GRASSLAND RESTORATION IN HETEROGENEOUS, CHANGING, AND HUMAN DOMINATED SYSTEMS

by

ALEJANDRO BRAMBILA

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Student: Alejandro Brambila

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This dissertation has been accepted and approved in partial fulfillment of the requirements for the Doctor of Philosophy degree in Environmental Sciences, Studies, and Policy by:

Bitty Roy	Chairperson
Lauren Hallett	Advisor
Lucas Silva	Core Member
Bart Johnson	Institutional Representative

and

Krista Chronister	Vice Provost for Graduate Studies

Original approval signatures are on file with the University of Oregon Division of Graduate Studies.

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DISSERTATION ABSTRACT

Alejandro Brambila

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Ecological restoration is a powerful tool to promote biodiversity and ecosystem function. Understanding underlying system variability and directional change can help predict outcomes of restoration interventions. Spatial or temporal availability of resources, for example, can lead to a similarly applied intervention having different outcomes. Similarly, as climate change shifts underlying competitive dynamics management strategies that worked in the past may no longer work. Human influence has played a major role in determining patterns of heterogeneity and novelty across systems, and human-dominated systems can provide opportunities for extending restoration impacts beyond wildlands.

Here, I examine how environmental variation, change, legacy and land use influence restoration outcomes in western U.S. grasslands. Specifically, I focus on semi-arid and Mediterranean grasslands of California, Oregon and Washington. These grasslands are invaded by introduced annual grasses, which threaten to displace native species and, especially in the perennial dominated north, transform ecosystem state and function. Each of the chapters presented in my dissertation ask a question that seeks to contextualize and improve grassland restoration across a variable landscape. In Chapter II, I examine how grazing herbivory enhances or dampens the effect of environmental variation on resource availability at different scales using data from a long-term cattle-herbivory exclusion study. In Chapter III, I ask how communities with variable starting conditions established by climate and management legacies

respond to restoration burning across regional climate gradient. In Chapter IV, I consider how warming impacts competitive outcomes between species representative of two potentially dominant functional groups. Finally, in Chapter V, I test the feasibility of expanding restoration into a novel agricultural context potentially compatible with native grassland vegetation. Throughout, I consider what each of these outcomes mean in a management context, and how they can be applied more broadly to improve restoration success.

This dissertation includes previously published co-authored material.

CURRICULUM VITAE

NAME OF AUTHOR: Alejandro Brambila

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene
Brown University, Providence RI

DEGREES AWARDED:

Doctor of Philosophy, Environmental Sciences, Studies, and Policy, 2022, University of Oregon
Bachelor of Science, Biology, 2012, Brown University

AREAS OF SPECIAL INTEREST:

Restoration Ecology
Community Ecology
Plant Ecology
Agroecology

PROFESSIONAL EXPERIENCE:

Graduate Research Fellow, University of Oregon 2020-2022
Graduate Teaching Fellow, University of Oregon. 2017-2019
Conservation Land Management Fellow, Chicago Botanic Garden and BLM. Marina and Alturas, CA. 2016-2017
Habitat Restoration Specialist, Save the Bay. Oakland, CA. 2015-2016
Research Internship, Flombaum Lab, University of Buenos Aires, Buenos Aires, Argentina. 2014
Fulbright Fellow, University of Talca and Wines of Chile. Talca, Chile 2013

GRANTS, AWARDS, AND HONORS:

United States Department of Agriculture AFRI, Agroecosystems Program. "Ecological intensification for a productive oak-hazelnut savannah landscape" PIs L. Hallett, L. Ponisio, L. Silva. $500K. *Proposal was inspired by my dissertation, and I contributed to the writing; as a graduate student I could not be listed as a PI.* University of Oregon. 2021-2024

UO Peter O'Day Fellowship for graduate student and undergraduate mentee research collaboration. University of Oregon. 2020

NSF Graduate Research Fellowship. 2020

UO ENVS Seed Grant for Applied Science. "Resolving conflict between oak conservation and organic hazelnut production". PIs. L. Hallett, A. Brambila, T. Larson, B. Miller. $9,750 University of Oregon 2018-2019

California Native Plant Society Salley Casey Shooting Stars Fellowship. "Urban ecology of western Santa Clara valley native oaks." A. Brambila. $1,500. 2015

UO Promising Scholars Award for incoming graduate students from diverse backgrounds with strong academic promise. University of Oregon. 2017

Fulbright Fellowship. University of Talca, Chile. 2013

PUBLICATIONS:

Brambila, A., Reed, P.B., Bridgham, S.D., Roy, B.A., Johnson, B.R., Pfeifer-Meister, L., Hallett, L.M. 2022 Disturbance: a double-edged sword for restoration in a changing climate. *Restoration Ecology*

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Finally, my fifth chapter on restoration in Hazelnut orchards grew out of a broader hazelnut agro-ecology research program in the Hallett Lab. Our first project took place at My Brother's Farm and was made possible through much support and planning with the Larson brothers, especially Taylor, and their families. The study described in my fifth chapter took place at Lane-Massee Farms, owned by Lynnea and Paul who adjusted their farming practices and allowed us to introduce new species to their property in the name of science. This work would not have been possible without the efforts of my undergraduate mentees, Marissa Lane-Massee, Drew Donahue, Calvin Penkauskas, and Ari Brown, who put in countless hours, made these projects their own, and taught me about hazelnut farming, pollinators, birds and mushrooms.

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CHAPTER I

INTRODUCTION

Ecological restoration is a powerful framework for ecosystem management that acknowledges and seeks to reverse anthropogenic degradation of natural systems (Clewell et al. 2004; Hobbs & Norton 1996). In a world with extensive habitat loss and degradation, restoration is a vital extension to conservation that activates ecosystem management and allows landscape managers to identify and work towards specific outcomes (Young 2000; Thorpe & Stanley 2011). While restoration targets are informed by historical conditions and processes, historical fidelity is not always possible or even desirable (Suding & Hobbs 2009; Standish et al. 2014; Case & Hallett 2021). Anthropogenically-driven changes to underlying conditions including climate change, novel species introductions and competing historical and modern land uses can limit potential outcomes. At the same time, the active management and goal-setting implicit in restoration can provide a valuable guide for managing novel ecosystems and community assemblages over time, especially in contexts with competing uses (Seastedt et al. 2008; Hobbs et al. 2009). While there have been many restoration successes, ecosystems are heterogeneous and changing, complicating simple prescriptions. Understanding how to apply and adjust restoration practices across variable contexts will be necessary to achieve desired outcomes in a diverse and changing world.

Underlying environmental variability is a key driver of management outcomes. Heterogeneity in resource availability and climate across regional gradients (Tilman 1982), within sites (Harrison 1997; Tuomisto 2010), or across years (Reyer et al. 2013) can shift relative species fitness, resulting in similar management actions having divergent outcomes. Similarly, climate change is shifting baseline conditions (Intergovernmental Panel on Climate Change 2014; Anderson 2016), and interventions that have worked in the past may not under novel conditions. While managers and restoration practitioners may not be able to control underlying ecosystem variability, understanding where and how management interventions lead to different outcomes can increase predictability.

Although environmental heterogeneity and environmental change structure natural systems and drive novelty, management and contingency matter. Starting conditions, disturbances and deliberate or non-deliberate species introductions can influence eventual community composition (D'Antonio & Vitousek 1992; Hayes & Holl 2003; Hobbs & Huenneke 1992). Restoration ecology seeks to harness these processes to promote native species, biodiversity and desired functions and services (Hobbs et al. 2007; Young et al. 2017). The lessons learned from balancing environmental constraints and contingency in managing and restoring wildlands can also be applied to human-dominated systems. While these systems present additional constraints and have not always been managed for ecological value, identifying compatible anthropogenic land use types can expand the reach of restoration beyond traditional natural systems to provide habitat and ecosystem functioning across the broader landscape.

Semi-arid and Mediterranean grasslands in the western U.S. have high biodiversity, endemism, and provide important ecosystem services and cultural values. Throughout their range, these grasslands are under pressure from extensive habitat loss, fragmentation, species invasion and ongoing climate change which is intensifying summer heat and drought. These landscapes have spatial and temporal (both inter and intra-annual) variability in environmental conditions, land use, and resulting plant communities. Conservation and restoration of native grasslands are a priority throughout the region. The goal of my dissertation is to examine elements of how outcomes of active management in these grasslands interact with climate, resource availability and land use, to increase predictability, identifying effective management practices, and expand the reach of restoration into more human-dominated contexts.

In Chapter II of my dissertation, "Herbivory enhances the effect of environmental variability on plant community composition and beta diversity" I examine how an anthropogenic land use, cattle grazing, affects different scales of diversity across a spatiotemporally heterogeneous landscape. This chapter was co-authored with John W. Chesnut, Laura R. Prugh, and Lauren M. Hallett and was published in the Journal of Vegetation Science in 2020. The Carrizo Plain is a semi-arid grassland in southern California structured spatially by giant kangaroo rat mounds. These mounds have enhanced soil resource availability and support a distinct, set of species than inter-mound habitat. Plant communities are also structured spatially via interannual precipitation variability, with distinct species benefiting from wet and dry years. I analyzed data from a long-term grazing study at Carrizo Plain and asked how cattle grazing management affected alpha, beta and gamma diversity at the site.

In Chapter III, "Disturbance, a double-edged sword for restoration in a changing climate", I examine how community starting condition and climate warming influence the outcome of restoration burns in Pacific Northwest prairies. This chapter was co-authored with Paul B. Reed, Scott D. Bridgham, Bitty A. Roy, Bart R. Johnson, Laurel Pfeifer-Meister and Lauren M. Hallett. These grasslands are adapted to regular burning, which is used in a restoration context to allow fire-dependent native forbs to persist. As the climate warms, introduced annual grasses have become a novel threat, replacing the previously dominant perennial grasses and driving state change. I asked how burning affected community trajectory and seedling establishment across a latitudinal gradient and a range of starting conditions determined by variable warming legacies. This experiment took place in the context of a pre-existing multi-year climate-manipulation experiment established by my co-authors.

In Chapter IV, "Direct versus indirect effects of warming on competition and coexistence between an introduced annual (*Lolium multiflorum)* and a native perennial (*Festuca roemeri*) grass in the Willamette Valley, Oregon", I developed a competition experiment and used a demographic modeling approach to understand how warming was affecting annual and perennial grass competition, and the potential for state change in Pacific Northwest prairies. This chapter was co-authored with Chhaya Werner, Jeff Diez, and Lauren M. Hallett. My experiment established various competitive scenarios with different densities of annual seeds and perennial plugs and seeds in warmed and ambient plots. We used fecundity and survival data to parametrize Beverton-Holt competition models and then simulate populations of each species with and without interspecific competition. We asked whether warming had direct or indirect effects on perennial population persistence and interpreted these results in a management context.

In Chapter V, "Feasibility of native cover crops in hazelnut orchards of varying ages in the Willamette Valley, Oregon," I capitalize on a potentially compatible land use to expand restoration of Pacific Northwest prairie species beyond traditional wildlands. This chapter was co-authored with Ari Brown, Marissa Lane-Massee and Lauren M. Hallett. To determine the compatibility of hazelnut orchard management with native understory vegetation, I introduced various native species across orchards of different ages and respective canopy covers and manipulated the typical mechanical disturbance intensity. I asked both which species could survive in different contexts and how they impacted factors relevant to farm productivity and ecosystem functioning.

Chapter VI summarizes the results of these studies.

CHAPTER II

HERBIVORY ENHANCES THE EFFECT OF ENVIRONMENTAL VARIABILITY ON PLANT COMMUNITY COMPOSITION AND BETA DIVERSITY

From Brambila, A., J.W. Chestnut, L.R. Prugh, L.M. Hallett. 2020. Herbivory enhances the effect of environmental variability on plant community composition and beta-diversity. Journal of Vegetation Science 31(5):744-754 (Invited paper for special issue).

Contributions

L.P. and J.B. developed the research design and implemented the experiment; A.B. and L. H. conceived of the research idea; L.P. and J.B. collected data; A.B. performed statistical analyses; A.B., with contributions from L.H., L.P., J.C., wrote the paper; all authors discussed the results and commented on the manuscript.

Introduction

Understanding the factors that shape biodiversity over space and time is a central problem in ecology. Bottom-up resource availability and top-down consumer pressure are two key drivers that structure species diversity and interactions (Tilman 1982; Mittelbach et al. 2001; Grime 1979; Buckling et al. 2000) Both drivers are classically associated with a unimodal diversity relationship, such that diversity peaks at intermediate levels of resource availability and consumer pressure. While these processes were initially identified in isolation, more recent theory indicate that they are linked, with herbivory enhancing diversity under high resource conditions and decreasing diversity under low (Worm et al. 2002; Hillebrand et al. 2007; Borer et al. 2014). However, support for this theory is mixed, leading to debate around the context (Mittelbach et al. 2001; Harrison et al. 2003) and mechanism (Koerner et al. 2018) of resource-consumer-diversity relationships. Potential explanations for this theory focus on the switch from belowground competition in resource-poor contexts to aboveground competition for light and space in resource-high contexts and the role of dominant versus rare species in each context (Osem et al. 2002). Milchunas et al. (1988) suggest that herbivory and low water resource conditions lead to convergence of plant communities with similar avoidance and tolerance strategies.

Systems with high spatiotemporal variation in resource availability may lead to divergent resource-consumer-diversity relationships within the same site. For example, herbivory may have a differential effect on community dynamics in high versus low resource years and/or patches. Moreover, these dynamics may change with spatial versus temporal resource variation. For example, productivity (Huxman et al. 2004) and species richness (Hawkins et al. 2003; Kreft & Jetz 2007) are both highly responsive to precipitation across spatial gradients, but their sensitivity to temporal variation in precipitation depends on the environmental context. Specifically, xeric sites exhibit higher sensitivity than mesic sites to intra-annual precipitation variability in both productivity (Huxman et al. 2004) and richness (Adler & Levine 2007; Cleland et al. 2013). As such, the positive effect of herbivory on diversity may increase with spatial variation but be overwhelmed by temporal variation in resource availability. Finally, there may be an interaction in which herbivory more strongly moderates diversity in relation to temporal resource variability in high rather than low resource areas.

In systems characterized by high spatiotemporal resource variability, herbivory may alter both local and landscape diversity patterns. Classically, resource-consumer-diversity relationships have focused on patterns in alpha diversity. However, in patchy resource environments, herbivory may also alter landscape patterns of community dissimilarity and dispersion between and within different resource patch types (Tuomisto 2010; Vellend 2001; Anderson et al. 2011). Further, these dynamics may only manifest once a baseline level of resources are available. Incorporating data across a range of temporal environmental conditions may more accurately describe communities in variable systems by taking into account changes in species composition across time, whether at the local or landscape level (Avolio et al. 2015). Permanent plots stratified across spatially heterogeneous landscapes and repeatedly sampled across a range of temporal environmental variation can help develop an understanding of a hierarchy of factors structuring plant communities.

The Carrizo Plain, an arid grassland in Southern California, is an excellent system to test how herbivory moderates diversity under high spatiotemporal resource variability. First, like many western grasslands, the Carrizo Plain experiences high precipitation variability, and water is a major limitation to plant productivity. Multiple year droughts are interspersed with wet spells, altering both total plant productivity and functional group representation (Grinath et al. 2018). Second, the Carrizo Plain is characterized by high spatial resource availability due to the presence of Giant Kangaroo Rats (*Dipodomys ingens*), an ecosystem engineer that forms evenly spaced mounds over six meters in diameter around its burrows (Grinnell 1932). The mounds increase soil nutrient availability and support more productive plant communities compared to the spaces between mounds, particularly in wet years (Prugh & Brashares, 2012). This spatial resource heterogeneity leads to distinct on-mound plant communities compared to the surrounding inter-mound space (Grinath et al. 2019). In addition to ecosystem engineering, the GKR is a major source of herbivory through seed predation (Gurney et al. 2015). Cattle grazing, which is common in the Carrizo Plain and surrounding areas, adds to overall herbivory pressure although GKR regularly consume more biomass than cattle (Endicott et al. 2016).

Here we use a long-term (10 year) cattle grazing removal experiment at the Carrizo Plain to assess how cattle grazing (as additional herbivory pressure above baseline GKR herbivory) alters productivity, species diversity and community composition in relation to spatial and temporal resource variability. We hypothesize that given the site’s aridity, productivity will increase both on and off-mound with interannual variation in rainfall, although reduced soil resource availability off mound will limit the increase in productivity off-mound leading to increased resource heterogeneity in wet years. Alternatively, the response of productivity to resource conditions could be unimodal, with compensatory growth making up for losses to herbivory in the highest resource conditions. Across variable resource conditions, we expect that grazing will generally reduce productivity, although we expect this effect to vary in its magnitude with minimal effects in low resource conditions, and increasing as there is more total productivity. Because Carrizo Plain is an arid system with generally low average moisture conditions, we expect that diversity will generally increase with precipitation, especially off-mound where resource-acquisitive dominants may be limited by existing soil nutrients as well as precipitation . According to linked resource-herbivory theory, we expect that grazing will reduce diversity under low resource (precipitation and soil nutrient) conditions by increasing mortality but increase diversity in high resource conditions by reducing aboveground competition. Across this heterogeneous landscape, we expect minor effects of grazing on beta-diversity in dry years as the whole site is moisture limited, and a homogenizing effect in wet years as cattle increase diversity on higher resource GKR mounds, but decrease it off-mound. Below, we test these patterns both at the local and landscape level and relate them to underlying shifts in species composition and productivity.

Methods

STUDY AREA

The Carrizo Plain is the largest remnant of the San Joaquin Valley grassland ecosystem type. The plain is located in the southern part of the valley and is characterized by an arid Mediterranean climate with mild wet winters and hot dry summers. Average annual precipitation is 190 mm, nearly all of it falling during the growing season which begins in October and ends in April. Annual precipitation is highly variable; during our study the maximum amount of precipitation fell in 2010-2011 (410 mm), and the minimum in 2013-2014 (46 mm) (1998-2017; MesoWest CAZC1, 35.10N, 119.77W). Our study site, Center Well pasture is located within the Carrizo Plain National Monument. The site has been intermittently grazed by cattle since the 1800s, and it was cultivated for wheat and barley from 1890-1974. Contrasted with neighboring pastures that retain a significant native perennial grass cover (i.e. *Poa secunda*), the Center Well plant community within our site is primarily composed of annual forbs (*Erodium cicutarium, Lepidium nitidum*) and exotic annual grasses (i.e. *Bromus madritensis, Schismus arabicus, Hordeum murinum* (species names: Baldwin and Goldman 2012)). The site is within the endangered Giant Kangaroo Rat's (GKR) core habitat, whose mounds cover roughly 50% of the soil surface (Gurney et al. 2015). In addition to the GKR there are various rare and endangered endemic plant species concentrated in the Carrizo Plain, of which one, *Monolopia congdonii,* is found in Center Well pasture.

SAMPLING DESIGN

Four pairs of 1.96 hectare (140m x 140m) control and exclosure plots were randomly placed within the ~5 km x 5 km Center Well pasture. Control plots allowed continued cattle grazing access, and exclosure plots were fenced to eliminate cattle herbivory (but not GKR). Pairs were oriented in a random compass direction and separated by a 60 m buffer. Within each plot, eight 1m x 1m quadrats were established to monitor plant communities. These were stratified so that four quadrats were randomly placed on GKR mounds and four were off mounds. Taken together, cattle grazing and GKR mound status comprised our four experimental treatment groups: grazed on-mound, grazed off-mound, ungrazed on-mound, and ungrazed off-mound. Here and throughout, "ungrazed" refers to cattle grazing, and not the presence of GKR or other potential herbivores (i.e. insects). Over time as GKR had continued access to the plots, some mounds shifted and affected quadrats were reclassified, leading the design to become slightly unbalanced by the end of the experiment (Appendix S1). In 2015, new quadrats were established in the cattle exclosure plots, replacing the old plots and rebalancing the on to off mound ratio in these plots. Plant communities were assessed at peak productivity (late March to early April) in one square meter quadrats using pin-frames. Pins were dropped from above spaced evenly every 10 cm within the quadrat for a total of 81 pin drops. Each first hit was recorded, and one additional hit was recorded for each species that occurred in the quadrat but was not hit. Aboveground net primary productivity (ANPP) was clipped at peak in April, in rotating 1/4m x 1/4m plots adjacent to quadrats. This biomass was dried and then weighed for analysis. Cattle grazing occurred in the spring, after April community and ANPP monitoring. Cattle were only grazed in wet years, specifically 2008-2011 and 2016-2017. To account for legacy effects of grazing we included all years in our analysis based on exclosure status rather than only including data from actively grazed years. We sourced growing season precipitation data from the University of Utah's Meso-West station CACZ1 (35.10N, 119.77W) in the Carrizo Plain.

ANALYSIS

Design/Rainfall

We used R for all statistical analyses (R core team, version 3.4.2). To address temporal variability in water resources, we aggregated rainfall from the summer before to the summer after growth (i.e., previous year July to July) to capture growing season rainfall (95% of precipitation falls from October to April). We categorized years as wet or dry if they were +/- 0.5 standard deviation from mean rainfall over the course of the experiment. We considered 2010, 2011 and 2017 as wet years (all grazed) and 2013, 2014 and 2015 as dry years (not grazed). All other years were considered "normal" and excluded from wet or dry categorical analyses as normal year results were intermediate and not significantly different from all year results. Given a major drought that took place during the experiment, we also explicitly analyzed plant communities in 2014, the driest year of the drought, and 2017, the wettest year after the drought to evaluate drought-recovery specific responses.

Productivity

To test how grazing and spatiotemporal resource availability altered ANPP, we used a linear mixed effect model with precipitation (continuous), grazing (grazed or excluded), GKR mound status (on or off mound), and a grazing x mound interaction as fixed effects and year and quadrat nested within plot-pair as random effects using the function "lmer" in the R packages "lme4", and "lmerTest" (Bates et al. 2015; Kuznetsova et al. 2017). To test whether the interaction between grazing and mound (each combination of grazing and mound status) was affected by precipitation, we subsequently analyzed ANPP using ANOVA with grazing (grazed or excluded), GKR mound status (on or off mound) and their interaction as fixed effects and year (when more than one year was used in the model) and quadrat nested within plot-pair as random effects within just wet years, just dry years, and within 2014 (the strongest drought year) and 2017 (the wettest year post-drought). To address interactive group differences, we used post-hoc Tukey comparisons using the function “glht” in the R package “multcomp” (Hothorn et al. 2008b). To estimate p-values we used Satterwaithe’s approximation of degrees of freedom.

Diversity

We quantified alpha diversity as Shannon diversity within each replicate quadrat and year using the function “community_diversity” from the R package “codyn” (Lauren Hallett et al. 2019). To assess whether the effects of grazing and spatiotemporal resource availability on ANPP affected quadrat-level diversity, we tested precipitation, grazing and mound status on Shannon diversity in parallel models to our ANPP analysis.

To better understand spatial resource and herbivory interactions at the landscape scale, we characterized beta diversity by assessing how grazing treatment, mound status and their interaction led to compositional turnover across the site. We visualized spatial beta diversity using a four-dimensional nonmetric multidimensional scaling (NMDS) using the “metaMDS” function in the R package “vegan”. To test for significant differences between treatment communities we ran perMANOVA using the “adonis” function in the package “vegan” (Oksanen et al. 2017). Second, we characterized beta diversity as dispersion within each grazing x mound treatment. This allowed us to test whether grazing homogenized communities within a treatment category, and whether this effect varied by spatial resource conditions. We tested for significant differences in community dispersion around centroids for each treatment using the function “betadisper” in the R package “vegan”. Parallel to ANPP and alpha diversity analyses, we conducted both beta diversity analyses across all years, and then within wet versus dry years and within 2014 versus 2017. To quantify relative effect sizes of composition and dispersion differences, we used the function “multivariate_difference” in the R package “codyn” (Lauren Hallett et al. 2019).

Composition

Finally, we considered how individual species and groups of species responded to variable resource and herbivory conditions, and how these species drove local and landscape diversity patterns. We aggregated individual species counts into total counts of three plant functional groups - native and introduced grasses and native forbs - within each year and quadrat. For each of these three groups we tested effects of precipitation, grazing and mound status on their percent cover in models parallel to our ANPP analysis. For native forbs, we related cover to precipitation with a quadratic rather than a linear model based on maximum likelihood best fit. To identify species with particularly strong affinity for a treatment combination we identified indicator species using the function “multipatt” from the R package “indicpecies” (De Caceres & Legendre 2009) using the correlation index function corrected for unequal group sizes. We ran this analysis for all years, wet and dry years separately and within 2014 drought and 2017 wet year post-drought. We used a linear mixed effects model to test the relationship between introduced grasses and ANPP with percent cover of introduced grasses (continuous), grazing (grazed or excluded), GKR mound status (on or off mound) and a grazing x mound interaction as fixed effects and plot-pair as a random effect using the function “lme” paralleling our analysis of ANPP.

Results

Productivity

Across all years, ANPP was strongly linked to precipitation, increasing 0.81g/m^2 per mm of rainfall (F=10.29$_{1, 7.95}$, P=.012, Figure 2.1) and mound status (F=9.79$_{1, 121.3}$, P=.002). In a reduced model with precipitation removed to test for interactive effects of GKR mound and grazing, grazing did not change the mean value of ANPP but increased the heterogeneity of ANPP, significantly elevating ANPP on-mounds but reducing it off-mounds across years (77.44 g/m^2 difference between on and off-mound, P=.011). This on-mound effect was approximately twice as high in wet years (167.81 g/m^2 greater on-mound compared to off, P=.007) and the difference was greatest in the wet year post-drought, 2017 (407.36 g/m^2 greater on-mound compared to off, P=.001) (Figure 2.1). Compared to grazed plots, exclosures had more similar (not significantly different) ANPP on and off mound.

Diversity

Precipitation was also a major driver of increased quadrat-level Shannon (alpha) diversity (F=8.69$_{1,7.9}$, P=.018). In our two-way grazing x GKR mound model, alpha diversity was slightly higher in exclosures across all years (exclosure treatment difference=0.07, F=12.65$_{1, 65.4}$, P<0.001). This effect was consistent in dry years, but disappeared in wet years when considered independently (Figure 2.2). In wet years, however, diversity was significantly (F=4.29$_{1, 183.1}$, P=.039) lower on mound compared to off.

We addressed beta-diversity both as between-treatment community differences and within treatment community dispersions (differences between replicate communities within the same treatment). There were not significant perMANOVA differences between treatment communities except in 2017, when both mound (P=.0001) and grazing treatment (P=.0001) main effects led to community differentiation (Figure 2.3). As such, there were minimal treatment differences (see Appendix S2 for effect sizes). However, the sizes of these effects were elevated in wet years, especially the interactive grazing effect off-mound. Mirroring significant perMANOVA differences, the effect sizes were more pronounced in 2017, the post-drought wet year. By contrast, dry years had generally intermediate effect sizes. Full community difference results can be seen in Appendix S2.

Beta diversity patterns differed within each treatment group. Grazing led to significantly more dispersed communities across all years (P=0.015) (Appendix S2). Generally, on-mound grazed communities were the most dispersed. In wet years, dispersion was driven by mound differences and grazing effects were marginal. In the wettest post-drought year, 2017, the effect of grazing was greater compared to wet years generally, increasing dispersion on-mound and homogenizing off-mound communities. In dry years (including the driest year, 2014), communities were relatively homogeneous, with the exception that on-mound grazed communities had high dispersion (as in all years). Full dispersion results and effect sizes can be found in Appendix S2.

Composition

Percent cover of the four introduced annual grass species (Figure 2.4a) responded positively to precipitation ($F=5.69_{1, 108.9}$, P=0.018) and there was an interactive effect mirroring the effect on biomass whereby grazing led to a significant difference on and off-mound (difference=5.5%, P=0.004) across all years, while there was no significant difference between mound status when not grazed . The effect of grazing was consistent in dry years (4.1%, P=0.035) and increased in magnitude in wet years, although it was not significant (7.0%, P=0.076). This effect disappeared in 2014 during the drought (P=0.547), and was largest in 2017 post-drought (21.2%, P=0.003). The three most abundant introduced grasses were *Hordeum murinum, Schismus arabicus,* and *Vulpia myuros*. *Schismus* and *Vulpia* cover were not significantly affected by treatment. *Hordeum* emerged as an indicator species for on-mound communities whether grazed or not, and was found on mound with significantly higher cover across all years (9.2%, $F=12.53_{1, 141.4}$, P<.001), in wet years (19.72%, $F=10.80_{1, 47.5}$, P=.001), and in 2017 (21.05%, $F=11.52_{1, 42.4}$, P=0.001); but not in dry years or in 2014. Native grasses (mainly one species, *Vulpia microstachys*, which was an indicator species for all but ungrazed on-mound communities) generally increased with precipitation and were higher on mound, but these results were not significant when random effects of year and location were considered (Figure 2.4b).

Native forbs, the most species rich group (n=25), had a unimodal response to precipitation as a continuous variable where their cover peaked at intermediate levels of precipitation, although as with native grasses, this effect was not significant (Figure 2.4c). As a group, native forb cover did not respond to grazing or mound status. Certain species did, however, have specific responses. The four most common native forbs were all indicator species. *Guillenia lasiophylla* was an indicator of ungrazed, on-mound communities, *Lepidium nitidum* indicated grazed off-mound communities, *Lasthenia minor* indicated ungrazed communities generally, and *Trichostema lanceolatum* indicated ungrazed off-mound communities. The less common *Trifolium gracilentum* and *Microseris elegans* also emerged as indicators of ungrazed off-mound communities. While some of the more common species responded positively to grazing, less common native forbs, aggregated as “wildflowers”, were less abundant on-mound than off across all years (1.22% lower, $F=11.25_{1,917}$, $P<0.001$), and in dry years responded negatively to grazing off-mound (2.60% lower, $F=11.5_{1,58}$, $P<0.001$).

Overall, biomass was positively correlated with percent cover of introduced annual grasses across mound and grazing statuses ($F=56.1_{1,530}$, P=2.2e-13), although its effect size varied. The effect was approximately five times stronger (coefficient 0.49 vs 0.11) when grazed vs ungrazed, and while there was a significant relationship on-mound, there was no consistent relationship off-mound. In summary, biomass was most strongly correlated with introduced grasses in grazed-on-mound quadrats, and least correlated in grazed-off-mound quadrats.

Discussion

Theoretical (Proulx et al. 2006; Proulx & Mazumder 1998; Hillebrand et al. 2007; Milchunas et al. 2002) and empirical developments (Asgari & Steiner 2017; Groendahl & Fink 2017; Guerry & Menge 2017) have led to a general expectation that the effect of herbivory on diversity shifts with resource availability. Here, we tested whether resource-consumer-diversity relationships vary in a highly-patterned system with variation in both water resources (temporally) and soil nutrients (spatially). We focused on an arid grassland in which an ecosystem engineer creates high spatial resource variability at a relatively small scale in an otherwise (aspect, slope) homogenous landscape, and in which rainfall is highly variable. Over the course of our study, which included wet periods and a severe, multi-year drought, species diversity and productivity both linearly increased with precipitation. Despite periods and patches of high resource availability, cattle grazing had a small but consistently negative effect on alpha diversity across all years, as theory would predict under consistently low resource conditions (Tilman 1982). This suggests that average resource conditions in this arid system may be more important than resource variability for local resource-consumer-diversity relationships. However, on high resource patches and especially in wet years, both productivity and beta diversity were enhanced by cattle grazing, in part because grazing was associated with patchy distributions of introduced annual grasses. As such, our findings suggest that resource-consumer-diversity relationships may shift when assessing local versus landscape-level diversity.

Working across a range of spatiotemporal water availability, previous studies have shown that grazing effects do in fact vary within a site (Osem et al. 2002; Carmona et al. 2012; Rota et al. 2017). Specifically, these studies find that grazing has the greatest effect on diversity at high resource conditions, although this effect was variable. While Osem (2002) and Carmona (2012) found increases in diversity, Rota (2017) saw a decrease. This is likely due to differences in palatability of dominant and rare species. For example, if the dominant species is a palatable, resource-acquisitive grazing tolerator (as in Carrizo), grazing may increase diversity; but if rare species are more suited to high resource conditions and are not resistant to grazing, grazing may decrease richness. For this reason, it may be important to consider measures of diversity that include evenness.

Productivity and local diversity consistently increased with precipitation, even in the wettest years of this study. This suggests that precipitation was a dominant limiting resource on plant productivity across years, and that peak theoretical diversity likely did not occur across this landscape (Goldberg & Miller 1990; Grime 1979; Noy-Meir 2003). This is consistent with studies that have found evidence for water limitation throughout North American grasslands generally (Webb et al. 1983; Sala et al. 1988), and a dominant intra-annual effect on precipitation on both diversity (Cleland et al. 2013) and productivity (Huxman et al. 2004) in arid systems. While a strong effect of precipitation is not a surprise in our arid system, this effect was consistent regardless of spatial variability or grazing status, suggesting that precipitation is not only a limiting factor, but the major factor structuring plant communities in this system. While soil nutrients did matter (there was greater diversity off-mound than on in wet years), their spatial variability may be dampened as nutrient availability can be restricted by moisture limitation (Cardinale et al. 2009). While these results are consistent with a recent study showing that precipitation plays a substantial role in structuring plant communities in Carrizo, lag effects can lead to unexpected patterns via thatch accumulation in subsequent years (Grinath et al. 2018). In this case, grasses can create a positive feedback where, once established, they increase their dominance over time. Prolonged droughts may function to interrupt and balance this cycle, or as in Sasaki et al. (2009) grazing in wet years can reduce thatch accumulation.

Cattle grazing had a small but significant negative effect on alpha diversity regardless of spatial and temporal resource variability. Given the high degree of spatiotemporal resource variability in the system, it was notable that the consumer effect was stable across conditions. This suggests that, at least in arid systems, resource-consumer-diversity predictions may be most appropriate in relation to average resource conditions, under which herbivory would be expected to further reduce population sizes and increase likelihood of local extinctions (Worm et al. 2002; Hillebrand et al. 2007). In variable but arid systems, periods of high resource conditions may not be enough to shift the community to space and light limitation (Noy-Meir 2003). As such, there may not be a strong mechanism for grazing to enhance diversity under periodic as opposed to sustained resource availability This is consistent with results from previous studies on grazing and spatiotemporal resource variability that found greater effects of interactive effects of consumer pressure in relation to spatiotemporal resource variability under slightly higher average resource conditions such as semiarid or mesic grasslands (Carmona et al. 2013, 2015; Milchunas et al. 1988). That said, arid systems are often managed for the expectation that grazing has a stronger negative effect under drought conditions, and the Carrizo Plain is no exception. Consequently, it is possible that even greater reductions in local diversity would have occurred if the site were grazed during the drought. While our experimental design is unable to test these effects, it demonstrates that even a carefully managed grazing program can lead to reductions in diversity in arid systems.

Although cattle grazing had a consistent negative effect on local diversity, it enhanced landscape level beta diversity, especially under high resource conditions. When grazed, on and off-mound communities diverged, particularly in wet years in an effect that peaked after recovery from the drought in 2017. Focusing exclusively on alpha diversity overlooks these landscape effects, which are driven by community compositional difference on and off-mound (Avolio et al. 2015; Anke Stein et al. 2014). By taking into account between-treatment community distances, we found that grazing increased beta diversity, potentially acting as a mechanism for increased species coexistence at the landscape scale (Amarasekare 2003; Chesson 2000). This community divergence was linked to an increased divergence in productivity in grazed plots in wet years. This result complicates the theoretical resource-consumer-diversity patterns expected whereby consumers affect diversity by reducing productivity (Bartolome et al. 1980). Cattle do not consume plants randomly, and through selective feeding they can increase productivity by stimulating the growth or dominance of herbivory tolerant or less-favored species (Koerner et al. 2018). Grazing also can affect plant growth through increasing nutrient cycling by modifying root to shoot ratios, impacting soil texture, and digesting plants into feces

(Peco et al. 2017) If cattle preferentially spend time on GKR mounds, they may further concentrate nutrients across the landscape, exaggerating the differences in nutrient availability on and off-mound. Grazing also increased within-treatment beta diversity (dispersion) particularly in on-mound communities. This again aligns with previous work in variable resource habitats where high-resource conditions are more affected by grazing, but in this case the resource in question is soil fertility rather than moisture. While between-treatment beta diversity represents a directional, systematic effect of grazing across the landscape, dispersion represents random-patchy effects of grazing. For example, grazing disturbance can create opportunistic habitat for grazing tolerant species or refuges for rare species (ex: *Monolopia congdonii)* by creating gaps for colonization and increasing resource turnover (D'Antonio et al. 1999).

To understand how scales of diversity interact across our site, we considered species composition. For alpha diversity to stay the same or decrease while beta diversity increases, we expect to see species sorting into landscape patches where they can successfully compete and persist. Specifically, theory predicts that superior competitors for scarce resources will succeed in low resource conditions, and more acquisitive species will better compete for light and space in high resource conditions (Harpole & Tilman 2007; Cardinale et al. 2009; Borer et al. 2014). The two main types of plants present in our pasture were annual grasses (native and exotic), which both responded positively to increased precipitation, and annual forbs, which represented most of the species diversity and whose percent cover peaked at intermediate precipitation but declined in the wettest years. This unimodal response to increasing resources suggests a transition from abiotic limitation to biotic limitation, and that in high resource contexts grasses tend to outcompete forbs. In fact, introduced annual grass cover drove beta diversity patterns in high resource contexts. Their cover was highest on mound and in wet years, coinciding with highly productive conditions. This result is consistent with observations at Carrizo Plain throughout the 20th century (Grinnell 1932; Schiffman 1994) and in western grasslands generally (Huenneke et al. 1990; Weiss 1999). Our indicator species analysis showed that in addition to outcompeting forbs in optimal conditions, these resource-acquisitive exotic grasses (i.e. *Hordeum*) drove the main native grass, *Vulpia microstachys* off-mound. While specific native forbs tended to have more idiosyncratic responses to grazing and mound status, these responses demonstrate filtering by some criteria. Further research is necessary to determine the likely resource and herbivory resistant trait-mediated responses of individual species. Consistent with previous studies in Carrizo Plain (Kimball & Schiffman 2003), but contrary to the typical pattern found across California grasslands (Safford & Harrison 2001; Hayes & Holl 2003), grazing reduced cover of most forbs (and *Vulpia*), particularly in wet years, potentially because these native species did not evolve with cattle grazing. It is possible that our study differed in this respect due to a first-hit sampling design, which may capture the dynamics of tall grasses but underestimate understory forbs in years with high grass cover.

In a study of the effects of GKR foraging and mound formation on precipitation legacies, Grinath et al. (2018) also found that GKR mounds led to more introduced annual grasses in wet years. While in our study, cattle grazing exaggerated these differences, Grinath et al. (2018) found that GKR foraging effectively suppressed introduced grass cover. These differences may be due to cattle vs. GKR feeding preferences, coevolutionary histories with forage species, or direct interactions between cattle and GKR. GKR are substantial grazers in Carrizo Plain, and regularly remove more ANPP than cattle (Endicott et al. 2016). While GKR will selectively forage some species over others, a feeding preference study found they preferred (*Bromus, Schismus*) or did not avoid (*Hordeum*) introduced annual grasses (Gurney et al. 2015). As granivores, GKR remove reproductive propagules of plants they consume, while cattle do feed on seeds but prefer leaves over reproductive stems (Reppert 2007). Cattle organize their foraging activity primarily at the community/patch level, a tendency that is likely exaggerated in Carrizo with cattle spending most of their time on GKR mounds where there can be much higher productivity (Senft et al. 1987). This may help explain the dispersion of on-mound communities, which was driven by a few sites that became highly dominated by *Hordeum*.

In our assessment of the effects of herbivory on plant community dynamics in Carrizo Plain, our results demonstrated that it is important to not only consider general resource availability, but spatial and temporal variability within a site. Across our analyses, the effect of cattle grazing was often subtle and depended on an interaction with spatial and/or temporal resource availability as well as the status of GKR. the other major herbivore in the system. For example, the most dramatic beta-diversity and ANPP differences arose in 2017 following the severe drought that drastically reduced GKR populations (Grinath et al. 2018). Results from experimental GKR exclosures support the dominant role of GKR in controlling development of grass dominance in high resource conditions (Prugh & Brashares 2012). Ultimately, cattle grazing decreased diversity at the alpha level, but increased diversity by increasing patchiness across the landscape, both between mounds and inter-mounds and across mounds themselves. Taking within-site heterogeneity into account allowed for a more nuanced exploration of effects on plant diversity, and considering species-specific responses gave further insight into how plant communities were being affected and leading to divergent productivity and diversity responses. These results show how grazing exaggerates heterogeneity of plant communities across the landscape at Carrizo plain, particularly in high-resource years, and provide context for managers of arid landscapes concerned with grass invasion or native plant conservation.

Bridge

Understanding how a management activity (i.e. grazing) interacts with underlying within-site heterogeneity can help predict the outcome of this activity. As in this study, heterogeneity can be defined by ecosystem engineers or precipitation variability. Understanding heterogeneity, both within and across-site is also important to understand for the implementation of restoration activities. In the following chapter, I consider how heterogeneous starting conditions established by variable warming and drought legacies affect the outcome of restoration burning across a latitudinal climate gradient.

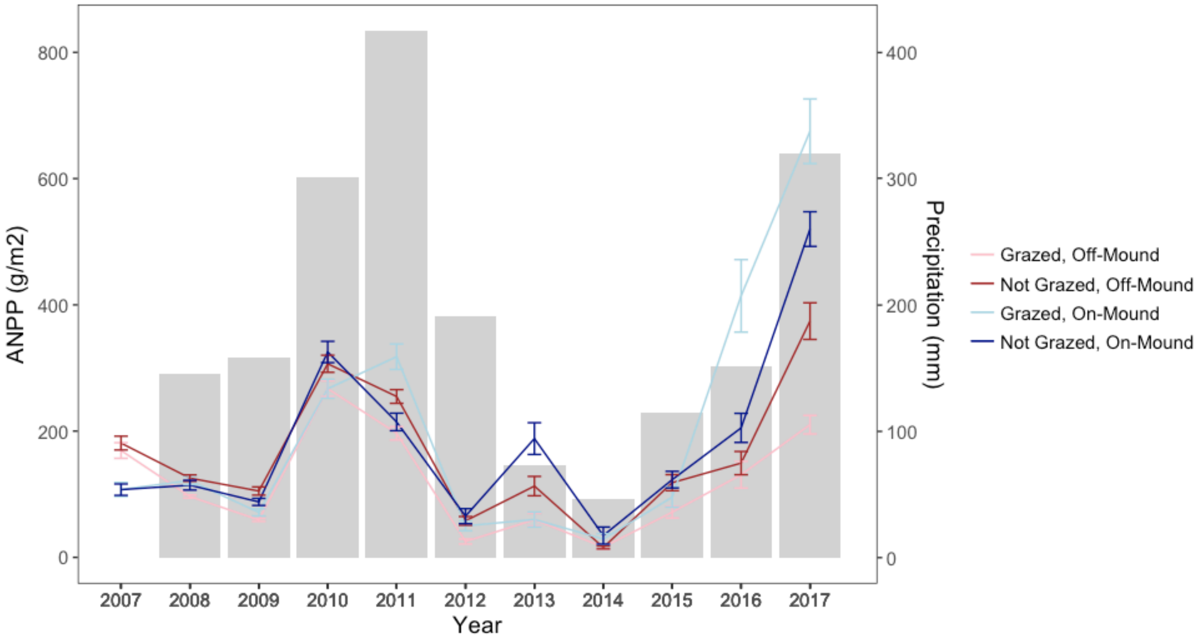


Figure 2.1: Aboveground net primary productivity over time and in relation to grazing treatment and mound status (± SE, colored lines), and annual precipitation (grey bars).

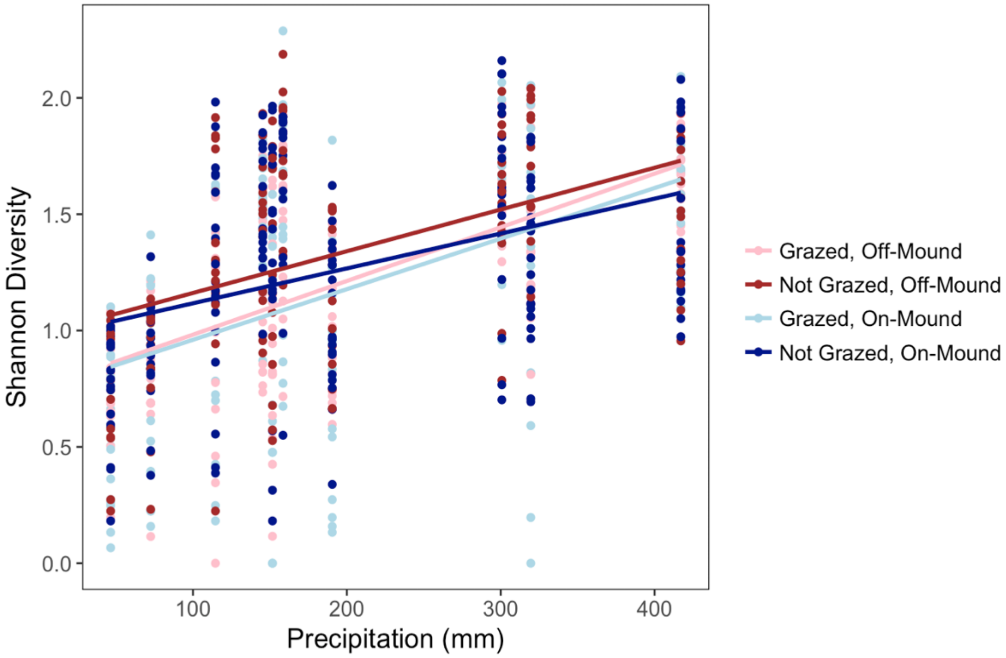


Figure 2.2: Shannon diversity of annual plants in relation to precipitation and grazing treatment and mound status.

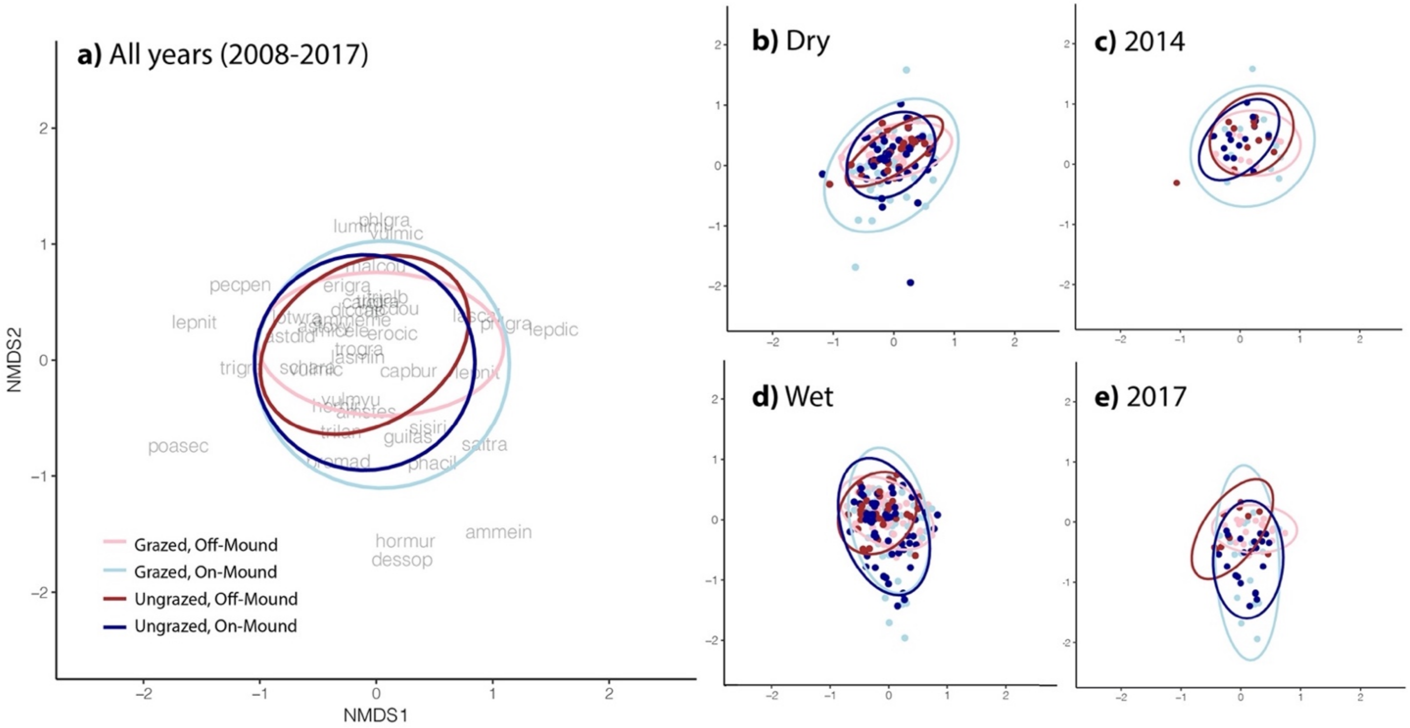


Figure 2.3: NMDS ordinations of communities by treatment in (a) all years showing ellipses and species positions; (b) dry years; (c) 2014, the driest year over the course of the experiment; (d) wet years, and (e) 2017, the wettest year emerging from the drought. See appendix 3 for species codes and information.

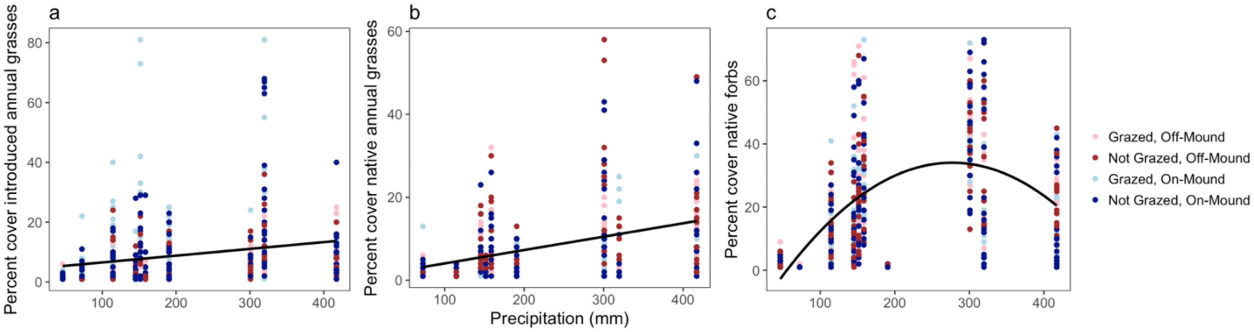


Figure 2.4: Functional group responses to precipitation and in relation to grazing treatment and mound status.

CHAPTER III

DISTURBANCE, A DOUBLE-EDGED SWORD FOR RESTORATION IN A CHANGING CLIMATE

Contributions

PBR, SDB, BAR, BRJ, and LPM established the underlying experimental infrastructure; AB and LMH conceived and designed the research; AB performed the experiments, analyzed data and wrote the manuscript with input from all authors.

Introduction

Disturbance is a key tool for ecological restoration, but one that can lead to unintended outcomes. Burning, grazing, mowing, and herbicide application are common restoration disturbances used in conjunction with seed addition to manipulate the trajectories of existing plant communities by freeing up space and increasing available resources for target species (Hobbs et al. 2007; Flory & Clay 2009; Papanastasis 2009). Where communities have evolved with disturbance, reintroducing aspects of the historic disturbance regime is often necessary to maintain populations of disturbance-adapted species (Leach & Givnish 1996; Macdougall & Turkington 2007; Peco et al. 2017). However, the same type of disturbance can have different outcomes depending on the biotic, abiotic and historical context of a given system (Temperton et al. 2004; Hilderbrand et al. 2005; MacDougall & Turkington 2006). As global change shifts underlying environmental conditions, often with no historic analog, the potential for unexpected outcomes of restoration disturbance may increase (Valladares et al., 2015).

Fire is widely used to support direct seeding establishment in the restoration of native grasslands west of the Cascade Mountains in the Pacific Northwest (PNW) of the United States. Historically, Native Americans managed grasslands in this region with fire, fostering a diverse mix of native annual and perennial forbs growing among native perennial grasses (Boyd 1999). Frequent fire both maintained the open character of prairies and savannas by decreasing woody invasion and allowed for the persistence of diverse disturbance-adapted forbs (Dunwiddie et al. 2014). The traditional indigenous fire disturbance regime was altered by European settlers in the mid 1800s, who also introduced grazing-adapted perennial grasses as forage for cattle (Rundel et al. 2016; Christy & Alverson 2011). Following further fire suppression in the early 20th century, those prairies not already lost to land-use change were greatly reduced by forest encroachment, while introduced perennial grasses came to dominate remnant prairies at the expense of native plant species (Maret & Wilson 2005; Christy & Alverson 2011). In recent decades, awareness of the ecological and cultural value of native grasslands has grown, stimulating an increase in restoration activity throughout the region (USFWS 2008). Today, prescribed fire followed by direct seeding of native forbs and grasses is one of the most successful tools for managing ground layer plant communities in grassland restoration (Hamman et al. 2011; Nuckols et al. 2011).

While fire is an important restoration tool in PNW grasslands, increasing pressures of species invasion (D’Antonio & Vitousek 1992; Ricciardi 2007) and climate change (Dalton et al. 2021) are shifting baseline conditions globally and locally, making outcomes less predictable**.** Disturbance-mediated invasion is not rare (Hobbs & Huenneke 1992), especially where invaders are disturbance-adapted, seral species, or have feedbacks that modify disturbance regimes (Balch et al. 2013). Where annual cheatgrass (*Bromus tectorum*) is invading in the Great Basin, for example, both fire and anthropogenic grazing disturbances have become threats (Brooks et al. 2004; Mack 1981). In California grasslands, historical grazing and tilling disturbance allowed for the rapid state-change of perennial to annual grass dominance (HilleRisLambers et al. 2010). Today, disturbance used in restoration to reduce the dominance of introduced annual grasses can precipitate a second wave of invasion by other, more noxious annual grasses (George et al., 2007). Similarly, disturbance has the potential to interact with climate, a strong driver of grassland community composition in the PNW. Here, plants experience a Mediterranean climate with warm, dry summers and cool, wet winters. Climate change is expected to cause mean annual temperatures to increase by 2.7 to 6°C, leading to an earlier start to the growing season and subsequent longer dry period (Dalton et al., 2017). An earlier, warmer growing season can decrease native species population growth rates, and increases the potential for introduced annual grasses to expand within the PNW (Dennehy et al. 2011; Pfeifer-Meister et al. 2016; Reed et al. 2021c), as they complete their entire life-cycle before the onset of the intensifying summer drought (Clary 2008; HilleRisLambers et al. 2010). This dynamic is evident across a latitudinal climate gradient, in which annual grasses have become dominant in California while perennial grasses still dominate more northern PNW grasslands (Christy & Alverson 2011).

Understanding where environmental conditions benefit forbs and perennial grasses, versus annual grass expansion, will be key in determining where fire and seed addition will be most effective in the future. Western PNW grassland restoration typically seeks to reduce the dominance of highly competitive introduced perennial grasses in favor of native perennial grasses, and in doing so reestablish diverse native communities (Stanley et al. 2008; Sinclair et al. 2006). Native perennial grasses continue to persist across a wide range of environmental conditions, and restoration from introduced perennial grass to native perennial grass dominance through disturbance and seed addition is often successful (Stanley et al. 2011; Wilson & Clark 2001). As the PNW climate becomes increasingly favorable for introduced annual grasses, however, there is a risk that restoration practices such as burning, which have historically assisted in the recovery of native perennial grasses, may initiate an alternative trajectory toward persistent introduced annual grass dominance. The level of risk depends on climate and the community starting conditions: whether a site under consideration for disturbance is already dominated by native or introduced perennial grasses, or by introduced annual grasses. These annual grasses germinate and grow quickly, outcompeting seedlings from other functional groups by drawing down resources early in the season and eventually forming a thick thatch layer (Jackson 1985; Clary 2008; Reed et al. 2021b). Instead of creating an opportunity for desired species to establish, burning where introduced annual grass seeds are present may increase their dominance. While negative impacts of introduced perennial grasses on overall diversity are well understood (Dunwiddie & Delvin 2006; Dennehy et al. 2011), diversity loss and changes to ecosystem functioning would likely be greater under introduced annual grass dominance (Reed et al. 2021c; Palmer et al. 1997). These changes include increased fire frequency, soil carbon loss, an increase in noxious weeds, increased erosion, a shortened forage season, and reduced biodiversity (D'Antonio & Vitousek 1992; Carlsen et al. 2000; Maret & Wilson 2005).

Here, we assessed the risk of annual grass invasion versus the benefits of restoring forbs and native grasses following burning across a latitudinal climate gradient, variable drought conditions, and a range of starting communities. Our first hypothesis was that, although burning would consistently increase forb cover, the risk of conversion to introduced annual grasses would vary with latitude (Figure 3.1). Specifically, we expected that burning would reinforce introduced annual grass dominance in warmer latitudes, whereas perennial grasses would maintain dominance in cooler latitudes. We expected the drought treatment would increase annuals, especially in the south. At intermediate latitudes we expected a less deterministic climate influence would increase the relative importance of community starting conditions, with burning increasing the dominance of introduced annual grasses where they were already established. Second, we hypothesized that burning would always increase establishment of sown seeds, but that this effect would be strongest in cooler latitudes for native species. Further, we hypothesized that community starting conditions would alter seedling establishment, with greater recruitment in communities dominated by perennial grasses than by annual grasses. Consequently, we expect that whether the benefits to native seedling establishment outweigh the risks of conversion to annual grass dominance requires consideration of both climate and starting community.

Methods

Experimental Design

Our experiment took place at three sites distributed across a latitudinal climate gradient in the Pacific Northwest from southwestern Oregon to central-western Washington (Table 1) from 2018 to 2020. The southern site, located in the Illinois River watershed, Oregon (42.2°N), experiences the warmest and driest summers and is a part of the Takilma cobbly loam soil series. The central site, located in the southern Willamette Valley near Eugene, Oregon (44°N), experiences intermediate climatic conditions, and has Hazelair silty clay loam soil. Finally, the northern site, located in the Puget Trough near Olympia, Washington, experiences the coolest temperatures and least-severe summer drought, and is on Cathcart medial-loam soil.

Our experiment capitalized on previous restoration efforts and climate manipulations that resulted in a range of starting conditions. Prior to our experimental burning and seeding, 60 plots of 7.1 m^2 across a latitudinal gradient underwent two restorations in 2009 and 2014. Plots were cleared with herbicide and seeded with native prairie species including native perennial grasses and native annual and perennial forbs, followed by experimentally applied warming, drought and irrigation from 2010-2012 and 2015-2018 (Pfeifer-Meister et al. 2016; Reed et al. 2019, 2021b). The most recent set of manipulations from 2015-2018 included four treatments: ambient, drought (60% of ambient precipitation), warming by 2.5 °C and warming + enough irrigation to offset the drying effect of the warming treatment, each replicated 5 times per site (Reed et al. 2019). All sites were initially dominated by perennial pasture grasses and experienced the same restoration and climate treatments, however, sites had very different trajectories with subsequent annual grass dominance in the south and perennial grass dominance in the north (Pfeifer-Meister et al. 2016; Reed et al. 2021c). Within sites, warming had a positive effect on introduced annual grasses mediated by a reduction in soil moisture, increasing the range of starting conditions at each site (Reed et al. 2021c), although we did not see significant differences in this study (Supplemental Figure 3.2). While heating and irrigation ceased in 2018, we retained the five drought treatment plots to assess whether post-burning trajectories were sensitive to precipitation amount.

Across the resultant range of variation in starting conditions, in 2018 we installed a fully-factorial experiment with site, burning, seeding, and drought as factors. To evaluate the effects of burning on functional group cover, we nested two 1-m^2 paired burned and unburned subplots separated by a 10 cm buffer within each of the 60 existing plots. These were established along a north-south axis in the western half of each plot. We burned between October and November 2018 using a 1-m^2 aluminum burn-box (Figure S3.1). We burned in low wind conditions between late morning to early evening. Fuels were ignited with wax paper or a propane torch, and we relit fires if they went out before all herbaceous fuels were consumed. Each site was burned on the earliest fall day permitted by local fire restrictions (Southern: November 3, Central: October 11, Northern: October 1). Fires removed all thatch and exposed mineral soil but did not cause mortality to most perennial species, which began to resprout quickly.

To assess the effects of starting composition, drought and burning on seedling establishment, we further divided burned and unburned subplots into six 33 cm x 33 cm seeding microplots. We randomly assigned microplots to one of six seed mixes (Table 2): 1. control (no seed added); 2. *Festuca roemeri* alone (native perennial grass, NPG); 3. *Danthonia californica* alone (NPG); 4. *Koeleria macrantha* alone (NPG); 5. introduced perennial grasses (*Schedonorus arundinaceus, Agrostis capillaris, Dactylis glomerata*); or 6. mixed annual and perennial native forbs (*Achillea millefolium, Agoseris grandiflora, Cammasia quamash, Clarkia purpurea, Collinsia grandiflora, Drymocallis glandulosa, Lomatium nudicale, Lomatium utriculatum, Acmispon americanus, Lupinus bicolor, Microseris lacinata, Plectritis congesta, Prunella vulgaris, Tritilea hyacinthea, Zigadenus venenosus*). We included both native perennial grasses and introduced perennial grasses to compare their relative establishment rates, calculated as the probability of germination and surviving their first growing season. The forb mix, consisting of native species commonly used in restoration, was included to test the ability of burning to increase native diversity in different contexts of background grass dominance. Each microplot (excluding control) was seeded with a total of 8 g m^{-2} of seed, divided evenly across species (either alone or in combination) by weight, within ten days of each burn. Each combination of site, burn treatment (subplot), and seeding (microplot) was replicated twenty times overall, with five replicates in each of the most recent climate legacy (warming, warming + precipitation) and within the two ongoing (ambient, drought) treatments.

Community measurements

To evaluate community trajectories, we estimated percent cover by functional group of interest (introduced annual grasses, perennial grasses, and forbs) in each 1 m^2 subplot at peak standing biomass in June 2019 at all sites. As our community measurements were focused on the functional annual-perennial transition we did not distinguish between species origin (native, introduced) for perennial grasses. A full list of species present in this experimental system can be found in the supplement of Reed (2021c). Cover measurements were repeated in 2020 to evaluate persistence of burn effects on seeded species, but only at the central site. To evaluate seedling establishment, we inventoried all individuals or culms (for perennial grasses) of seeded species in each 33 cm x 33 cm microplot at the peak of the growing season in June. Where seedlings were very abundant and evenly distributed within a microplot, we subsampled the center 11 cm x 11 cm of the microplot and weighted seedling abundance by proportion of total area covered. To calculate seedling establishment in 2019, we divided the number of individuals (or culms) by the original number of seeds added the previous Fall.

Analysis

All analyses were carried out using R version 3.6.2 (R Core Team, 2019), and scripts have been published GitHub accessible at: https://github.com/HallettLab/hops. Datasets are also available for download at:
https://portal.edirepository.org/nis/mapbrowse?scope=edi&identifier=1029&revision=1. To evaluate when burning initiated transitions between introduced annual grass, perennial grass, and

forb-dominated states across the latitudinal climate gradient, we first characterized burned and unburned communities based on the relative cover of each of these three groups. We then created a Bray-Curtis dissimilarity matrix of both unburned and burned community subplots across all three sites in 2019. These were then sorted into clusters using agglomerative hierarchical clustering by the complete linkage method using "cluster" (Maechler et al. 2015). To identify the optimal number of clusters, we used the elbow method in the package "factoextra" (Kassambara et al. 2017). To confirm that our clusters were significantly different, we ran mixed models using the R package "nlme" (Pinheiro et al. 2019) with functional group and cluster as interacting fixed effects and subplot nested within plot as a random effect. We used Tukey post-hoc tests from the package "multcomp" (Hothorn et al. 2008a) to identify differences in cover. We also used PERMANOVA, with cluster as a fixed effect and subplot nested within plot as a random effect, to verify differences in clusters. We then counted the number of within-plot transitions between clusters due to burning.

To address potential legacy effects of previous climate manipulations on functional group representation, as well as the ongoing effect of drought treatments, we used continuous multivariate methods with site and climate manipulation treatment as fixed factors. Functional representation was relativized as a proportion of total cover for each functional group within each subplot, and these 'functional communities' were ordinated in multivariate NMDS space using the package vegan (Oksanen et al. 2017). We tested for significant differences between unburned subplots by site and climate manipulation treatment, with subplot nested in plot as random factors using PERMANOVA. Because the only ongoing manipulation, drought, showed no significant effect on community composition, our analyses consider these climate manipulations only as a historical driver of variable starting conditions and suggest that burning effects may be robust to some degree of rainfall variability.

To test whether burning increased introduced seedling establishment, and whether starting community composition modified these effects, we focused on four response metrics: native perennial grass establishment rate, introduced perennial grass establishment rate, forb establishment rate and forb Shannon diversity. We initially calculated the establishment rates of each species by dividing the number of individuals present at peak biomass in Spring 2019 by the number of seeds added (estimated by weighing seeds in the lab). We then averaged species' level establishment within each focal group, and calculated Shannon diversity among the forb species using the R package "codyn" (Hallett et al. 2019). We used mixed effect models to assess responses, with site and burn treatment as interacting fixed effects and subplot as a random effect. To evaluate the effect of starting community composition on seedling establishment, we tested for differences in each metric by unburned subplot community cluster. Because we wanted to evaluate the effect of starting composition independent of site, we used cluster as a fixed effect and site as a random effect.

At the central site we additionally compared two-year establishment success (calculated as the number of individuals that persisted until spring 2020 compared to seeds added) and assessed the response of individual forb species as well as overall functional group response. Here, we used year and burn treatment as fixed factors, and microplot nested in subplot as random effects. For all comparisons we used post-hoc Tukey tests.

Results

Starting Composition

In unburned control plots, introduced annual grasses dominated at the southern site, forbs were generally dominant or co-dominant with annual or perennial grasses at the central site, and perennial grasses and forbs dominated at the northern site (Figure 3.2a). While previous work has shown that warming and drought can amplify introduced annual grass dominance (Pfeifer-Meister et al. 2016; Reed et al. 2021c), our PERMANOVA analysis (Figure S3.2, Table S3.1) did not find significant differences at any site of the ongoing drought treatment (Northern: $P=0.897$, Central: $P=0.545$, Southern: $P=0.572$) or climate manipulation legacies as a whole (Northern: $P=0.929$, Central: $P=0.256$, Southern: $P=0.237$).

Cluster Characterization

We initially identified the optimal number of community clusters as three, at which point increasing partitions provided diminishing returns of explained variation (Figure S3.3a). We named these clusters: “Forbs Dominant”, which was dominated (61% average) by forbs (both annual and perennial); “Annual Grasses” which was dominated by introduced annual grasses (63% average); and “Perennial Grasses and Forbs” which had roughly equal representation of forbs and perennial grasses (~46% average, Figure S3.3b). Although we optimized within-cluster variation at three groups, we added a fourth group to better distinguish between levels of annual grass dominance, further dividing “Annual Grasses” into two ecologically relevant subgroups: “Annual Grasses Dominant” and “Annual Grasses and Forbs”. In the first group, “Annual Grasses Dominant”, introduced annual grasses represented a strong majority of relative cover (71.8% average), while in “Annual Grasses and Forbs” they were abundant but not the outright majority (48.8% average, Figure 3.2b). Our clusters were confirmed as significantly different by ANOVA of functional group relative cover (Figure 3.2b, Table S3.2) as well as PERMANOVA, where cluster explained more variation ($P<0.01$, $R^2=0.81$) than site ($P<0.01$, $R^2=0.68$, Figure 3.2a). Because we were interested in the expansion and persistence of introduced annual grass dominance, we proceeded with these four clusters, which explain similar levels of within-cluster variation as three clusters. Across all plots, seed addition did not affect community composition due to low survival rates, small stature, and rapid recovery of established plants post-burn.

Fire Effects

Although we expected burning to increase introduced annual grass dominance in the south and increase forb representation in the north, we instead saw a general pattern of burning reducing introduced annual grass dominance, with increased forb and some perennial grass representation across sites (Figure 3.3). While there were no “Annual Grasses and Forbs” or “Annual Grasses Dominant” clusters in the northern site, the number of plots in both these and the “Annual Grasses Dominant” cluster were reduced by burning at the central and southern sites. All sites saw increases in the “Forbs Dominant” cluster membership with burning. Only the central site had representation of all four clusters, where seven out of twelve possible unique cluster transitions occurred (four occurred in the south and two in the north).

Overall, burning improved native perennial grass and introduced perennial grass seedling establishment (Figure 3.4a, b). The lone exception was that native perennial grasses never established at the hot, dry southern site, even when burned. Following a similar pattern, burning significantly increased the establishment of forbs and Shannon diversity at the central and northern sites, while having no effect at the southern site (Figure 3.4c, d, Table S3.4). At the central site, all but one forb species showed a trend toward increased establishment with burning, although the magnitude of this effect varied widely and was not always statistically significant (Figure S3.4). Initially, introduced perennial grasses had the highest burned and unburned establishment rate, but by 2020, net survival dropped to a similar level as the best-surviving native perennial grass, *Festuca roemeri*. This species greatly benefited from burning, and the initial effect of the burn lasted through 2020. By contrast, another native perennial grass, *Danthonia californica*, did not benefit from burning and had low but consistent establishment and net survival. Lastly, the native perennial grass, *Koeleria macrantha,* showed a strong initial response to burning similar to pasture grasses, but had low net survival through 2020.

Although seeding success was overall lower in unburned plots, existing vegetation more strongly modulated success in these plots. Annual grasses tended to suppress seeding success; for example, introduced perennial grasses and forbs both showed higher establishment in communities that were not in the "Annual Grasses Dominant" cluster (Figure 3.5). More specifically, introduced perennial grasses had higher establishment in "Perennial Grasses and Forbs" and "Forbs Dominant" clusters, and forbs had higher establishment in the "Perennial Grasses and Forbs" than the "Annual Grasses Dominant" cluster (Table S3.3). Seeded forb Shannon diversity was also higher in the "Forbs Dominant" than "Annual Grasses Dominant" cluster. In contrast with introduced perennial grasses, native perennial grass establishment did not significantly differ by starting condition in unburned plots.

Discussion

Overall, our results supported our expectation that burning can bolster perennial grass and forb cover and establishment from seed, but that climate and starting community condition can influence its efficacy. Contrary to our expectation that burning would reinforce introduced annual grass dominance in warmer climates, we saw increased forb and perennial grass representation across all sites. However, at the central site this was an average trend composed of individual plot transitions both towards and away from introduced annual grass dominance, and there was one transition towards annual grasses at the southern site. Site-specific variation in response to fire can help guide and prioritize the use of prescribed burns. While we found that burning disturbance can lead to positive restoration outcomes across the regional gradient sampled, practitioners will need to weigh specific benefits, costs and risks.

The strong latitudinal effects we observed indicate that restoration goals and strategies may need to vary based on climate and existing introduced annual grass abundance, and that these dynamics may continue to shift in all parts of the region under increased warming. Warmer-latitude PNW grasslands could see accelerated transition to annual grass dominance with increasing disturbance, as observed in our southern site, and whether grasslands are dominated by annual or perennial grasses can have major effects on ecosystem functioning (Palmer et al. 1997). Annual grass dominance can increase fire frequency, soil carbon loss, noxious weeds, and erosion, while also shortening the forage season, and reducing biodiversity (Carlsen et al. 2000; Maret & Wilson 2005; Anke Stein et al. 2014; D’Antonio & Vitousek 1992). Therefore, managers of introduced perennial grasslands may need to re-evaluate where the additional benefits provided by native perennial grasses outweigh the risk of conversion to introduced annual grass dominance. In addition to increased plant community diversity, the discontinuous cover of native perennial bunchgrasses provides habitat for native species of grassland obligate endemic species of ground-nesting birds including the streaked horned lark and Oregon Vesper sparrow (Altman 2000, 2011) and invertebrates like Fender’s blue and Taylor’s checkerspot butterflies (Schultz et al. 2011). By contrast, rhizomatous introduced perennial grasses create dense continuous cover that reduces habitat value for grassland species. A site-by-site review of our results can help understand the relative level of risks and rewards of using fire on restoration outcomes.

It is unlikely that fire and seeding alone are sufficient to return introduced annual grass-dominated southern sites to perennial grass dominance. While burning did not increase annual-grass dominance as expected, no plots transitioned to perennial dominance and burning had no significant impact on native perennial grass or forb seedling establishment. While there was an increase in introduced perennial grass establishment with burning, it was still a minor contribution to overall cover and did not affect cluster membership. In southern sites, perennial grass recovery may be bolstered by more labor and cost-intensive restoration methods such as irrigation or planting plugs instead of seeds (Hedberg & Kotowski 2010; Lindh 2018). A forward-looking strategy might also include assisted migration of perennial species or populations from the south that are better adapted to future climate change, although these practices carry risks of their own, such as genetic dilution of locally-adapted native populations or invasiveness (Aitken & Whitlock 2013; Butterfield et al. 2017). Within the regional gradient of our experiment, the annual grass-dominated southern site represents a condition that will likely become more common in the PNW as climate change shifts current climatic conditions northward. Here, the reduced efficacy of burning must be weighed against the greater benefits and reduced labor of focusing on cooler-climate sites that still have a large perennial grass component.

Meanwhile, our results at the cool, northern site reaffirm what PNW restoration practitioners already know: burning is still a useful tool for enhancing diversity of disturbance-adapted forbs and aiding in the establishment of native perennial grasses. Even with a warming climate, for the foreseeable future there will likely remain sites where local climate gives healthy populations of perennial grasses a competitive advantage over introduced annual grasses. If properly identified and monitored, these sites represent a low-risk, high-reward scenario for burning disturbance to restore native perennial grasses and forbs.

While our northern and southern sites had relatively consistent starting communities across plots, the less-deterministic central site had plots occupying each of our four clusters ("Annual Grasses Dominant", "Annual Grasses and Forbs", "Perennial Grasses and Forbs", and "Forbs Dominant). Where multiple community states occupy the same climate, as here, they are considered resilient if they are able to re-establish dominance following disturbance (Holling 1973, Suding & Hobbs 2009). Intact vegetation provides resistance to invasion, and resilience to disturbance allows for recovery of existing vegetation following disturbance (Condon et al. 2011). These concepts are operationalized in the Great Basin, where the increased resilience and resistance of native vegetation in cooler and wetter sites across the landscape helps prioritize preventative and restoration efforts (Chambers et al. 2020, 2014). We expected that fire could be used as a management disturbance to purposefully overcome introduced annual grass resilience, or unintentionally overcome perennial grass resilience, allowing for rapid state change. In fact, after one burn, we saw only a moderate level of state-change at the central site. Specifically, we saw a small shift away from introduced annual grasses, a net result of transitions both toward and away from annual dominance post burn. This may suggest some level of resilience for both community types, or a slow transition process driven by perennial grass seedlings. Further research is needed to determine whether communities fully recover, and whether any resilience is robust to repeat or more intense disturbance.

While burning did not lead to complete state change at the central site, it played a large role on seedling establishment. Overall, introduced perennial grasses had the greatest initial increase in establishment when burned, although this was reduced to the level of native *F.*

roemeri by the second year. *Danthonia californica* was not affected by fire, suggesting it may be an appropriate candidate for restoration where fire risk is high due to introduced annual grass presence or proximity to human settlement. However, another study found that continuing monitoring uncovered a benefit for the species from fire in the form of pathogen reduction (Roy et al. 2014). The variability of starting conditions present at the central site also demonstrated the key role of community on seedling establishment. While native perennial grass establishment was not affected by starting communities, introduced perennials, and forbs to an even greater extent, established at higher rates in perennial grass or forb-dominated plots. This suggests that in intermediate sites which are not dominated by introduced annual grasses, seeding may be successful even in the absence of disturbance, potentially helping to reduce the threat of introduced annual grass invasion. Where climate conditions are intermediate, considering interannual and spatial climate variability will also be important for predicting fire disturbance outcomes. Here, it may be important to plan restorations so that they include disturbance only in years with cooler growing seasons that approximate conditions further north or to focus on sites with more suitable microclimates. This is potentially a realistic option in the PNW where the El Niño Southern Oscillation and the Pacific Decadal Oscillations flip between cold wet growing seasons and warm dry ones (D'Arrigo et al. 1999; Lindh et al. 2018).

At face value, our results suggest that burning has generally positive effects and the rewards likely outweigh risks across the regional gradient sampled. However, after twelve years of experimental clearing, restoration and climate manipulation, the communities and histories of our plots are relatively uncommon in the context of current PNW grasslands as a whole. All of our sites were originally dominated by introduced perennial grasses, and even at the southern site undisturbed surrounding grasslands have remained so (Pfeifer-Meister et al. 2016, Reed *unpublished data*). Fully interpreting our results requires understanding why our plots were invaded by introduced annual grasses, and what this means for disturbance risks. While introduced annual grass invasion in our plots was exacerbated by climate manipulations that reduced available soil moisture (Reed et al. 2021c), we found site to be the best predictor for introduced annual grass dominance. For example, all of our southern-site starting communities in 2018 were dominated by introduced annual grasses regardless of climate treatment legacy, demonstrating that ambient conditions at lower latitudes can already support annual dominance. The existence of both annual-grass (in our plots) and perennial-grass (in surrounding pasture) dominated states in the south limits our interpretation of risks to only sites that are already dominated by introduced annual grasses and highlights the added risk of multiple disturbances. In fact, our results suggest that warmer sites with existing perennial populations are likely at highest risk of conversion following disturbance.

Taken as a whole, our results suggest that using fire to reestablish native grasses and forbs across our regional gradient can risk conversion to introduced annual grass-dominated assemblages, especially in warmer sites. Although annual grass dominance may be difficult to recover from, there is little risk but some potential gain in subsequent disturbance. More research into the ecosystem services provided by introduced annual grass-dominated and perennial-grass-dominated grasslands will further inform practitioners making decisions that affect state-change dynamics. With the increased threat of introduced annual grass expansion, managers will need to critically consider the desirability of different potential ecosystem states, as well the risk of different types of intervention. In managing ecological systems, both action and inaction have risks. Increasingly, climate change is altering local understandings of the risks and benefits of intervention. The Pacific Northwest is only one of many regions experiencing novel environmental conditions coupled with new waves of species invasions. Our study serves as an example of how the outcomes of disturbance intervention must be contextualized in terms of site history and regional context. Contextualizing management will not entirely eliminate the uncertainty surrounding restoration in a changing world, but it can help reduce it. Rather than inaction, we advocate for informed decision-making to improve long-term restoration success.

Bridge

This study demonstrated that contextualizing the impacts of restoration intervention in time and space can help understand the risk that a specific site will be part of a larger predicted trend. In this case, a perennial to annual transition is underway across western Pacific Northwest grasslands. We saw that once established the annual state is quite resilient to burning disturbance, but so are perennials. In the following chapter, we consider how warming is driving this shift. Specifically, we ask whether warming directly negatively impacts perennials, or indirectly via strengthened competition from annuals. We consider what each of these outcomes mean in a management context.

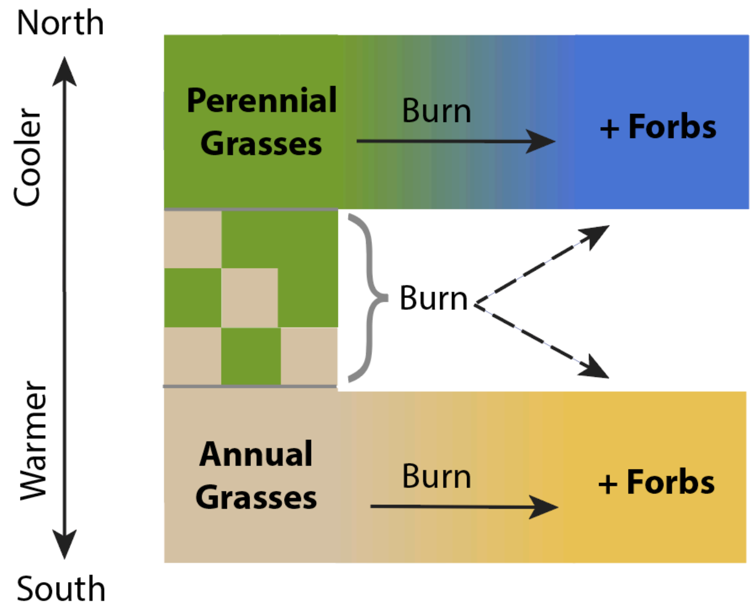


Figure 3.1: Expected effects of burning (arrows) on annual grass (tan) and perennial grass (green) dominated communities which were associated with a latitudinal climate gradient (left). We expected burning would consistently increase the proportion of forbs, while climate would reinforce the dominant grass type in warmer (annual grasses) and cooler (perennial grasses) climates. At intermediate latitudes, variation in starting community composition and intermediate climate conditions was expected to support increases in either annual or perennial grass cover following burning.

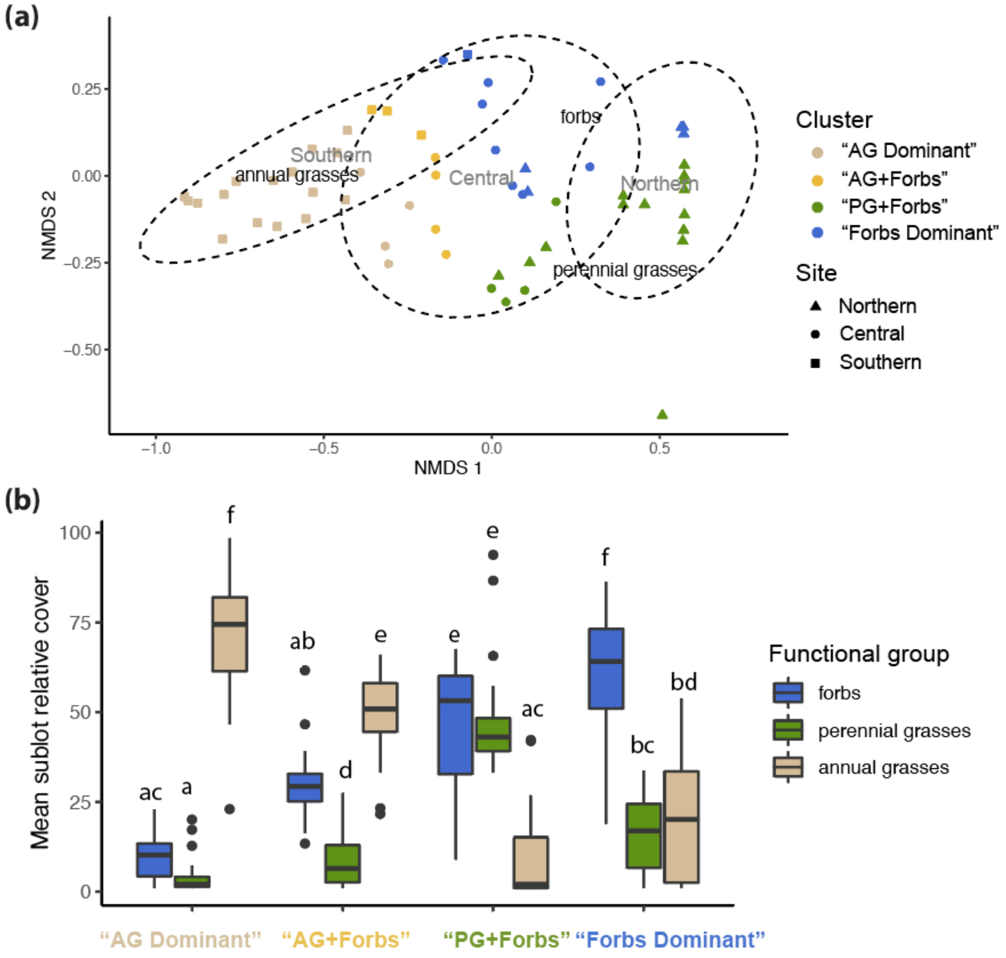


Figure 3.2. (a) NMDS ordination of subplot communities by site (shape) and cluster (color). Black text represents relative loadings of functional groups in ordination space. These include annual grasses (NMDS1: -0.543, NMDS2: -0.001), perennial grasses (NMDS1: 0.339, NMDS2: -0.300), and forbs (NMDS1: 0.232, NMDS2: 0.207). Ellipses represent multivariate normal distribution 95% confidence intervals by site and are labeled at their centroids with grey text. **(b)** Cluster composition as defined by the range of average relative functional group representation at the subplot level across all sites in burned and unburned subplots. Letters denote significant ANOVA differences in functional group cover both within and across clusters.

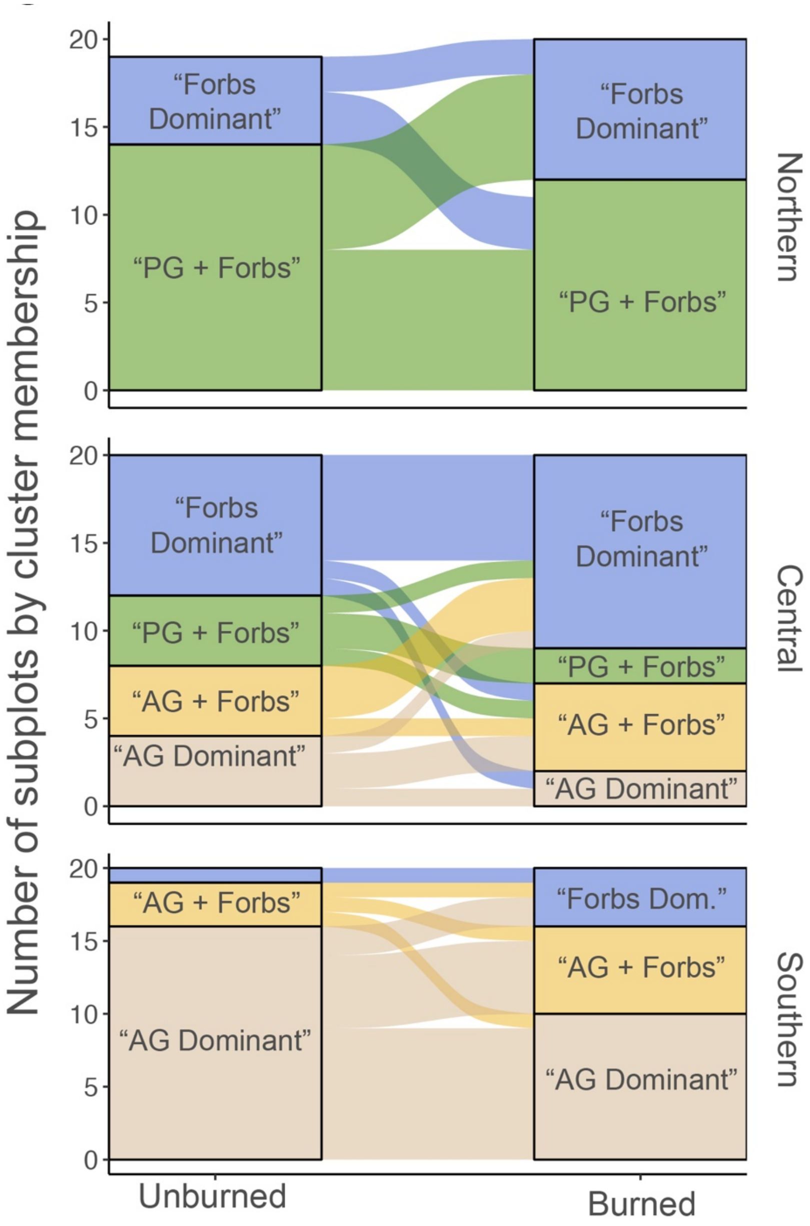


Figure 3.3. Paired unburned and burned subplot transitions based on cluster membership in 2019. All sites saw more transitions towards forbs and away from annual grasses with burning. Specifically, the "Forbs Dominant" cluster always increased in membership, and when present the "Annual Grasses Dominant" cluster always decreased in membership. Overall, the central site had the greatest diversity of cluster memberships (all four), as well as most total (ten) and unique (seven) transitions. Note: n=19 in Northern unburned due to missing data for one plot.

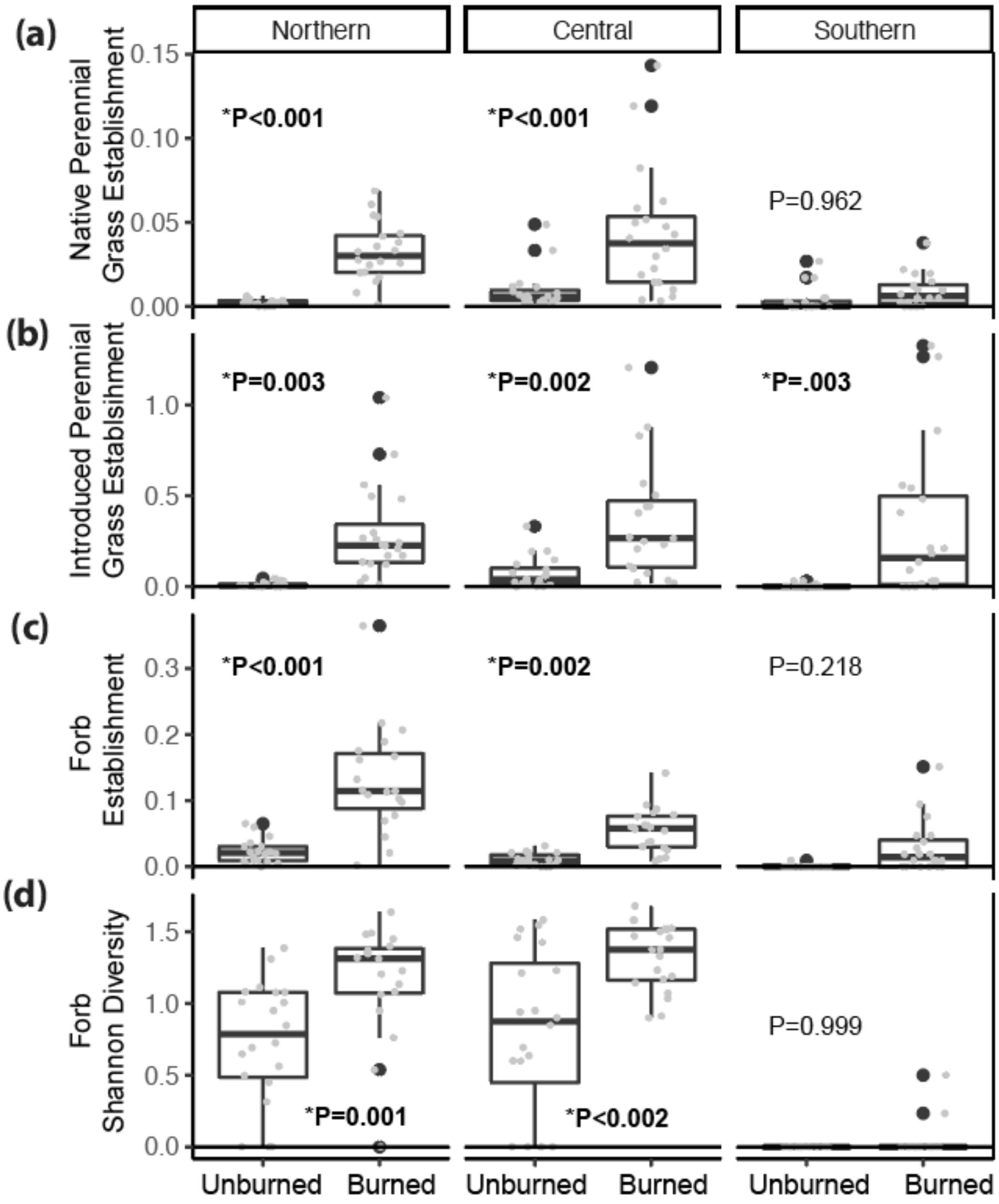


Figure 3.4. Establishment (proportion of added seeds surviving as seedlings in spring 2019) of (a) native perennial grasses, (b) introduced perennial grasses and (c) forbs in burned and unburned subplots. Burning increased seedling establishment except for native perennial grasses and forbs in the southern site. Burning also increased forb seedling Shannon diversity (d). These effects were most pronounced in the north while few forbs survived in the south.

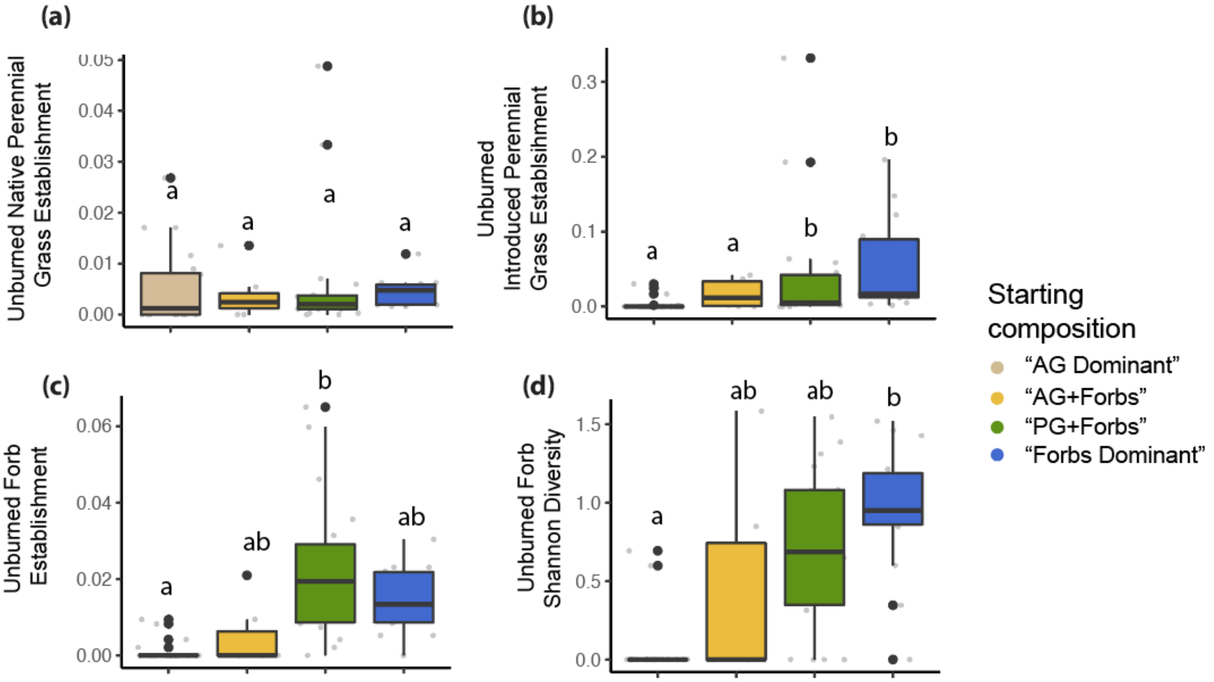


Figure 3.5. Seedling responses by starting community composition as defined by unburned subplot cluster membership in 2019. Responses include (a) native perennial grass establishment rate (seedlings in June 2019/seeds introduced) (b) introduced perennial grass establishment rate, and (c) forb establishment rate and (d) Shannon diversity of seeded forb seedlings. Letters represent the result of mixed models for each response metric with cluster as a fixed factor and site as random.

Table 3.1. Experimental site location and environmental context. Elevation data are from the USGS spot elevation tool TNM elevation map: 1/3 arc-second resolution (https://apps.nationalmap.gov/elevation/). Precipitation and air temperature 1981-2010 averages, and yearly data are from Oregon State PRISM model (http://www.prism.oregonstate.edu). Soil taxonomy and series information are from the Natural Resources Conservation Service, United States Department of Agriculture (USDA), Web Soil Survey (http://websoilsurvey.nrcs.usda.gov/).

			Experimental Site		
			Southern	**Central**	**Northern**
Manager			Siskiyou Field Institute	The Nature Conservancy	Capitol Land Trust
Latitude			41.27811	44.02615	46.86415
Longitude			-123.642278	-123.182171	-122.958918
Elevation			282m	168.8m	78.6m
Monthly Air Temp (°C) (PRISM)	Averages (1981-2010)	max	20.2	17.3	15.9
		min	4.4	5.4	5.3
		mean	12.3	11.4	10.6
	2019 mean		12.8	11.3	10.1
	2020 mean		13.6	12	10.7
Annual Precipitation (mm) (PRISM)	Average (1981-2001)		1434	1134	1240
	Aug 2018 - Aug 2019		1881	924	1055
	Aug 2018 - Aug 2020		1369	848	1358
Soil	Taxonomy		Loamy-skeletal, mixed, superactive, mesic Entic Ultic Haploxerolls	Very-fine, smectitic, mesic Vertic Haploxerolls	Medial, mixed, mesic Typic Haploxerands
	Series		Takilma cobbly loam	Hazelair silty clay loam	Cathcart medial-loam pasture

Table 3.2: Species seeded into five of six 33 cm x 33 cm micro-plots within paired burned and unburned subplots. Seed mixes were created to evaluate burn effects on native and introduced perennial grass seedling establishment, as well as native forb establishment and diversity. Each microplot was seeded with eight grams of seeds, evenly divided by weight among species. Native perennial grasses were each seeded independently in their own microplot, while three pasture grasses were seeded together into one plot and the 15 forbs were seeded together into one microplot. A sixth microplot was not seeded.

Seed mix	Species	Longevity	Origin	Grams/species
Koeleria macrantha	*Koeleria macrantha*	Perennial	Native	8 grams
Festuca roemeri	*Festuca roemeri*	Perennial	Native	8 grams
Danthonia californica	*Danthonia californica*	Perennial	Native	8 grams
Introduced perennial grasses	*Schedonorus arundinaceus,* *Agrostis capillaris,* *Dactylis glomerata,*	Perennial Perennial, Perennial	All introduced	2.67 grams
Native forbs	*Acmispon americanus,* *Clarkia purpurea,* *Collinsia grandiflora,* *Lupinus bicolor,* *Plectritis congesta,* *Achillea millefolium,* *Agoseris grandiflora,* *Cammasia quamash,* *Drymocallis glandulosa,* *Lomatium nudicale,* *Lomatium utriculatum,* *Microseris lacinata,* *Prunella vulgaris,* *Tritilea hyacinthea,* *Zigadenus venenosus*	Annual, Annual, Annual, Annual, Annual, Perennial, Perennial, Perennial, Perennial, Perennial, Perennial, Perennial, Perennial, Perennial, Perennial	All native	0.53 grams

CHAPTER IV

DIRECT VERSUS INDIRECT EFFECTS OF WARMING ON COMPETITION AND COEXISTENCE BETWEEN ANA INTRODUCED ANNUAL (*LOLIUM MULTIFLORUM*) AND A NATIVE PERENNIAL (*FESTUCA ROEMERI*) GRASS IN THE WILLAMETTE VALLEY, OREGON

Authors and affiliations:

Alejandro Brambila[1,2], Chhaya Werner[1, 3], Jeff Diez[1,2], Lauren M. Hallett[1,2]

1. Institute of Ecology and Evolution, University of Oregon
2. Environmental Studies Program, University of Oregon
3. Botany Department, University of Wyoming

Contributions

A.B. and L.M.H. developed the research design. A.B. implemented the experiment, performed statistical analyses with support from C.W. and J.D. and wrote the paper with support from all authors. All authors discussed the results and commented on the manuscript.

Introduction

Climate change is driving widespread changes to ecosystems (Bellard et al. 2012; Feeley et al. 2020). As novel conditions differentially affect species fitness, patterns of competitive dominance or coexistence can shift, occasionally driving rapid state-change (Moore et al. 2003; Standish et al. 2014). One striking example is in western Pacific Northwest grasslands, where warming is associated with a transition from perennial grass to introduced annual grass dominance (Pfeifer-Meister et al. 2016; Reed, Pfeifer-Meister, Roy, et al. 2021). Predicting where and how these transitions will take place is difficult, as warming affects the entire community and interactions between species simultaneously; however, accurately predicting these transitions can be vital to planning management prevention and mitigation strategies. For example, direct negative effects of warming on the extant community may be impossible to prevent at a local scale without broad environmental manipulation, whereas indirect effects mediated by invasive species may be altered by management. When state transitions are between different life history strategies, such perennial grasses and annual grasses, understanding how direct and indirect effects accrue across vital rates of each life stage is essential for targeted management.

Warming has the potential to alter community composition by directly or indirectly affecting the fitness of individual species, making it important to holistically study climate change impacts on multi-species communities (Farrer et al. 2014). For example, as warming impacts species' survival and fecundity, some may experience direct physiological impacts resulting in local extinctions, changes in abundance, or unstable populations (Lambers 2015; Thomas et al. 2004). Alternatively, the effects of climate change can be mediated through interactions with other community members (Ives 1995; Tylianakis et al. 2008), potentially leading to outcomes that differ from expectations based on direct effects alone. These indirect effects can result from either shifting competitor abundances or changes in per capita competitive effects, or a combination (Gilman et al. 2010; Adler et al. 2009). For example, in a warmer climate per capita competition for water could become more intense, and in the Pacific Northwest annual grass dominance has been associated with the rapid drawing down of soil moisture early in the season leading to reduced native biodiversity (Reed, Pfeifer-Meister, Roy, et al. 2021). Understanding the relative importance of these direct and indirect effects has important management implications for methods and prioritization of interventions.

Identifying which vital rates drive system change, and how these are affected by direct and indirect pathways, is critical for effectively targeted management. For example, restoration efforts often focus on seeding and seedling success, but adult survival can be most important for the long-term viability of perennial species (Franco & Silvertown 2004; Mordecai et al. 2015). Similarly, even when restoration efforts plant adult plugs instead of seeds, there may be a a lag period before the juvenile plugs are as established and competitive as extant adult grasses. As such, additional management may be necessary for juvenile plugs, and protection of existing stands may be more effective than restoration. The importance of perennial life stage on competitive ability is supported by California systems where both annual and mature perennial dominated grasslands have shown resistance to invasion (Corbin & D'Antonio 2004; Seabloom et al. 2003). In fact, historical agricultural plowing to eliminate native vegetation best predicts which grasslands lack perennials in California today (Stromberg & Griffin 1996). Adult perennial robustness has also been observed in the Pacific Northwest, where wet prairie perennial seedlings showed reduced fitness in competition with annuals, but competitor removal had no effect on survival of adults in the field (Pfeifer-Meister et al. 2008). Differences in life stage responses to warming might lead to different initial versus ultimate responses (e.g., if seedlings respond favorably but adults negatively). Differences in life history strategies might also lead to divergent vulnerabilities to change; for example, perennial grasses must survive summer heat and drought which can be particularly challenging in their first, non-reproductive year, while annual grasses avoid this stressor by completing their life cycle in one fall to spring growing season. As such, it is important to both understand the relative importance of each vital rate for overall population growth, and to disentangle the effects of warming on each life stage to predict the timescale of a state change and effectively managing it.

Western Pacific Northwest grasslands have a Mediterranean climate, defined by mild, wet winters and warm, dry summers (Rundel et al. 2016). These perennial grasslands have a unique, fire-dependent flora and fauna (Shelvey & Boyd 2006) which provide multiple ecosystem services including pollination, cattle pasture, carbon sequestration and indigenous cultural value (Hamman et al. 2011; Menke 1992). Development, agriculture and industry have reduced and fragmented grasslands to a fraction of their former extent, while loss of prescribed fire, agricultural disturbance and species invasions have led to novel species assemblages. Today introduced perennial pasture grasses dominate grasslands north of Oregon's Willamette Valley, while introduced annual grasses often dominate to the south. Recognizing their value, conservation and restoration efforts are underway to protect and expand these native perennial grasslands often using a combination of disturbance (mowing, burning, solarization) and seeding of native forbs and perennial grasses. Under climate change, this region is experiencing hotter, drier, and longer summers (Dalton et al. 2017). Both latitudinal and experimental evidence suggest that this warming is driving state change to annual dominance, with potential concerns of biodiversity loss and changes to ecosystem function (Palmer et al. 1997; Corbin & D'Antonio 2004; Carlsen et al. 2000; Maret & Wilson 2005; Claudia Stein et al. 2014). Understanding how direct and indirect warming effects alter vital rates, and how this aggregates to affect population trajectories, could refine grassland management by differentiating between communities made up of seedlings, plugs and established adults and annual presence affects them.

Here, we took a population modeling approach based on data gathered from a controlled experiment that manipulated temperature and competitor density to examine direct and indirect effects of warming on a native perennial grass (*Festuca roemeri)* and an introduced annual grass (*Lolium multiflorum)* in western Oregon. Specifically, we asked to what extent warming directly impacted *Festuca*, or indirectly affected it via effects on *Lolium* abundance or competitive ability (Figure 4.1). We used parametrized competition models to explore how warming affects population trajectories and competitive outcomes. We asked 1) How do direct and indirect effects of warming impact equilibrium populations and growth rates of each species? and 2) How sensitive are these outcomes to shifts in vital rates? We carried out our experiment over two years, allowing adult perennial parameters to vary across years to compare juvenile plugs to more established adults. Generally, we expected that warming would increase the *Lolium* population size and growth rates relative to *Festuca,* increasing the chance of annual dominance, and that more established adult *Festuca* would better resist annual invasion.

Methods

Experimental Design and Data Collection

To test for direct and indirect effects of warming, we grew the perennial *Festuca roemeri* seedlings and adults in warmed and ambient conditions across various competitive scenarios with a common annual grass, *Lolium multiflorum.* We identified a grassland site dominated by introduced perennial grasses near Eugene, Oregon in the Southern Willamette Valley, a transition zone where both annual and perennial dominated communities are found. Our experimental design consisted of various controlled competitive scenarios between annual seeds, perennial seeds, and perennial plugs in both warmed and ambient conditions. Our goal was to parametrize Beverton-Holt competition models for each species which could then be used to assess to what degree warming affected population growth rates with and without interspecific competition, and whether competitive exclusion, coexistence, or priority effects were expected.

A 10 m by 30 m area was mowed in Spring 2019. Clear plastic was installed over the entire area and the plot was solarized for six months. The plastic was removed in September 2019, at which point all vegetation was dead. Surface litter was raked off the site, and any remaining litter was incinerated with a propane torch, exposing mineral soil. Twenty-four hexagonal 2 m^2 macro-plots were established, separated by 1m buffers. Twelve macro-plots were assigned to be warmed with the remainder at ambient conditions. Warming was implemented using modified International Tundra Experiment (ITEX) chambers, commonly used to raise internal air temperature at high latitudes (Henry and Molau 2003; Marion et al. 1997). We adapted our ITEX chambers to the temperate climate (Aronson & McNulty 2009; Buhrmann et al. 2016), adjusting height and opening diameter and adding temperature stabilizing mass as in Godfree et al (2011). We constructed hexagonal chambers with a 3 m diameter using Palram®, angle aluminum and zip ties, adding 18 black 3.5 gallon buckets around the perimeter as thermal mass (Figure S4.1). To verify that our warming treatment was effective over the course of our experiment, we randomly selected six warmed and six ambient macroplots and installed one Thermicron iButton (maximintegrated.com) to monitor air temperature (at 30cm) and one belowground to measure soil temperature (at 5cm) at the northern end of the plot to minimize shading. The 24 iButtons were synchronized and programmed to record temperatures every four hours.

Within each warming treatment, seven competitive scenarios (Table 4.1) were randomly assigned to four replicate sub-plots to evaluate demographic responses of each life stage to varying densities of conspecific and heterospecific competitors. Our competitive scenarios included three background equilibrium density treatments, three 50:50 treatments and one low competition treatment. Equilibrium density treatments had either annuals, seedling perennials, or adult perennials at high density (6 g/m^2 for seeds, 10 $individuals/m^2$ for adults) with two phytometers of each other competitor (four of each in the adult background treatment). The three 50:50 treatments were each evenly divided between two of the three competitors at approximately half their density in the equilibrium plots ($2g/m^2$, 6.06 $adults/m^2$). The low-density treatment had no background competitor, only two phytometers of each competitor, widely spaced to avoid competition. Each phytometer was established by adding six seeds and then thinning to one individual if multiple emerged. For the competitive scenarios of "no background", "annual background", "perennial seedling background" and "perennial adult background", macro-plots were divided into two 1 m^2 subplots. For three "50:50" competitive scenarios macro-plots were divided three ways into 0.66 m^2 segments. For a layout of plot treatment assignments see Figure S4.2.

We sourced *Lolium* seed that was grown in the Willamette Valley from a local feed store, and purchased *Festuca* from Heritage Seedlings, a native seed purveyor in Salem, OR. We grew out adult plugs from May through August 2019 in the University of Oregon greenhouses, and then hardened them off for two weeks outdoors. Following removal of solarization plastic, we transplanted plugs and allowed them to establish for one month, during which time two failed transplants were replaced. In November 2019, we broadcasted annual and perennial seeds and randomly selected phytometers. Seed heads were removed before maturation in Spring 2020 and surviving perennial seedlings were removed immediately before broadcasting seed at the same rate for the second year of the experiment in September 2020.

To assess demographic responses to competition and warming, we monitored survival and fecundity of each life stage over two years. In June each year, we estimated *Lolium* and adult *Festuca* fecundity by counting their reproductive tillers. Because there were many *Lolium* individuals, we counted tillers at the plot level, while for *Festuca* we associated tillers with each individual. We then counted seeds on 20 random tillers per species from warmed plots and 20 from ambient plots and calculated mean values to convert from tillers to seed production. On average, *Lolium* tillers had 30 spikelets with 11 florets, and festuca had 25 spikelets with 6 florets. Simple ANOVA suggested no significant difference in seeds per tiller in warmed versus ambient plots. *Festuca* seedling survival to adulthood was calculated at the plot level by counting the number of seedlings present one year after they were sown.

Population Model Structure

We used discrete-time Beverton-Holt models used in similar analyses (Mordecai et al. 2015; Larios et al. 2017; Lauren M. Hallett et al. 2019) to describe population growth of each species in competition with no migration. For the annual, *Lolium*, we calculated per-capita population growth as the number of seeds produced over the number of seeds added. To account for the perennial life history of *Festuca*, we assumed seeds that survive their first year become adults, and therefore modeled population growth using two models. In the first, seed production is determined by adult fecundity as we assumed that seedlings do not produce seeds in their first year. In the second, the adult population increases as added seeds survive to adulthood. Each population growth model was also influenced by interannual seed or adult survival, respectively, and competitive interactions. With subscript *a* representing annual *Lolium* seeds, *s* representing *Festuca* seeds, and *p* representing *Festuca* adults, the population growth models are:

$$Eq. 1 - Annuals: \quad N_a(t+1) = N_a(t) * (1 - g_a)s_a + N_a(t)\lambda_a \frac{1}{1 + \alpha_{aa}N_a(t) + \alpha_{ap}N_p(t)}$$

$$Eq. 2 - Perennial\ seeds: \quad N_s(t+1) = N_s(t) * (1 - g_s)s_s + N_p(t)\lambda_p \frac{1}{1 + \alpha_{pa}N_a(t) + \alpha_{pp}N_p(t)}$$

$$Eq. 3 - Perennial\ adults: \quad N_p(t+1) = N_p(t)s_p + N_s(t)s_{sp} \frac{1}{1 + \alpha_{sa}N_a(t) + \alpha_{ss}N_s(t) + \alpha_{sp}N_p(t)}$$

Each equation calculates a population, N_i, at a time (t + 1) given $N_i(t)$, competitor densities, and demographic parameters including establishment, g_i; fecundity in the absence of competition, $\boxed{\lambda}_i$; interannual survival, s_i (note: s_s represents interannual ungerminated seed survival and s_{sp} represents seed survival to adulthood); and the competitive effect of population *j* on *i*: $\boxed{\alpha}_{ij}$. *Lolium* population growth depends on the interannual survival of seeds that did not germinate plus fecundity reduced by intraspecific competition and competition from adult perennials. Similarly, *Festuca* seed availability depends on seedbank survival (s_s) and adult fecundity reduced by intraspecific competition and competition from *Lolium.* Finally, the adult *Festuca* population depended on interannual adult survival and the survival of seeds to adulthood (s_{sp}) reduced by competition from all three life stages. Due to their small size in their first year and delayed emergence, we did not expect *Festuca seedlings* would meaningfully compete with adults or *Lolium,* but that they would with other seedlings.

Parameter Estimation

To estimate fecundity, survival and competition parameters in warmed and ambient plots, we fit models using a Bayesian approach in R (R Core Team 2019) and Stan using the package “rstan” (Stan Development Team 2022). For each model, we ran three Markov chain Monte Carlo chains with 5,000 warm-up and 5,000 sampling iterations to determine posterior distributions. We fit independent models for each life stage (*Lolium*, *Festuca* adults, and *Festuca* seedlings) allowing competition, fecundity and seedling survival to adulthood parameters to vary by warming treatment. We fit separate models using data from 2020 and 2021 independently to compare the fecundity and competitive effects of juvenile adult plugs and more established perennial adults, resulting in a total of six model fits (three life stages x two data years).

To interpret our experimental design and adapt our collected data to the model assumptions, some data cleaning and manipulation was necessary. To account for variable subplot size, counts were adjusted to densities on a per square meter basis. Because of the high numbers of seeds added, annual fecundity and perennial adult survival models were run using subplot level average data, while perennial fecundity was estimated at the individual adult level. For annuals, per-capita fecundity was calculated as the proportion of seeds produced over seeds added. Perennial seedling survival was calculated as the proportion of new adults the following year over the number of seeds added. Adult perennial per capita fecundity was simply entered as seed counts per individual. Competitor densities were generally calculated as starting density of seeds or plugs added to a given subplot per meter squared. The exception to this was where phytometers of different life stages had been intentionally spatially separated, we reduced their competitive density to zero. Specifically, in our ‘no competition’ treatment, we assumed zero competition between phytometers of different life stages, in the seedling background competition treatment we assumed no competition between annual and adult perennial phytometers, in the annual background treatment we assumed no competition between adult and seedling perennials, and in the adult background treatment we assumed no competition between annuals and perennial seedlings. Finally, because annual and seedling phytometers were thinned to four (in seedling and annual background) or eight (in adult background) stems, we adjusted these densities based on a seeds:stems conversion factor calculated as independent mean values for each species from their respective background plots.

Across life stages, model structure and priors varied. To account for differences in posterior distributions of fecundity versus survival estimates, our annual and perennial seed model posteriors were poission distributed, while our perennial adult model used a gaussian distribution. Across models, we allowed lambdas, alphas and perennial seedling survival to vary according to warming treatment by defining intercept (ambient) and slope parameters for each, where the warmed parameter value was defined as the intercept + slope. Because biological reality requires positive lambda and survival, and we assumed no facilitation, we constrained these priors to positive values using exponential transformations: *exp(ambient + slope * warmtrt)*. We set generally uninformative, normally distributed priors for most parameters. Priors for lambda values and perennial seedling survival were centered near mean field observations. Differing posterior distributions of these parameters across years suggest that they were not overly constrained. All of our alpha intercept priors were *normal(-2, 1)*, which translated to *normal(0.13, 2.7)* post exponent transformation. Slopes for all parameters were centered on zero at *normal(0, 1)*. In addition to our modeled parameters, we incorporated germination and seed survival parameters from the literature for both species. While our adult *Festuca* survival rate was 100%, we used a literature derived figure of 97.5% to account for small sample size. A full accounting of model parameters, priors, and definition can be found in Table S1.

Model Analyses

Using our estimated parameters, we performed several comparisons of species performance in warmed and ambient conditions to determine relative fitness. These included comparisons of raw parameter values, equilibrium population densities, growth rates when rare (GRWR) to determine coexistence, and sensitivities of GRWR to key demographic parameters. To directly compare raw parameter values, we randomly selected 1000 iterations from the sampling portion of the posterior distribution of each model. We then ran two way ANOVA with warming treatment and year to test for significant interactions. Group differences were evaluated using the function emmeans() with Tukey post-hoc transformation from the package ‘lsmeans’(Lenth 2016).

Because we were primarily interested in interannual differences due to maturation of adult perennials rather than interannual climate variability, we averaged mean estimates for all parameters not directly involving adult perennial competition or fecundity (Table S4.1). For parameters that were averaged across years, these average values were used in simulations for both years. Parallel analyses allowing all parameters to vary by year can be found in supplemental materials (Figures S4.6 and S4.7) To calculate equilibrium population size for each species in the absence of interspecific competition, we ran our population growth models with mean parameter estimates for each combination of warming treatment and year until population stabilized. Because *Festuca* populations depend on both seeds and adults, both models were run in parallel.

To test for coexistence, we calculated GRWR for each species when its competitor was at equilibrium in each combination of climate and year. Taken together, GRWR of both species in a set of conditions determines whether species coexist (both species have positive GRWR), one competitively excludes the other (only one species has positive GRWR), or whether priority effects drive outcomes (both species have negative GRWR). To simulate annual invasion, we introduced one seed of *Lolium* into an equilibrium population of *Festuca* seeds and adults and ran our population models with mean parameter estimates for 300 years. Perennial invasion was identical, but instead of adding one seed we added one net individual divided into fractional individuals ($N_p + N_s = 1$) proportional to the ratio of seeds to adults at equilibrium. The annual GRWR was calculated as the natural log of seeds in year two over year 1, and the perennial GRWR was calculated as the dominant eigenvalue of the transition matrix between seed and adult life stages (Mordecai 2013). Finally, we performed a sensitivity analysis where we reduced each parameter by 5% to see which parameters had the greatest relative impact on coexistence and equilibrium population sizes.

Results

Overall, our modeling predicts that the introduced annual grass, *Lolium*, can invade into equilibrium populations of the native perennial, *Festuca*, across a range of conditions, while *Festuca* may not always be able to do the same, resulting in either coexistence or annual dominance. In general, our successfully implemented warming (Figure S4.1) directly and indirectly benefited *Festuca* and had a negative effect on *Lolium.* Finally, maturity level and survival of perennial adults had substantial impacts on population outcomes for both species.

While annual populations were largely driven by intraspecific competition, perennial populations were more impacted by adult maturity level (i.e. year), climate, and the interaction of climate and interspecific competition. Apart from perennial seedlings of juvenile plugs (-33% in 2020), warming directly increased perennial equilibrium populations of juvenile and established adults (+25% each) and seedlings of established adults (-17% in 2021) in the absence of interspecific competition, and directly decreased annual populations (-35%, Figure 4.2a). These patterns arose despite increases to annual fecundity and decreases to perennial fecundity in warmed conditions that were offset by increased intraspecific competition among annuals and increases in perennial seedling survival (Figure S4.2).

In the presence of interspecific competition, perennial equilibrium populations were greatly reduced after 300 years under ambient conditions; to nearly zero in the case of juvenile plugs (0.018/m^2 versus 7.56/m^2 warmed) and their seedlings (8.66/m^2 versus 30,445/m^2 warmed) in 2020, and to a steady but reduced level for established adults (1.55/m^2 versus 11.6/m^2 warmed) and their seedlings (4,723/m^2 versus 226,623/m^2 warmed) in 2021 (Figure 4.2b). As annuals were primarily affected by intraspecific competition and only minorly by competition from established adult perennials, they saw only minor reductions to equilibrium populations under interspecific competition with the greatest effects driven by the large established adult population in warmed plots in 2021. The reduction to equilibrium populations due to interspecific competition (i.e. indirect effects) can be seen in Figure 4.2c.

Consistently positive GRWR for annuals, and varying positive and negative GRWR for perennials result in either coexistence or perennial exclusion depending on climate and adult maturity (Figure 4.3). Specifically, warmed conditions always resulted in coexistence. Under ambient conditions both juvenile perennial adults (Figure 4.3a) and mature perennial adults (Figure 4.3c) had negative growth rates, resulting in eventual competitive exclusion. However, perennial growth rates were one to two orders of magnitude smaller than the annual's suggesting that while they were being excluded it was taking place very slowly. As seen in Figure 4.2, after 300 years of competition with a negative growth rate, approximately 10% of mature perennials persisted.

Sensitivity analysis revealed that GRWR of both species was primarily driven by adult perennial survival, s_p (Figure 4.4). Reducing this vital rate by 5% led to large decreases in perennial (-0.049 ambient, -0.037 warmed) and large increases in annual (+0.653 ambient, +0.876 warmed) GRWR. These decreases to perennial GRWR due to reduced adult survival were, in fact, greater than their baseline GRWR. Other vital rates that had substantial impacts on perennial GRWR when reduced included perennial fecundity (negative), annual fecundity (positive), and annual intraspecific competition (negative, Figure 4.4a). These effects were all greater when warmed compared to ambient, contrasting with the reduced impact of adult survival when warmed. Annual GRWR was also impacted by reductions in perennial seedling survival (positive), annual fecundity (negative), perennial seedling-seedling competition (negative) and competition from adult perennials (positive, Figure 4.4b). In contrast to perennials, annual GRWR was more sensitive to adult perennial survival under warmed conditions, again reflecting greater interspecific competition with warming.

Discussion

Our results surprisingly suggest that warming neither directly nor indirectly threatens native *Festuca* populations, which instead may benefit directly from warming through increased seedling survival and indirectly through reduced competitive strength of *Lolium*. Our results demonstrate the value of a holistic modeling approach over a simple comparison of annual and perennial fecundities in warmed and ambient conditions that would have suggested a negative impact on perennial populations. While warming did have a direct negative effect on *Lolium*, its ability to invade and reduce the population of perennials regardless of perennial age and climate conditions has important management implications. The ability of more established perennials to persist, and the importance of these adults for perennial population stability also highlights the importance of perennial age and life stages for restoration and conservation outcomes.

The net positive effect of warming on *Festuca* and net negative on *Lolium* contrasts with expectations from local (Reed, Pfeifer-Meister, Roy, et al. 2021; Reed, Peterson, Pfeifer-Meister, et al. 2021), and broader grasslands where annuals increasingly dominate in hot-dry summers (Compagnoni & Adler 2014; Lenz et al. 2003; Clary 2012). Instead, direct and indirect effects of warming were consistently beneficial for perennials, with the only exception that warming decreased seed production in juvenile perennial adults. Despite the expectation that the ability to escape drought should benefit annuals under heightened stress (Ludlow 1989; Levitt 1985), our results highlight interspecies variation in functional traits and responses within broad functional groups (Balachowski et al. 2016). While *Lolium* is common in the Willamette Valley, it dominates in wet, nutrient rich conditions where it is a dominant competitor (Pfeifer-Meister et al. 2008). *Festuca*, by contrast, has an extensive root system and is drought tolerant, and commonly found on thin, rocky soils (Darris et al. 2012). Higher soil moisture (in the ambient treatment?) may have also corresponded with higher nitrogen availability (Jackson et al. 1988), which *Lolium* can take rapid advantage of. While our experiment and simulations consistently elevated temperature, seasonality and timing of heat and drought events also matter. For example, if spring or summer temperatures rise beyond annual tolerances, these high heat events could be particularly detrimental to annual populations. Despite our unexpected results, independent consideration of direct and indirect competitive effects was highly informative. While direct effects on *Festuca* growth rate and equilibrium population were minor, a strong interaction between climate and annual competition led to substantially *Festuca* lower populations in the conditions that supported higher *Lolium* abundance. Since *Lolium* could always invade, its competitive strength and population abundance in different climatic conditions is an important management consideration.

Perennial age was also an important in competition outcomes, with implications for population management in conservation and restoration contexts. While is it well-known that plugs often outperform seedlings in a restoration context (Hedberg & Kotowski 2010), our results show that established second-year *Festuca* plugs substantially outperformed juvenile first-year plugs both with and without annual competitors. We likely underestimated this effect, since we replaced transplants that failed within the first month, artificially inflating first-year survival rates. This suggests that where the investment is made to use expensive plugs in a restoration project, it may be worth investing additional effort to ensure they establish and grow--for example, by coupling transplanting with one to two years of competitor removal. It also suggests that conservation of mature existing individuals may be more effective in some cases than restoration plantings. This situation implies a priority effect, which is possible when adult perennials hold ground against invaders while seedlings are outcompeted (Werner et al. 2016, Young et al. 2017). Even though our GRWR analysis did not find direct evidence for theoretical priority effects very slow perennial growth rates (in some cases populations were still slowly declining after 300 years of annual invasion) result in priority effects in application. In a practical context, these very slow transitions can look and act like stable states (Seabloom et al. 2003). While we only monitored adult perennials for two years, improved adult fitness in subsequent years would increase the likelihood of coexistence or priority effects. Finally, over many years significant climate variability should be expected which can both impact coexistence (Chesson 2000), and also provide windows for intervention. For example, if warming enhances *Festuca* seedling survival, but also increases competition from annuals, these may be good years to clear *Lolium* and seed *Festuca*.

While adult survival provided perennial population stability, these populations were more sensitive to adult mortality than any other vital rate, with a sustained 5% reduction of adult survival resulting in population collapse. Our results are consistent with previous grassland annual-perennial coexistence studies (Mordecai et al. 2015; Larios et al. 2017) and even population modeling of long-lived animal species (Crowder et al. 1994; Crouse et al. 1987). These studies on sea turtle conservation demonstrated that a shift from conserving the least sensitive life stage (eggs) to more sensitive life stages (large juveniles and adults) would better help populations recover. Adoption of these methods has shown to be effective in this system (Crowder et al. 1995), again reinforcing our management recommendation to invest in adult perennial conservation or ongoing maintenance of restoration projects. These efforts could include monitoring individuals over time, targeted weeding around adults especially in years with strong interspecific competition (Young et al. 2017), and reducing potentially lethal disturbance. In fact, in portions of our experiment excluded from our analyses, we witnessed mean area disturbed by gophers in one year to be 40%, a far greater reduction than modeled in our sensitivity analyses.

In a warming climate, predicting the effects competition between dominant species of alternate ecosystem states will be an ongoing challenge. While general patterns like the annualization of Pacific Northwest grasslands emerge, unexpected outcomes like ours demonstrate the value of competitive population modeling and may provide insights for using particular species for certain sites. Here, the perennial *Festuca* proved to be resilient to warming, whereas the annual *Lolium* was more sensitive. Perennials may continue to struggle, with increased competition even under current climate conditions, but established adult populations can resist state change in the absence of disturbance. Long, slow transitions may also hide underlying shifts in small population growth rates, which may allow for rapid state change following disturbance. Because dominant species often determine ecosystem function and diversity, these transitions can have broad lasting effects. Understanding how perennials and annuals compete can help retain these desirable species and services. Management is often reactionary, and on a perennial timescale that may be too late. Our ability to manage remaining Mediterranean grasslands under novel climate conditions will determine the future of this system in the PNW.

Bridge

In this study, we demonstrated the value of taking a demographic approach to model populations in competition. We found a surprising result where our selected perennial fared better in warmed conditions than ambient, and our annual fared worse, but only slightly so. This highlights the importance of considering species as individuals, rather than simply broad functional groups. At the same time, we found that the annual was already able to invade, and even competitively suppress the native perennial at ambient conditions. This strong competitive effect is troubling for the conservation and restoration of native grasslands. In the following chapter, we consider an alternative form of restoration that may be able to extend restoration impact: using native vegetation as understory cover crops in an agricultural setting.

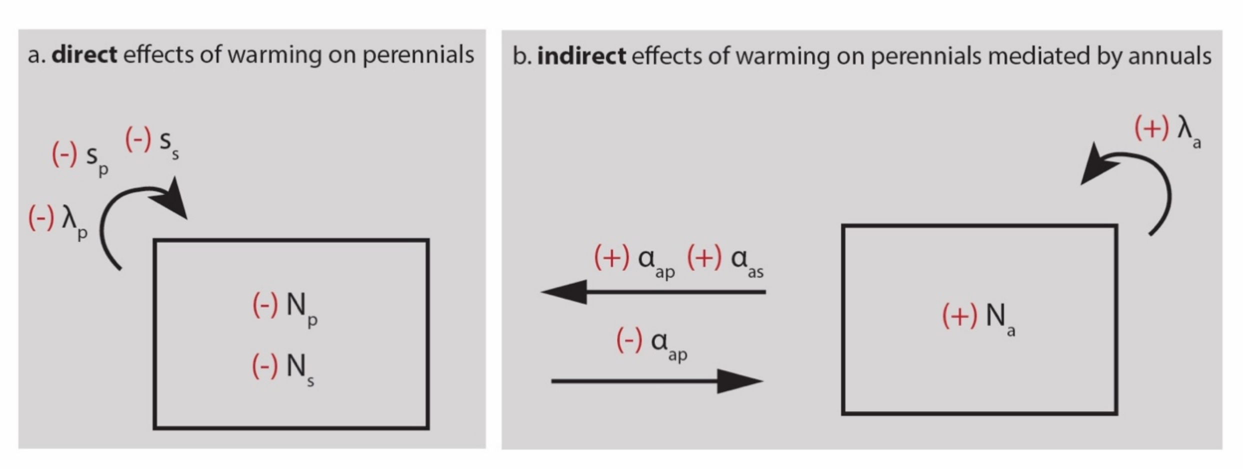
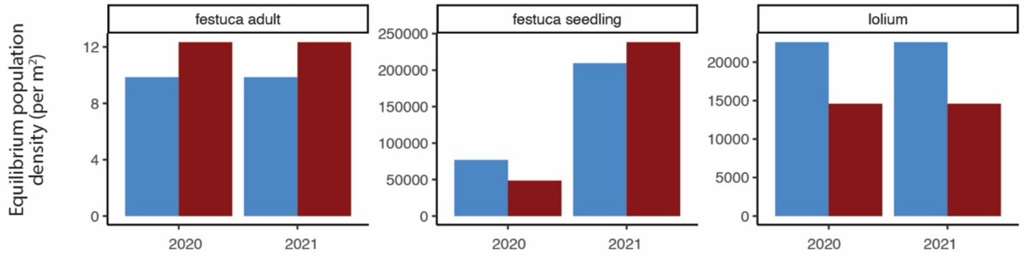
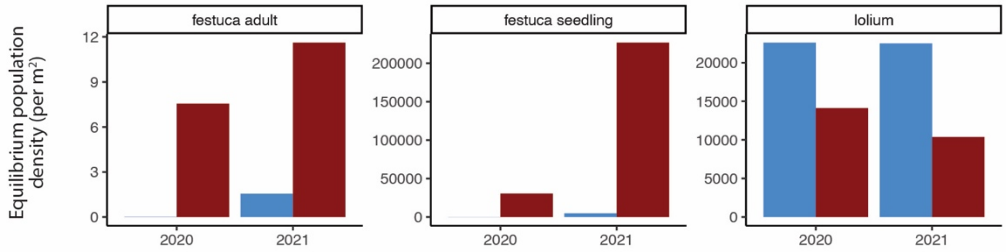


Figure 4.1. Potential direct (a) and indirect (b) impacts of warming on perennial versus annual dominance are shown in red. Vital rates and population sizes (*N*) are shown in black. Lambdas (*y*) represent fecundity, *s* represent survival, and alphas (*a*) represent competitive coefficients. Subscripts refer to either adult perennials (*p*), seedling perennials (*s*), or annuals (*a*). Our first goal it to understand the relative influence of direct negative warming effects (-) on perennial equilibrium population size and growth rate via reduced survival and fecundity versus indirect negative warming effects via increased annual fecundity or relative competitive superiority. We also asked how sensitive populations were to changes in each vital rate.

a. Equilibrium density with only interspecific competition



b. Equilibrium density with inter and intraspecific competition



c. Proportion of inter and intraspecific equilibrium density over intraspecific-only equilibrium density

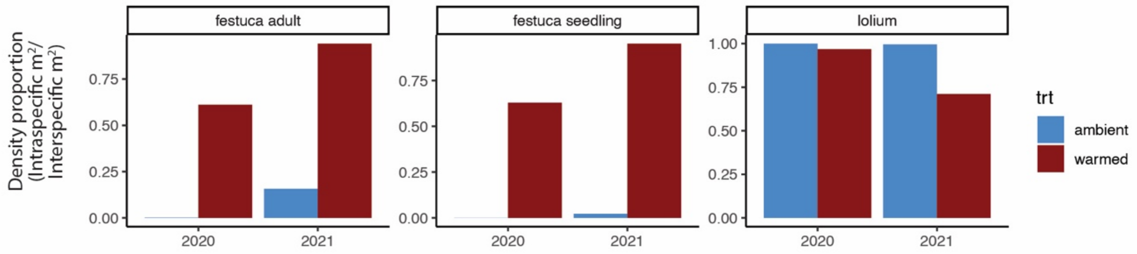


Figure 4.2. Equilibrium population size simulated using mean parameter values after 300 years of population growth in warmed and ambient conditions using data from 2020 (juvenile plugs) vs. 2021 (mature adults). a) Population in the absence of interspecific competition. b) Population with inter and intraspecific competition. c) Proportion of full intraspecific only equilibrium density under intra and interspecific competition.

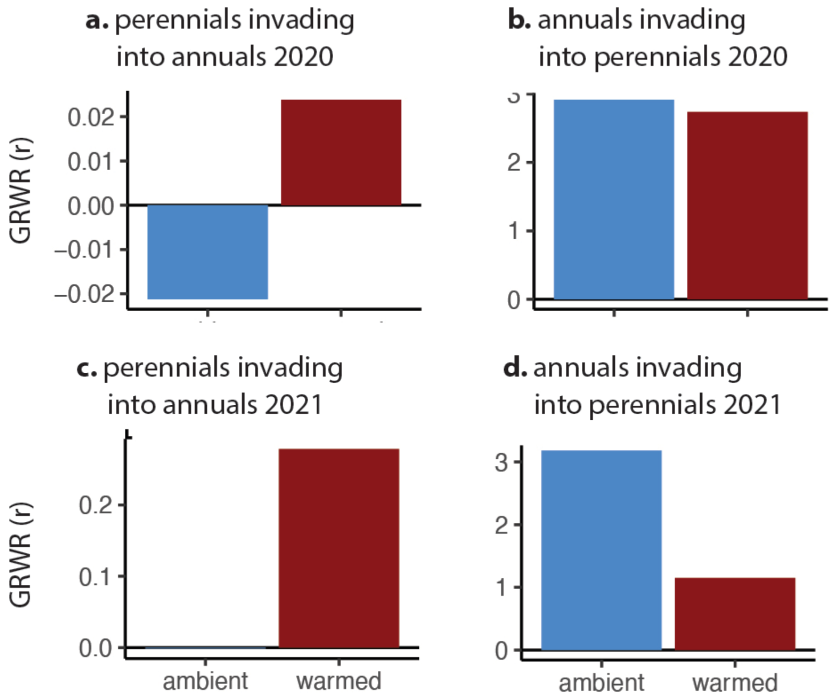


Figure 4.3. Growth rate when rare of each species in ambient (blue) and warmed (red) conditions. Warming benefits perennials at the expense of annuals. Panels a) and c) show perennial GRWR as they invade into annuals and panels b) and d) show annual GRWR as they invade into perennials. Annuals can always invade, and in warmed conditions, all species coexist. In 2020 juvenile perennial plugs are competitively excluded by annuals in ambient conditions, while mature adults coexist under the same conditions in 2021.

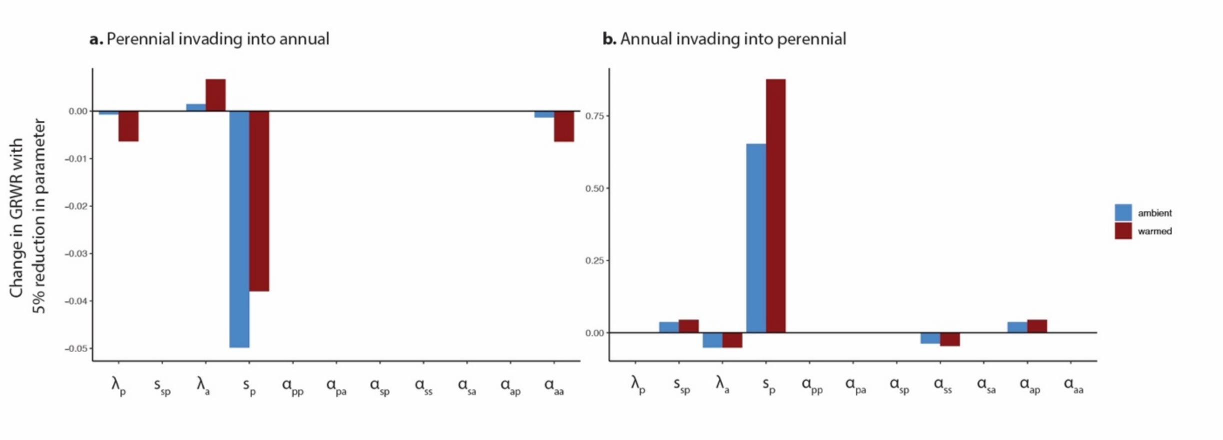


Figure 4.4. Effect of reducing parameter values by 5% on growth rate when rare (GRWR) of perennials invading into annuals (a), and annuals invading into perennials (b) in each warming treatment. To calculate each GRWR, selected parameter was reduced by 5% while all others were held constant. Resulting GRWR for 2020 and 2021 were averaged. Blue bars represent change in GRWR under ambient conditions, red represents warmed conditions. Parameters include λ_p, adult perennial fecundity, s_{sp}, perennial seedling survival to adulthood, λ_a, annual fecundity, s_p, adult perennial survival, a_{pp}, adult perennial per capita intraspecific competition, a_{pa}, annual per capita competitive effect on adult perennials, a_{sp}, adult perennial per capita competitive effect on seedling perennials, a_{ss}, seedling perennial per-capita intraspecific competition, a_{sa}, annual per capita competitive effect on seedling perennials, a_{ap}, adult perennial per capita competitive effect on annuals, and a_{aa}, annual intraspecific competition.

Table 4.1. Each competition treatment consisted of varying densities of perennial adults, annuals and perennial seedlings. One treatment with no competition and three plots with equilibrium background densities of one species took up 1m^2. Background densities were established by weight at 6g/m2 in these plots. Three 50:50 plots were seeded at 3g/m2 in 0.66m2 plots, or a total of 2g of seeds per plot. Number of individuals added was estimated by counting 1g of weighed seeds for each species and multiplying by seeded weight. Phytometer marked with an asterisk (*) represent number of target individuals post thinning. More seeds were added prior to thinning to ensure viable phytometers.

Competition Treatment	Plot Size (m2)	Species/Stage	Phytometer or Background	Individuals added (N)	Density (individuals/m2)
None	1	Adults	Phytometer	2*	2
		Annuals	Phytometer	4*	4
		Seedlings	Phytometer	4*	4
Adult Background	1	Adults	Background	10	10
		Annuals	Phytometer	8*	8
		Seedlings	Phytometer	8*	8
Annual Background	1	Adults	Phytometer	2	2
		Annuals	Background	2480	2480
		Seedlings	Phytometer	4*	4
Seedling Background	1	Adults	Phytometer	2	2
		Annuals	Phytometer	4*	4
		Seedlings	Background	6080	6080
50:50 Adults:Annuals	0.66	Adults	Background	4	6.1
		Annuals	Background	826	1240
50:50 Adults:Seedlings	0.66	Adults	Background	4	6.1
		Seedlings	Background	2026	3040
50:50 Annulas:Seedlings	0.66	Annuals	Background	826	1240
		Seedlings	Background	2026	3040

CHAPTER V

FEASIBILITY OF NATIVE COVER CROPS IN HAZELNUT ORCHARDS OF VARYING AGES IN THE WILLAMETTE VALLEY, OREGON

Authors and affiliations:

Alejandro Brambila[1,2], Ari Brown[1], Marissa Lane-Massee[1,2], Lauren M. Hallett[1,2]

1. Institute of Ecology and Evolution, University of Oregon
2. Environmental Studies Program, University of Oregon

Contributions

AB1, LMH conceived and designed the research; AB1, AB2, MLM performed the experiments. AB1, AB2, MLM analyzed data and wrote the manuscript with input from LMH.

Introduction

Throughout the 20th century, exponential growth in agriculture was responsible for the loss of approximately 40% of native habitat area globally (Ramankutty & Foley 1999; Hooke et al. 2012), and ongoing agricultural use can preclude efforts to regain native habitat through traditional restoration (Balmford et al. 2003; Armsworth et al. 2017). Where this is the case, managing working lands as agroecosystems provides a complementary method to help achieve landscape-level restoration goals (Barrett & Peles 1994; Tscharntke et al. 2005; Pywell et al. 2011). A transition to ecological intensification in place of traditional chemical and mechanical intensification can regain habitat value and potentially provide other co-benefits in farmlands (Doré et al. 2011; Bommarco et al. 2013; Tittonell 2014). Successful ecological intensification on farmland requires identifying plant species that can survive in an agricultural context without compromising (and ideally enhancing) crop productivity and ecosystem function. Here, we consider Oregon’s Willamette Valley hazelnut orchards a surrogate for native oak-prairie habitat. We use this system to explore the potential for cover cropping with native herbaceous species to support the restoration of diverse herbaceous understory and associated pollinator communities.

Successfully expanding ecological restoration into orchards first requires identifying native species that can survive the agricultural environment; we term these considerations the “survival criteria” (Figure 5.1a). Orchards are a good candidate for ecological intensification because tillage is reduced to minimize tree root disturbance, allowing cover crop vegetation to persist longer (Moretti 2021; Simoes et al. 2014; Stebbins 1971). Similarly, niche partitioning based on rooting depth reduces competition for water and resources between trees and cover crops (Parker & Meyer 1996; Atucha et al. 2013). Past work in Mediterranean olive and California almond orchards suggest that native species can coexist with productive trees (Cruz et al. 2019; Jiménez-Alfaro et al. 2020). At the same time, disturbance and shading in orchards can pose challenges for cover crop survival. Many crops, including hazelnuts, are harvested from the orchard floor, requiring it to be free of vegetation leading up to harvest (Olsen & Peachey 2013). This ground clearing can require flailing and scraping the soil, and a sustainable orchard cover crop must be able to withstand this level of disturbance. Species phenology can influence their disturbance response (Fernández Ales et al. 1993), and species capable of reproducing before ground clearing are more likely to be successful (Grime 1979). Second, mature orchards have dense, closed canopies that may constrain potential cover crops, whereas younger orchards provide more access to light. Successful cover crop communities must either be tailored to the age of the orchard or be tolerant of shifting light availability over time.

A second requirement for successful ecological intensification in orchards is that it does not complicate or burden farm labor and productivity without compensatory benefits; we term these factors the “agricultural criteria” (Figure 5.1b). Conventional cover crops are increasingly being adopted for their production benefits, including weed suppression, erosion control, and improvements to soil health that can increase soil moisture (Atucha et al. 2020; Gómez et al. 2009). Whether native cover crops can provide these benefits to the same degree depends on the effects of individual species and the overall cover crop composition (Storkey et al. 2015; Isbell et al. 2017). There is growing evidence that a diverse mix of native species can compete more strongly with weeds than conventional cover crops (Döring et al. 2012; Richardson & Pyšek 2006), and diverse species phenology can sustain green vegetation through the winter and help reduce erosion (De Baets et al. 2007). Persistent vegetation may also help increase soil moisture by shading the soil and reducing compaction that allows water to infiltrate (Gómez et al. 2011). On the other hand, any cover cropping system entails costs of seeds, fuel, and labor, and risks the cover crops competing with main crops or interfering with operations. Species phenology is therefore also important from the farmer’s perspective, as species must have senesced with minimal residual biomass to not interfere with harvest. Additionally, a cover crop that facilitates weeds or reduces soil moisture would not pass the agricultural criteria.

Finally, a native cover crop that meets both the survival and agricultural criteria must also be relevant to local restoration goals; we term these considerations the “ecological functioning criteria” (Figure 5.1c). In the Willamette Valley, Oregon, hazelnut orchards are particularly well-suited to support specialized and geographically restricted understory vegetation from oak-prairie habitats. Because of historical farmland development in the fertile valley bottom, today, oak-prairie communities are limited to marginal sites representing 2% of their historical range

(Wright 2020). These isolated populations are expected to decline under climate change as migration and gene flow are limited (Dunwiddie & Bakker 2011; Reed, Bridgham, Pfeifer-Meister, et al. 2021). Orchards may provide a suitable analog for the oak-prairie herbaceous flora, which is disturbance-adapted (Boyd 1999). These communities also exist across a continuum of woodland, savanna and prairie habitats distinguished by widely varying canopy density (TNC 2010) that mirrors the range of orchard canopy conditions. The recent rapid expansion of new orchards (NASS 2017) with open canopies mirrors open prairie and savannas, while more established orchards may support woodland species. Hazelnuts also share a similar leaf phenology with native oaks, maximizing light availability to the understory during active fall and spring growth periods.

Maintaining native understory vegetation is particularly important for pollinator populations, including native bees and flies, whose population decreases have been linked to land alternation for agriculture (Koh et al. 2016; Brown & Paxton 2009) and lack critical baseline population data (Kearns 2001). In the Willamette Valley, open oak-prairie habitats are particularly valuable for native pollinators (cite). Agricultural fragmentation of native vegetation threatens these native pollinators, especially in the context of climate change, as demonstrated by predicted declines *Bombus spp.* nationwide (Sirois-Delisle & Kerr 2018). While incorporating native plants with varied phenology into agriculture can support diverse pollinators (Haaland et al. 2011; Ponisio et al. 2016), pre-harvest pesticide use in hazelnuts restricts phenology to earlier flowering species. If late flowering cover crops are allowed to persist in orchards, this form of ecological intensification can instead become an ecological trap (Ganser et al. 2019). Today, conservation and restoration of herbaceous habitats and the pollinators that rely upon them is a regional priority. Expanding oak-prairie communities into hazelnut orchards may provide a novel opportunity to support these efforts.

We tested the potential for expanding restoration of Willamette Valley oak-prairie understory species and associated pollinators into hazelnut orchards as cover crops using our three criteria. First, we examined which species of native annuals and perennials can survive in an orchard context (Figure 5.1a; survival criteria), considering how canopy cover and disturbance intensity affect fitness. Second, we considered how these cover crops impact agricultural production (Figure 5.1b; agricultural criteria). Specifically, we considered their ability to exclude weeds, reduce erosion potential, and modify soil moisture. Finally, we assessed cover crop contributions to ecological functioning through their interactions with native pollinators (Figure 5.1c; ecological functioning criteria). Across each of the three criteria, we considered individual species' phenology and compared four cover crop scenarios: native perennials, native annuals, conventional cover crops, and an unseeded control. Overall, we expected native cover crops to be a promising strategy for ecological intensification, and a viable orchard floor management strategy for farmers.

Methods

Experimental Design

We compared the performance of four different cover crop seed mixes over a two-year period in hazelnut orchards: native perennials, native annuals, conventional cover crops, and a control. To assess our survival criteria, we nested seeding treatments within three levels of orchard floor disturbance (flailing which involved mowing the vegetation, flailing and scraping, which involved both mowing and ground leveling, and unmanaged/none) and replicated the experiment in three different ages of orchards with corresponding differences in canopy cover (15-year with an open canopy, 40-year with a nearly closed canopy, and 60-year with an intermediate canopy density). To assess our agricultural criteria, we measured how surviving species altered weed pressure, erosion potential, and soil moisture. To assess our ecological functioning criteria, we compared native plant and pollinator diversity to typical bare floor management. The experiment was based at Lane-Massee Farms north of Salem, Oregon, and agricultural treatments were implemented by the farm.

We replicated orchard floor disturbance treatments in a random-block design with six blocks per orchard for a total of 54 plots (3 treatments x 6 blocks x 3 orchards). Plot sizes corresponded to a planted orchard grid square of 6.1 m x 6.1 m. Within each block we implemented three different management plots: flailing, flailing and scraping, and unmanaged. Flailing typically takes place three times and consists of mowing to 4 cm, while scraping takes place once, between the first and second flailing, and consists of dragging a weighted box blade behind a tractor to level orchard soils. Flailing and scraping were chosen because they are necessary for harvest, and they potentially take place during the active growing and flowering season, therefore having the greatest potential to limit cover crop survival. Blocks were oriented along a north-south axis, and locations were selected to minimize environmental heterogeneity, avoid edge effects, and minimize impact on farm operations. The small size of the 15-year-old orchard limited placement options, and blocks had variable edge conditions. Throughout the experiment, orchard management otherwise largely continued as for the rest of the farm, consisting of numerous activities aimed at promoting tree health, production, and maintaining clean and level orchard floors to facilitate harvest (Table S1).

Within each management plot we nested four 2.5 m x 2.5 m seeding mix subplots: native annual forbs, native perennial forbs, conventional cover crops, and an unseeded control (Table 1). Seeding treatments were applied to consistent locations within management plots to avoid misidentification and facilitate data collection. Native species were purchased from Heritage Seedlings in Salem, OR and were selected by price, availability and expert opinion of potential success. We separated native annuals and perennials to compare performance across broadly differing life-history strategies. The conventional cover crops were suggested by Oregon State University extension (Olsen & Peachey 2013). Although all three orchards were managed for bare ground at harvest, some weeds were present. Subplots were seeded in October 2019 following Paraquat herbicide application and then incineration of standing biomass with a backpack flame weeder. Because the ability of conventional cover crops to persist in hazelnut orchards is already known, we did not seed them in unmanaged plots. In late December 2019, we removed a thick layer of fallen leaves from all plots to aid in seedling establishment.

Data collection

To evaluate seed mix and component species according to our survival criteria, we visually estimated percent cover of each target species at peak biomass in May 2020 and 2021. To quantify shading intensity, we estimated the canopy cover of each subplot at full leaf-out each year using Canopeo (Patrignani & Ochsner 2015), a mobile application that analyzes fractional green canopy cover from digital images with greater than 90% accuracy. Imagery was gathered at the subplot-level, using an iPhone held horizontally one meter above the orchard floor in the center of the plot. This process was carried out twice, due to an ice storm on February 13, 2021 that broke tree limbs, reducing canopy cover especially in the 40-year-old orchard.

We addressed our agricultural criteria by monitoring weed cover, total winter vegetation, and soil moisture across seed mixes. Weed cover (any non-seeded volunteers) was estimated concurrently with target species in spring, and winter vegetative cover was estimated in January 2021. To test the soil moisture response we, measured volumetric water content (VWC) to a depth of 15cm over two time periods: weekly from April-May 2020 and monthly from March-August 2021. During 2021 moisture data was not gathered in July due to logistical challenges. To minimize spatial variability in VWC, we replaced the probes of Campbell Scientific HydroSenseII moisture meter with 1 cm threaded bolds which were touched to two six inch steel box nails permanently embedded in the center of each subplot (Grinath et al. 2019). To calibrate the nail measurements, we took a subset of measurements with both nails and probes at the same location over time and fit a linear regression. Nail measurements were adjusted using this linear relationship. We also occasionally took measurements with the probes directly if nails were lost, damaged or removed by orchard traffic.

To identify whether and when individual species flowering fell within the allowable pre-flail and pre-pesticide period, which is relevant for all three criteria, we evaluated species phenology in each subplot from April through August, 2021.Each month, we recorded the life stage of each species present in each subplot in the following categories: pre-flowering vegetative, first flower, peak flowering, last flower, post-flower vegetative or senesced.First and last flower were both defined as approximately 10% of flower buds open. At peak flower, we estimated floral abundance as the number of inflorescences per target species as a multiple of fifty, with greater resolution from 1 to 49 in the following categories: 1, 2, 5, 10, 25.

Finally, to evaluate our ecological functioning criteria we monitored pollinator visitations in June and July of 2020, and monthly from April through August 2021 in each subplot with observational surveys to quantify abundance, and aerial net collections to allow to quantify diversity. Pollinator surveys took place in dry conditions with partial or no cloud cover. To facilitate observational surveys, pollinators were classified into morphospecies (Table 2).Over a two-minute period, an observer noted each time an invertebrate landed on a flower, recording both host species and pollinator morphospecies. Weed hosts were identified to genus or family. Collection also took two minutes, and only pollinators that landed on flowers were collected. We did not collect honeybees (*Apis mellifera*), a seasonally introduced species, and bumblebee queens (*Bombus spp.*) were collected for photos and subsequently released to avoid negatively impacting colony formation. Collected samples were classified to order using a dissecting microscope. Because Anthophila and Syrphidae are major contributors to pollination and pollinator diversity (Ssymank et al. 2008; Youngsteadt 2020), these clades were identified to genus using (Jackson 2019) and (Miranda et al. 2013).

Data Cleaning and Analysis

All data cleaning and analysis was carried out using R version 4.0.3 (R Core Team 2022). To determine relative establishment and survival criteria of native annual, native perennial, and conventional cover crops in relation to management disturbance and shading we first aggregated species cover at the subplot level; total cover could exceed 100% where multiple vegetation layers were present. We tested for significant differences between total cover of target vegetation using mixed models with seed mix, management, and orchard age (as a rough proxy for shading), as fixed factors, and year and block as random factors. Throughout our analyses, we implemented mixed models using the function lme() from the package nlme (Pinheiro et al. 2019) and evaluated significant differences between groups with post-hoc Tukey tests using emmeans() from the package lsmeans (Lenth 2016).

To evaluate the effect of shading on survival, we tested whether canopy cover affected vegetative cover using mixed models that included both linear and quadratic canopy terms as fixed effects and block as a random effect, dropping the quadratic term when it was not significant. We considered the quadratic term because it seemed plausible to expect a nonlinear relationship between canopy and cover. To account for any expansion or migration beyond initial seed mix subplots in year two, cover of the same species from adjacent subplots was aggregated, allowing cover to be over 100%. While the 40 and 60-year-old orchards had relatively consistent canopy cover, shading in a portion of the 15-year-old orchard was increased by rows of taller vegetation to the south. To adjust our canopy cover estimates to account for shade from these adjacent trees, we estimated the proportion of plots that were in shade from adjacent trees at noon during mid-spring monitoring.Shade affected approximately 60% of each of the southern subplots and did not affect any of the northern subplots. For all southern subplots in the 15-year-old orchard, we then weighted the measured canopy cover in the subplot by 40%, and the adjacent vegetation canopy cover by 60%.

To analyze agricultural criteria responses, we first calculated the difference between spring weed cover and total winter vegetation cover (as a proxy for erosion reduction) in each seed mix subplot relative to the unseeded control. To effects consistent across orchards, we ran mixed models that used the difference spring weed cover and total winter vegetation cover relative to the control as response variables, seed mix and year as fixed factors, and block nested within orchard age as random. Because canopy cover affected baseline weed pressure, bare ground, and the potential severity of erosion, we then evaluated cover crop effects across a canopy cover gradient that encompassed all three orchard ages. Subplot level canopy cover measurements were averaged to the plot level, and we tested for significance of linear regression of each response variable against canopy cover.While we only considered winter vegetation between the 2020 and 2021 growing seasons, we evaluated the response of weeds in both years to evaluate cover crops' ability to exclude weeds over a longer period.

To evaluate whether cover crops affect soil moisture levels that trees depend on, we compared the effect of seed mix on VWC using mixed models for each year independently with seed mix as the main effect and time period (week in 2020, month in 2021), orchard, and block as random effects. Once a calibration curve for adjusting nail measurements to probe measurements had been established (Figure S5.3), we used existing probe measurements when possible and calibrated nail measurements otherwise. To contextualize soil moisture with climate, we downloaded daily precipitation data from PRISM and calculated weekly mean precipitation during each sampling period (PRISM Climate Group 2022). Because shading has a strong influence on soil moisture, we could not disentangle the effects of shading and seed mix in the inconsistently shaded 15-year-old orchard which we dropped from all moisture analyses

For our ecological functioning criteria, we evaluated the abundance and phenology of cover crop flowering, and how pollinator populations responded to changing floral resources. To estimate flowering abundance of a seed mix we aggregated species-level peak flowering estimates within subplot and month plus 10% of peak estimates for species in first and last-flowering categories. To compare seed mixes, we constructed mixed models using orchard age and seed mix as fixed effects and block nested in month as random effects. To identify the peak month of flowering for each seed mix, we also created mixed models for each orchard with month and seed mix as main effects and block as random. Because flailing and scraping started between June and July monitoring, our models use data from all plots through June, and only from unmanaged plots after. To assess whether pollinator abundance and diversity corresponded to cover crop flowering phenology, we compared observational and collection data from timed pollinator surveys across seed mixes and orchard ages. We aggregated pollinator visitations from observational surveys by host (including weeds) at the subplot level in each month, comparing each seed mix to the control. We calculated pollinator richness at the same scale from collection surveys by counting the number of unique taxa observed.For each of these responses, we constructed models with the same predictive factors as our plant phenology models. To compare the relationship between floral abundance and pollinator visitations independent of time we ran a linear regression of floral abundance and pollinator visitations within each orchard. As conventional cover crops were not seeded in unmanaged plots, they are not represented in the analyses after June.

Results

Plant Survival Criteria

Native annual and perennial forbs across all management types had significantly higher total cover in the first year than conventional cover crops (+77%, p<.001; +81%, p<.001; Figure 5.2). Both native groups had mean total cover values above 100%, driven by the density of resulting vegetation which had multiple canopy layers. In the second year, total native annual forb (-76%, p<.001), and total native perennial forb cover (-24%, p=.027) was significantly reduced but total cover of the conventional treatment remained the same. At this point, total native annual cover was not significantly greater than the conventional treatment (+10%, p=.29), but total native perennial cover remained greater than the conventional (+68%, p<.001). Somewhat surprisingly, flailing or scraping did not have a significant effect on the total cover of any seed mix. Shading did affect total cover of all seeding treatments, with consistently higher cover in the more open-canopied 15 (+31%, p<0.001) and 60-year-old (+40%, p<0.001) orchards than the closed-canopied 40-year-old orchard.

Individual species varied widely in both their mean cover and their responses to canopy shading (Figure S5.2). In 2020, both native seed mixes were dominated by a subset of high-performing species, while others had only minimal representation. The native annual forbs, *Amsinckia* (10%), *Clarkia* (20%), *Collomia* (19%) and *Epilobium* (49%) were common, while *Lotus* (1%), *Gilia* (8%), *Plectritis* (6%) and *Sanguisorba* (3%) were relatively rare (Figure S2a). Native perennial forbs, *Achillea* (40%), *Eriophyllum* (12%), *Geum* (38%), and *Prunella* (23%) were common, while *Agoseris* (1 individual), *Lomatium* (3%), *Potentilla* (6%), and *Viola* (1%) were rarer (Figure S2b). Finally, the conventional cover crops *Hordeum* (13%) and *Avena* (17%) were common, while *Trifolium* (5%) and *Vicia* (7%) were rarer (Figure S5.2c).

Most common species had significant relationships with canopy cover in both years, with the exception of *Avena*, *Hordeum* in 2021, *Prunella* and *Achillea* in 2020, and species with negligible cover (Table S5.2). Some exhibited a negative relationship (e.g. *Amsinckia, Achillea*, *Eriophyllum, Prunella, Clarkia, Epilobium* and *Trifolium* in 2021, *Lomatium*, *Gilia*, and *Plectritis* both years, and *Hordeum* in 2020; Figure S5.2) while others exhibited a hump-shaped relationship with highest cover at intermediate canopies (e.g. *Collomia* and *Geum* in both years, and *Eriophyllum*, *Clarkia*, and *Vicia* in 2020; Figure S5.2). Most species had somewhat lower cover in 2021 than 2020. Two native annuals, *Clarkia* (-16%, P<.001) and *Epilobium* (-38%, P<.001) exhibited pronounced declines between years, whereas all four common native perennials and the conventional *Trifolium* remained fairly constant (+/-10%). See Table 1 for a summary of average cover, canopy response, and interannual population survival by species.

Agricultural Production Criteria

Native cover crops were associated with a decrease in weeds and an increase in winter vegetation cover, a proxy for erosion potential (Figure 5.3). At peak biomass in May 2020, weed cover was highest in the unseeded control plots (73%) and this was significantly reduced by each cover crop seed mix (Figure 5.3a). Native annuals had the strongest effect (-52%, p<.001) on weed reduction, followed by native perennials (-30%, p<.001), and conventional cover crops (-21%, p<.001). In 2021, weed cover in control plots was unchanged (74%), and conventional cover crops failed to substantially reduce weed cover at all. In contrast, native perennial cover maintained a consistent weed reduction effect (-39%, p<.001), and native annual cover also continued to reduce weed cover, albeit to a lower degree (-21%,p<.001).In 2020, annuals had a significantly stronger effect on reducing weeds at lower canopy cover than at higher canopy cover (weed/canopy slope: 0.35, p=.03), but this effect was not significant in 2021 or for perennials or conventional cover crops in either year. Winter vegetation, assessed in December 2020, was largely determined by the presence or absence of perennial vegetation. While annual seedlings were present in the winter, they did not make up meaningful cover, whereas native perennial cover crops and perennial weeds drove differences in winter cover. There was no significant difference in winter cover between the unseeded control (21%), the native annual plots (20%) or the conventional cover crop plots (17%) (p=0.99 and p=0.91, respectively; Figure 5.3b).Native perennials, however, had significantly higher winter cover than unseeded plots (p=0.004) at 36%. Perennial winter vegetation cover was also significantly negative related to canopy cover (p<0.001, slope=0.30, p=0.02).

Overall, cover crops had minimal effects on soil moisture, regardless of whether they were native annuals, native perennials or conventional (Figure S5.4a).Because soil monitoring took place across different timescales, we identified a common reference period of April 1 through May 17 for comparison (Figure S5.4, red boxes). Overall subplot-level soil moisture was driven primarily by rainfall availability over time, with time period being a significant factor in both 2020 and 2021 (p<0.001 in both cases). In 2020, there was a small but significant interaction between seed mix and month. Specifically, subplots with native annual cover crops had significantly higher soil moisture than unseeded control plots in weeks 3-6, and higher moisture than the conventional mix in weeks 4-6 (Table S5.3 for effect sizes and p-values).Likewise, native perennials also had higher moisture than both unseeded controls and conventional crops in weeks 4-6. In 2021, the only significant effect of cover crop type was that in June the conventional cover crop mix had higher moisture than the unseeded control and native annuals, but not native perennials (Figure S5.4a; Table S5.3). During the comparable reference period of April 1 through May 17, rainfall was much higher in 2020 (99mm) than 2021 (27mm, Figure S4b). In fact, in 2021 only 138mm of rain fell throughout the entire monitoring period from March through August. While VWC at the beginning of the reference period was similar across years, high rainfall in 2020 resulted in elevated VWC during the final three weeks of the reference period similar to levels in March in 2021.

Peaks in floral abundance, pollinator visitations and pollinator richness were generally within the allowable pre-flail period (Table S5.4), although the low flowering conventional crops (Figure 5.4) were cut short by flailing in July. Native annuals had their highest floral abundance in June in the 40-year-old orchard and in the 60-year-old orchard there were more flowers present in June than April or May, but not significantly more than July or August. By contrast, native annuals peaked in the 15-year-orchard in August. Insect visitations peaks (Table S5.5) generally mirrored peaks in floral abundance, with a June peak for conventional crops and native perennials in the 15-year-old orchard. In the 60-year-old orchard, there were also more visitations to native perennials in the May than April or August and more visitations to native annuals in June than April, May or August. Unseeded controls had consistently low visitation that did not vary significantly. Pollinator richness (Table S5.6) only varied in the 15-year-old orchard, where June represented a diversity peak for conventional and native perennials, and higher than May for the unseeded control.

Ecological Function

In addition to a general alignment between periods of high floral abundance and pollinator visitation, there was a significant direct association between floral resource provisioning and use as determined by linear regression in each of the fifteen ($p<0.001$, $R=0.77$), sixty ($p<0.001$, $R=0.66$), and forty-year-old ($p<0.001$, $R=0.58$) orchards (Figure S5.5). Estimates of floral abundance varied widely between orchard ages (15: 138 inflorescences, 60: 50, 40: 5) and seed mixes (native perennials: 133 inflorescences, native annuals: 31, conventional: -3).Aside from annuals vs. conventional, all contrasts were significant (Table S5.4). Pollinator visitation (Table S5.5) and diversity (Table S5.6) responses paralleled floral abundance as native perennials had higher values for both metrics than native annuals or conventional cover crops. There was also higher visitations in the 15-year-old orchard than 40 or 60, and declining pollinator richness from 15 to 60 to 40.

We collected pollinators from 25 unique taxa corresponding to 14 observational morphospecies categories (Table 5.2).Observations included 468 small black bees, 294 honeybees, 130 syrphid flies, 81 other flies, 59 big black bees, 30 bumblebees, and 52 ‘others’ from the remaining categories. Native perennials were visited by the largest proportion of small black bees (78%), other flies (81%), big black bees (74%), bumblebees (93%) and ‘others’ (86%). Honeybees visited native perennials (30%), weeds (31%), and conventional crops (28%) in roughly similar proportions. Syrphids primarily visited weeds (45%) followed by native perennials (36%). The native perennial, *Achillea*, had the highest number of visitations and supported the greatest taxonomic richness overall, but particularly in the 15-year-old orchard, while the native perennial, *Geum*, was highest in both measures in the 40 and 60-year-old orchards (Table 5.1).

Discussion

Our results suggest that Willamette Valley hazelnut orchards are a suitable analog for oak-prairie habitat and provide an opportunity to support ecological restoration of native herbaceous communities and associated pollinators.Native perennials are particularly well adapted to agricultural disturbances in hazelnut orchards, and their success relative to other groups was driven by a few overperforming species: *Geum, Eriophyllum, Prunella,* and especially *Achillea.* Except for *Geum*, which was well-adapted to high-canopy conditions, native cover crops performed best in low shade. These species had the highest cover, resulting in substantial weed and erosion reduction services, no soil moisture reduction, and the highest pollinator visitations and diversity. Three native annuals, *Epilobium, Clarkia,* and *Collomia*, drove high cover in the first year, but pollinator visitations and overall feasibility were limited by low interannual survival and late phenology. We recommend cover cropping using these high-performing species in newly established orchards to extend restoration impacts and bridge wildland habitat throughout the Willamette Valley.

Plant Survival Criteria

Surprisingly, flailing and scraping did not limit cover crop survival. While native annuals and conventional cover crops declined in 2021, there was no interaction with disturbance. Many native perennials reproduced before disturbance and rebounded quickly after, contributing to their success.Interpretation of our results is limited by our exclusion of a late winter herbicide application and an early flailing (Table S5.1). However, our experiment presupposes the need to exclude broad-spectrum herbicide, aiming to replace chemical weed reduction with biological competition. While later flowering species like *Clarkia* and *Epilobium* may have benefitted from delayed flailing, their low cover in 2021 suggests that other factors were more important for their survival. Their inability to reproduce may instead be caused by seedling competition with earlier species (Harris 1977; Blackford et al. 2020) or drought during seed formation (Samarah & Alqudah 2011). Disturbance may also provide a mechanism for dispersal. In 2021 we observed cover crops widely distributed around our blocks, suggesting that small plots can act as nuclei which expand over time (Corbin & Holl 2012; Rayburn & Laca 2013).

Orchard age and canopy cover were the primary drivers of cover crop survival. While individual species responses varied, all seed mixes benefited from open canopies. Therefore, the current rapid growth of the hazelnut industry (USDA 2017) represents an opportunity for ecological intensification, as new orchards can provide ideal conditions for decades before maturing. Admittedly, the small size of our young orchard could have allowed edge effects to influence our results, although we would expect the increased weed pressure (De Cauwer et al. 2008) and shade from adjacent trees to reduce cover crops survival, leading us to underestimate their potential. The two species that preferred intermediate canopy cover, *Geum* and *Epilobium*, validate our expectation that selecting diverse native species from corresponding habitats (oak woodlands) can increase the chance of success in these challenging conditions. However, *Geum*, had highly variable cover, suggesting other environmental factors (Telak et al. 2021) are relevant. These negative or intermediate-peaking cover responses suggest a stress-competition tradeoff (Grime 1977; Valladares et al. 2016) where better competitors dominated open conditions, and shade tolerators survived with light limitation. In the former category, *Achillea, Prunella*, *Eriophyllum* and the conventional *Trifolium* were the only species that substantially increased in cover across years. While our results support the interpretation that young orchards are the best candidate for ecological intensification, diverging species responses provide options for established orchards.

Agricultural Production Criteria

Our expectation that ecological intensification could meet agricultural criteria was supported by the fact that native perennials excluded weeds and reduced erosion potential most, followed by native annuals and then conventional cover crops. While native annuals reduced weeds most in the first year, native perennials did in the second, reflecting natural patterns where annuals take advantage of bare ground following disturbance and established perennials holding their ground are strong competitors (Harris 1977). Therefore, in orchards with high weed pressure that can interfere with harvest (Mennan & Ngouajio 2012), a combination of high performing annuals and perennials may be ideal to exclude weeds in the short and longer term. While all seed mixes were present over winter, only native perennials increased winter cover relative to unseeded plots and only in the youngest orchard. Fortunately, erosion controls are most needed in young orchards where tree canopies and roots stabilize soils less than mature orchards (Olsen & Peachey 2013). Complicating their undesirability, weeds provided a baseline of winter cover (20%) potentially reducing erosion risk themselves (Moreau et al. 2020). Finally, although hazelnuts are wind pollinated, farmers with diversified production can also increase yield from native pollinators that associate with native vegetation (Saunders et al. 1998; Klein et al. 2012; Lundin et al. 2017; Norfolk et al. 2016).

Native cover crops can also fail to meet agricultural criteria if they compete with trees or complicate harvest. Fortunately, cover crops never reduced soil moisture relative to controls. Instead, native seed mixes increased moisture during the wet spring of 2020, implying that excess rainfall infiltrated soils rather than running off. While we only measured soil moisture to a depth of 15 cm, our results are promising as this is the primary rooting zone of our herbaceous cover crops. By contrast, trees can access soil moisture in deeper horizons (Atucha et al. 2013). Despite our short experimental timeframe, over longer periods cover crops increase soil water holding capacity (Irmak et al. 2018), which will be increasingly important as climate change leads to drought that reduces yields and can kill young trees (An et al. 2020; Mingeau et al. 1994). Because we assumed that flailing and scraping would ensure bare orchard floors at harvest time, we did not directly evaluate cover crop impacts on harvest. We did observe, however, that vegetation in unmanaged plots became entangled with the harvester (Table 5.1). Additionally, when we reduced the number of flailing from three to two, woody debris was not sufficiently broken down and made its way into harvest bins. While we expect that thorough flailing will likely resolve these issues, care will be needed in the implementation of a cover cropping program and adaptive management may be necessary to ensure effective harvests.

Ecological Function

In addition to meeting survival and production criteria, native cover crops also supported the highest level of ecological functioning. Each population of a native species surviving in farmland can contribute to regional metapopulations, potentially rescuing threatened wildland oak-prairie remnants and increasing gene flow (Andren 1999; Vandermeer & Carvajal 2001). The profuse flowering of most native species before flailing also this improved the permeability of farmland facilitating insect dispersal which may aid in pollinator persistence under climate change (Sirois-Delisle & Kerr 2018). However, the weakened relationship between floral abundance and pollinator visitation in high-canopy orchards (Figure S5.5) suggests that pollinators are limited by shade and that younger orchards represent the best opportunity to support them. Surprisingly, limiting cover crop diversity may not substantially limit pollinator diversity and abundance. As we saw with *Achillea*, few hosts often supported most pollinator diversity in other agroecosystems (Haaland et al. 2011; Winfree 2010). Still, whether due to phenology mismatch (Rao & Stephen 2010) or preference, not all pollinators associated with Achillea (i.e. *Eucera* and *Osmia*), suggesting, as in Burkle et al. (2020) that host diversity can still be valuable. While conventional cover crops and weeds were disproportionately visited by non-native honeybees, suggesting that native vegetation was particularly valuable for native pollinators (Morandin & Kremen 2013), this utilization of weeds demonstrated the potential to increase ecological functioning by simply reducing weed control intensity. Any benefits to the native pollinator community will be lost, however, if pesticide use causes cover crops to become an ecological trap (Ganser et al. 2019). Novel non-spray pest disruptions, like biological control (Penkauskas et al. 2021) and mating disruptors (Miller 2018) can help reduce this risk, and coordination of disturbance and pesticide application can help ensure that attractive cover crops have been cleared before spraying.

Conclusions

Hazelnut orchards, especially those that are newly established, can play a valuable role in supporting the restoration and conservation of oak-prairie herbaceous understory species and the pollinators that rely upon them. These benefits to ecological function are not gained at the expense of agricultural production. In fact, ecological intensification can provide farmers valuable ecosystem services. Realization of these benefits will depend on collaboration between restoration practitioners, native seed nurseries and farmers to build capacity and bring native cover crop mixes to market. While agricultural landscapes are not always the cheapest and easiest place to restore, this experiment can serve as a model for other regions where specialized native flora and fauna are threatened by fragmentation and agricultural activity.

Figure 5.1. To transition from the current state of bare orchard floor management to the restoration of diverse native vegetation that supports pollinators, each cover crop species is assessed according to three criteria. First, potential cover crop species must meet survival criteria (a) with respect to variable light availability and the mechanical disturbances of flailing and scraping. Cover crops must also meet production criteria (b) with respect to orchard floor management; specifically with relation to weed exclusion, erosion potential and soil moisture. Finally, we compare the degree to which different cover crops support the abundance and diversity of native pollinators (c). The degree to which various species meet these criteria will narrow the potential species pool to the best candidates. Across each of these criteria we compare species of native annual forbs, native perennial forbs, and conventional cover crops with typical bare orchard floors.

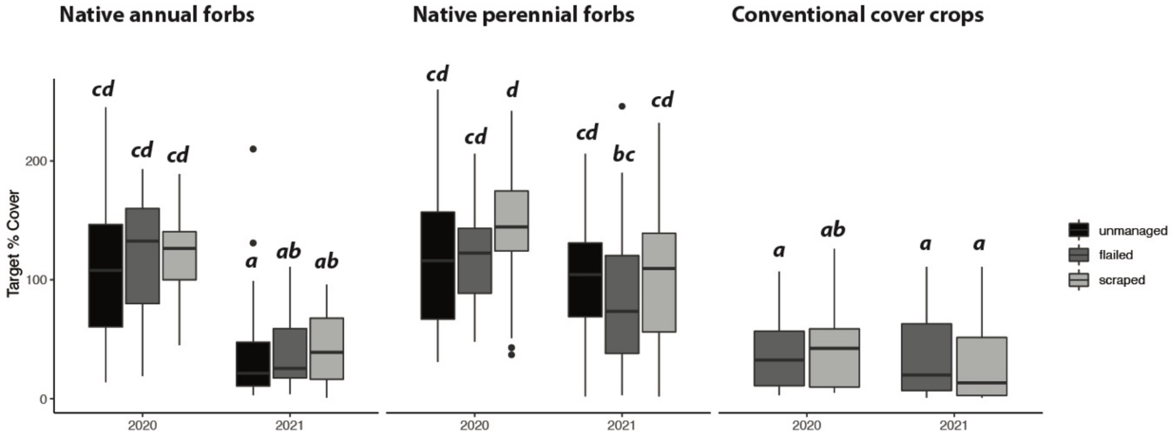


Figure 5.2. Aggregated target species cover by seed mix and in response to mechanical disturbance. Across all three cover crop seed mixes, flailing and scraping did not reduce target species cover relative to undisturbed plots. Perennials and annuals had similar levels of cover in 2020, which perennials maintained in 2021 while annuals declined. Conventional cover crops had the lowest aggregated cover across both years. Letters represent the result of mixed models with year, mechanical disturbance, and seed mix as fixed effects and orchard and block as random effects.

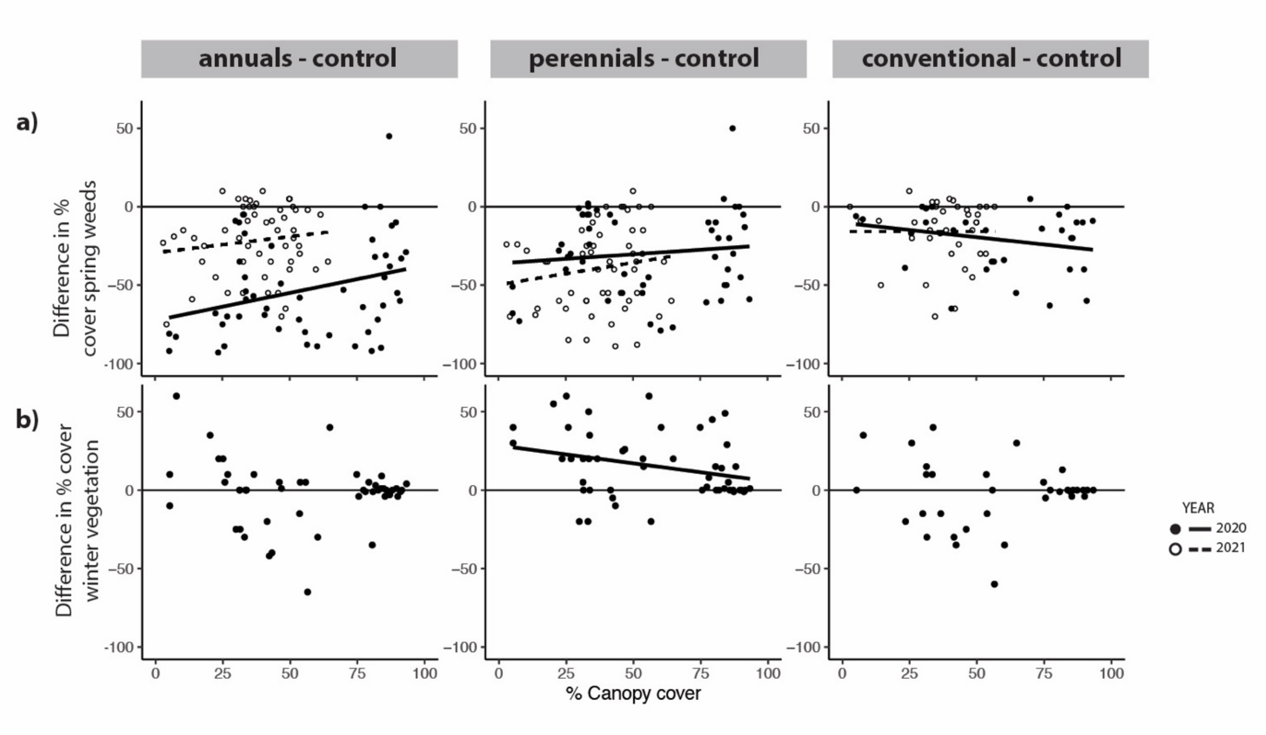


Figure 5.3. Effects of each seed mix relative to unseeded controls on a) peak weed cover and b) winter vegetation, production-related criteria for selecting cover crop species related to their weed exclusion ability and reduction of erosion risk. Closed points and solid regression lines represent data from 2020 and open points and dashed lines from 2021. Weeds were highest in unseeded control plots, and native annuals and native perennials reduced weed cover more effectively than conventional cover crops. Native annuals were especially effective under low canopy cover in the first year, and less so in the second. Native perennials were effective across a range of canopy cover conditions and remained so in the following year. Native annuals and conventional cover crops did not have significantly higher vegetative cover compared to control plots, native perennials did in open canopy conditions.

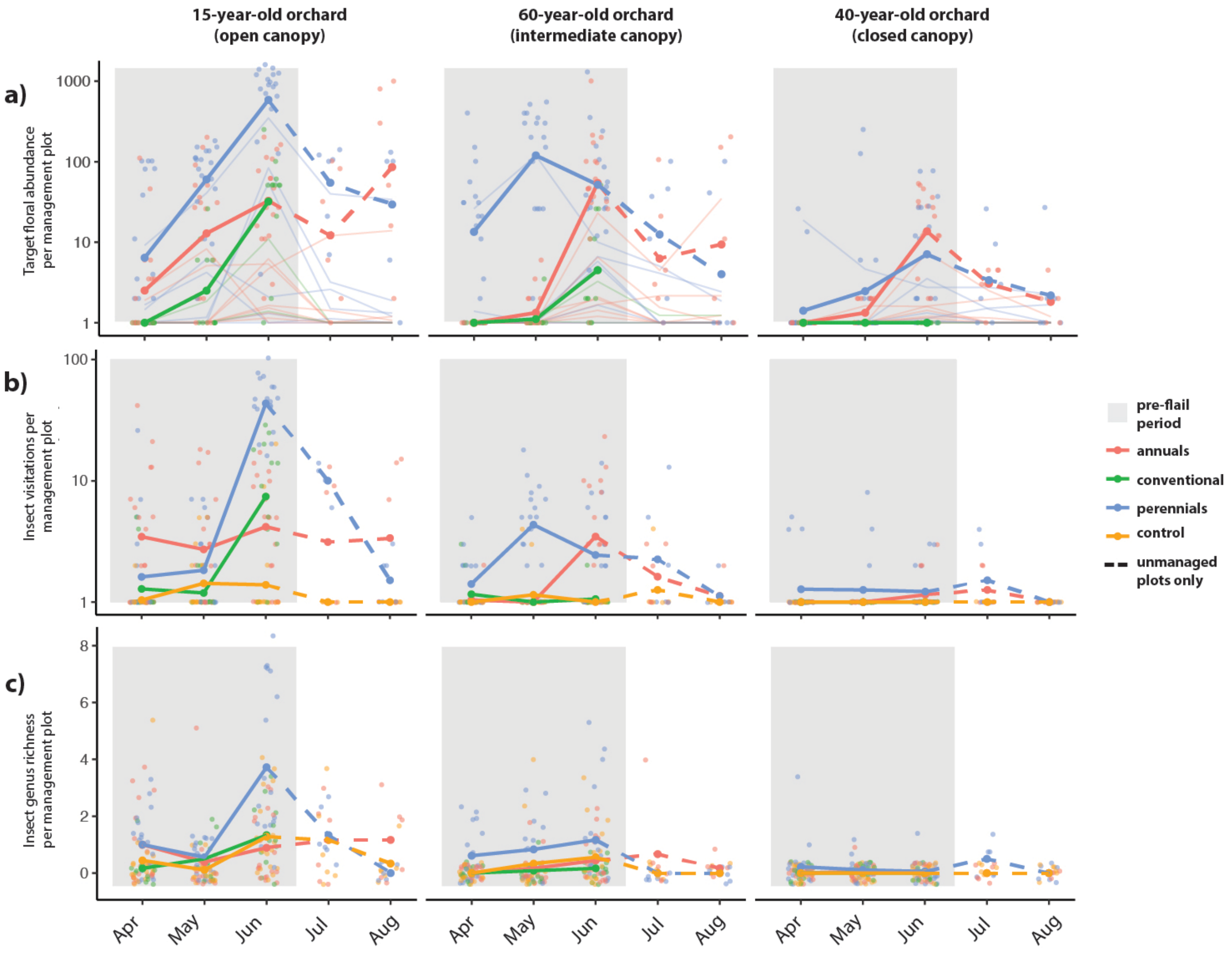


Figure 5.4: Floral abundance and associated pollinator visitations and diversity varies by orchard age and seed mix, but phenology is stable. Thick lines are colored according to seed mix and represent mean aggregated values for floral abundance a), pollinator visitations b) and pollinator diversity c) at the seed mix subplot level. The ‘control’ seed mix refers to unseeded subplots with only non-target plant species present. Translucent points represent individual subplot data, and thin lines in a) represent individual species’ mean flowering abundances. The gray area represents the ‘allowable flowering’ period before flailing and scraping were initiated. During this pre-flail period data from flailed, scraped and unmanaged plots are shown as solid lines, but once flailing was initiated only data from unmanaged plots are shown as dashed lines. All conventional plots were flailed, so there is no data for these plots outside of the pre-flail period.

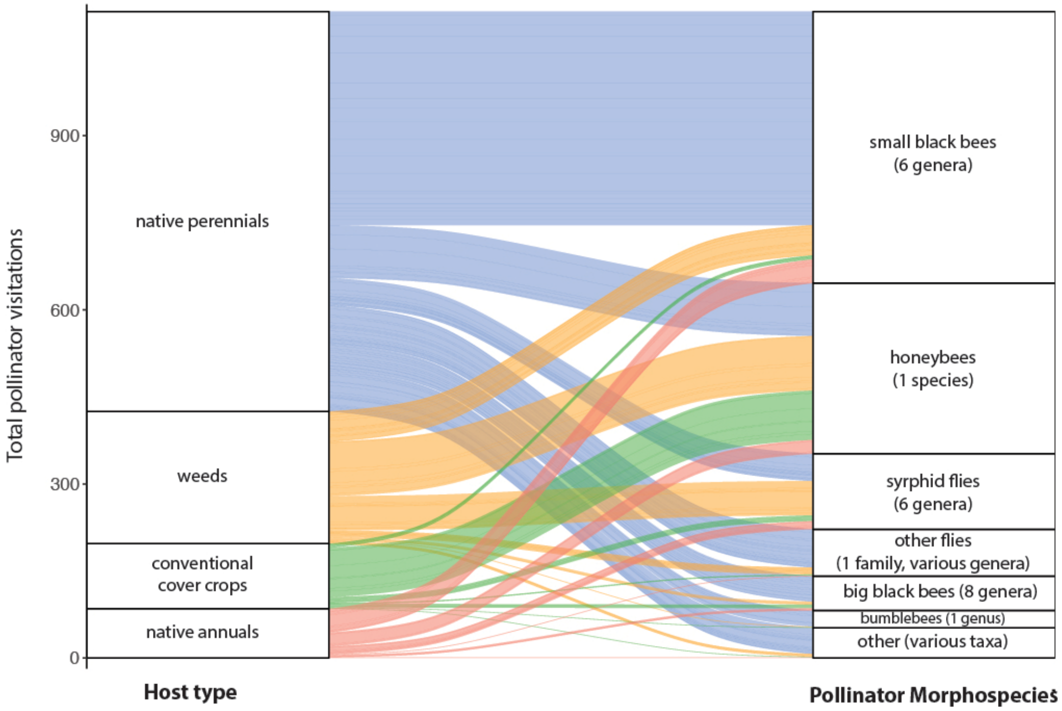


Figure 5.5: Pollinator morphospecies visitations to native perennial, native annual, conventional cover crop and non-target weed flowers across all orchards in flailed and scraped plots. Height of taxa labels and width of rivers correspond to total of visitation.

Table 5.1: Characteristics and performance of seed mixes and associated plant species. Agricultural criteria (winter vegetation, weed cover and soil moisture) are compared to unseeded controls at the seed mix level. At the individual species level, survival criteria include seed application rates, average cover each year, and canopy response (negative = declining cover with more shade, polynomial = greatest cover at intermediate shade, n/a = no relationship to canopy cover).Ecological functioning criteria are described with flowering period (months with flowers present), unique pollinator genera collected, and total pollinator visitation across all three orchards.

Seed mix	Winter vegetation (relative to control)	Spring weed cover (relative to control)	Moisture (periods different from control)	Harvest notes	Species	Price per Gram	Grams seeded	Seeds per Gram	Seeds per plot	Average cover 2020 (2021)			Canopy response	Flowering Period	Unique pollinator genera	Total pollinator visitaitons
										15	60	40				
Native Perennials	+15%	2020: -30% 2021: -39%	May 1 2020: + May 10 2020: + May 17 2020: +	In open canopy only *Achillea* trapped nuts and occasionally stuck in picker belt. *Geum* and *Eriophyllum* slightly trapped nuts.	*Achillea millefolium*	$0.198	6.25	3128	19550	40 (87)	45 (14)	34 (8)	negative	June	19	783
					Agoseris grandiflora	$0.694	6.25	604	3775	1 (0)	<1 (0)	0 (0)	n/a	n/a	1	0
					Geum macrophyllum	$0.220	6.25	1675	10469	10 (10)	52 (51)	52 (18)	polynomial		13	180
					Eriophyllum lanatum var. leuc	$0.320	6.25	2577	16106	5 (28)	22 (5)	8 (<1)	polynomial	June	5	44
					Lomatium nudicaule	$0.529	6.25	87	544	4 (10)	3 (<1)	2 (<1)	negative	April-May	3	10
					Potentilla gracilis	$0.231	6.25	3124	19525	2 (1)	11 (5)	6 (2)	n/a	June	1	1
					Prunella vulgaris var. lanceolata	$0.209	6.25	882	5513	24 (40)	18 (5)	26 (8)	negative	June	11	220
					Viola praemorsa (nuttalii)	$0.408	6.25	370	2313	<1 (0)	1 (<1)	1 (<1)	n/a		0	0
Native Annuals	-1% n.s.	2020: -52% 2021: -21%	April 24 2020: + May 1 2020: + May 10 2020: + May 17 2020: +	No harvest issues, some species still flowering at harvest.	*Epilobium densiflorum*	$0.132	6.25	1875	11719	34 (16)	64 (9)	49 (4)	negative/positive	June-Aug	4	81
					Clarkia amoenia ssp. lindleyi	$0.265	6.25	2274	14213	22 (8)	26 (3)	17 (0)	polynomial	June-Aug	6	38
					Collomia grandiflora	$0.176	6.25	268	1675	10 (8)	41 (23)	6 (1)	polynomial	June	5	2
					Amsinckia menziesii	$0.243	6.25	496	3100	19 (21)	4 (1)	6 (3)	negative	May-June	2	36
					Gilia capitata	$0.243	6.25	453	2831	11 (11)	9 (2)	5 (3)	negative	June-July	7	31
					Sanguisorba annua (Poteridium occidentale)	$0.172	6.25	535	3344	3 (<1)	3 (2)	3 (2)	n/a	June	0	0
					Plectritis congesta	$0.287	6.25	2891	18069	13 (7)	5 (<1)	2 (0)	negative	April-May	5	39
					Lotus purshianus (Acmispon americanus)	$0.231	6.25	195	1219	<1 (0)	1 (<1)	2 (<1)	n/a	June	0	0
Conventional	-4% n.s.	2020: -21% 2021: -13% n.s.	June 2021: +	*Avena* and *Hordeum* vegetation got stuck in the picker.	*Avena sativa* (annual)	$0.015	12.5	28	350	6 (4)	20 (8)	8 (0)	n/a	June-July	0	0
					Hordeum vulgare (annual)	$0.016	12.5	30	375	4 (8)	13 (5)	8 (0)	negative	June-July	0	1
					Trifolium repens (perennial)	$0.025	12.5	1710	21375	4 (26)	3 (4)	3 (<1)	negative	June-Aug	3	113
					Vicia angustifolia (annual)	$0.017	12.5	115	1438	2 (2)	10 (<1)	2 (0)	polynomial	July	0	0

Table 5.2: Description of insect morphospecies groups and associated collected taxa. Metrics of phenology and host preference include peak month (total visits across all orchards), most visited seed mix (total visits), most visited host species (total visits) and host attractiveness index, total visits per host per available flower. Note: weeds are distributed across seed mixes. *Species from these taxa are represented within multiple morphospecies categories.

Morphospecies	Description	Peak Month (visits)	Most Visited Seed Mix Subplot (visits)	Highest Host Attractiveness Index (visits/flower)	Most Visited Host Species (visits)	Order	Associated taxa
Small black bee	Bees less than ~ 0.75cm in size, that are mostly or entirely dark colored	June (547)	Native perennials (565)	_Plectritis_ (0.047)	_Achillea_ (359)	Hymenoptera	Andrenidae (_Andrena_*, _Panurginus_), Apidae (_Ceratina_*), Colletidae (_Hylaeus_), Halictidae (_Halictus_*, _Lasioglossum_),
Large black bee	Bees more than ~ 0.75cm in size, that are mostly or entirely dark colored	June (84)	Native perennials (82)	_Trifolium_ (0.006)	_Achillea_ (52)	Hymenoptera	Andrenidae (_Andrena_*), Apidae (_Ceratina_*, _Eucera_), Halictidae (_Halictus_*, _Lasioglossum_*), Megachilidae (_Anthidium_**, _Ashmeadiella_, _Osmia_*)
Bumblebee	Large (~3cm) bees with densely fuzzy hair on head, thorax and abdomen	June (69)	Native perennials (42)	_Prunella_ (.017)	_Prunella_ (61)	Hymenoptera	Apidae (_Bombus)_
Honeybee	Moderately large (~1.5cm) bees with a partially or mostly golden-colored abdomen and little hair	June (252)	Native perennials (160)	_Trifolium_ (.091)	_Achillea_ (138)	Hymenoptera	Apidae (_Apis mellifera_**)
Green bee	Highly metallic/reflective bees with a green reflection or colored integument	May (3)	Native perennials (2)	_Geum_ (<0.001)	_Geum_ (3)	Hymenoptera	Megachilidae (_Osmia_*)
Other bee	Insect with a recognizably Apoid body shape, but some other color (e.g. red, orange, tan)	June (8)	Native perennials (4)	_Achillea_ (<0.001)	_Achillea_ (4)	Hymenoptera	Apidae (_Nomada_)
Hymenoptera	Other members of Hymenoptera, not including bees (e.g. wasps, ants)	June (4)	Native perennials (6)	_Achillea_ (<0.001)	_Achillea_ (6)	Hymenoptera	Various
Syrphid fly	Flies distinguished by hovering movement and often by yellow and black patterns on abdomen	June (137)	Native perennials (112)	_Trifolium_ (0.010)	Weed (82)	Diptera	Syrphidae (_Eristalis_**, _Eupeodes_, _Platycheirus_, _Sphaerophoria_, _Syritta_, _Toxomerus_)
Other fly	All other flies not belonging to family Syrphidae	June (114)	Native perennials (121)	_Achillea_ (0.006)	_Achillea_ (95)	Diptera	various
Hemiptera	Insects with wings not covered entirely by a hard wing case (elytra) and with sucking mouthparts	July (29)	Native perennials (29)	_Achillea_ (0.002)	_Achillea_ (36)	Hemiptera	various
Lepidoptera	Butterflies and moths	June (17)	Native perennials (19)	_Prunella_ (0.004)	_Prunella_ (16)	Lepidoptera	various
Coleoptera	Insects with wings covered entirely by a hard wing case	June (18)	Native perennials (28)	_Geum_ (0.002)	_Geum_ (18)	Coleoptera	various
Dermaptera	Earwigs	May (1)	Native perennials (1)	_Achillea_ (<0.001)	_Achillea_ (1)	Dermaptera	various
Neuroptera	Lacewings	July (2)	Native perennials (2)	_Geum_ (<0.001)	_Geum_ (2)	Neuroptera	various

CHAPTER VI

CONCLUSIONS

Ecological restoration is a powerful framework for ecosystem management. While restoration intervention outcomes vary due to environmental variability, a changing climate, and land use contexts, understanding these relationships can help ensure effective restoration outcomes and even extend restoration beyond its traditional boundaries.

Over the course of my dissertation I considered how grazing management interacts with spatial and interannual resource availability (Chapter II), how prescribed burning affects seedling establishment and community trajectories across communities with variable starting conditions along an environmental gradient (Chapter III), how warming drives state change and to what extent contingency matters (chapter IV), and how restoration can be implemented in an anthropological landscape alongside production imperatives (Chapter V).

In Chapter II, I analyzed a long-term data set and showed that grazing ultimately decreased diversity at the local level but increased beta-diversity, especially in high-resource years. This increased heterogeneity can be helpful for native plant conservation and controlling widespread dominance of invasive annual grasses.

In Chapter III, I carried out prescribed burns on communities with variable starting conditions across a latitudinal gradient. I found that except for in hottest and driest conditions, burning increased seedling establishment but only had minor impacts on overall community trajectory. Contrary to my expectations, burning did not precipitate large-scale state change, but instead initially dominant functional groups remained dominance. This study helped quantify risks and rewards of prescribed burning for restoration, demonstrating that while burning does not have imminent risks, the level of reward is highly dependent on current climate and past management context.

In Chapter IV, I implemented a controlled competition experiment wherein I established various competitive scenarios with annual and perennial grasses grown at different densities in warmed and ambient conditions and monitored survival and fecundity. The population growth models that I fit and used for simulations revealed a surprising result where annuals could already invade and outcompete juvenile perennials, but a shift towards warmed conditions allowed perennials to persist. Perennial populations were highly sensitive to adult survival, and the annual competitive effect was largely driven by their ability to restrict perennial fecundity in ambient conditions. This result suggests annuals will continue to successfully invade, but specific well-timed management interventions such as planting and maintaining plugs by weeding in cooler, wetter years could help perennials persist.

Finally, in Chapter V, I tested whether hazelnut orchards could serve as a proxy for native herbaceous grassland species and pollinators that rely upon them. I found that in fact, several species could survive typical hazelnut mechanical disturbance, persist in low to moderate shade, provide farmers with valuable ecosystem services and increase ecosystem functioning.

Taken as a whole, these results demonstrate the importance of considering environmental heterogeneity and change when considering a restoration or management action. These results provide actionable recommendations and information for land managers and demonstrate an example of a way to expand restoration beyond wildlands. At the same time, they open the door to new potential questions. For example, to what extent can our observations regarding annual and perennial dynamics in the Willamette Valley be extrapolated across a landscape with diverse environmental characteristics? How would different species, or a greater diversity of annual and perennial species jointly respond to warming? How will native plant and pollinator populations respond to other challenges of the agricultural landscape such as pesticide and fertilizer applications? These questions can be addressed by future research.

APPENDIX A

SUPPLEMENTARY INFORMATION FOR CHAPTER II

Figure S2.1: Quadrat classification over time by block.

Table S2.1: Beta diversity statistics for main and interactive effects in all years, wet years, dry years, 2014 and 2017. perMANOVA statistics test the hypothesis that community centroids in multivariate space are statistically different. Betadisper statistics test the hypothesis that both community types have different levels of variance across replicates. Codyn statistics are effect size indices from 0-1 of either community difference (analogous to perMANOVA) or dispersion (analogous to betadisper). Default first comparison in contrast is more dispersed unless underlined.

Context	**Treatment**	**Contrast**	**PERMANOVA**			**betadisper**	**codyn differences**	
			F	***P***	***R2***	***P***	***Community***	***Dispersion***
All years	grazing main	grazed-un		*n.s.*		0.015	0.11	0.002
	grazed	on-off mound		*n.s.*		*n.s.*	0.11	0.02
	ungrazed	on-off mound		*n.s.*		*n.s.*	0.12	0.03
	mound main	on-off mound		*n.s.*		*n.s.*	0.10	0.03
	on-mound	grazed-un		*n.s.*		*n.s.*	0.11	0.002
	off-mound	grazed-un		*n.s.*		*n.s.*	0.12	0.009
Wet years	grazing main	grazed-un		*n.s.*		*n.s.*	0.14	-0.02
	grazed	on-off mound		*n.s.*		*n.s.*	0.17	0.06
	ungrazed	on-off mound		*n.s.*		*n.s.*	0.20	0.08
	mound main	on-off mound		*n.s.*		*n.s.*	0.18	0.07
	on-mound	grazed-un		*n.s.*		*n.s.*	0.13	-0.02
	off-mound	grazed-un		*n.s.*		0.056	0.17	-0.005
Dry years	grazing main	grazed-un		*n.s.*		*n.s.*	0.13	0.03
	grazed	on-off mound		*n.s.*		*n.s.*	0.17	0.08
	ungrazed	on-off mound		*n.s.*		*n.s.*	0.13	0.01
	mound main	on-off mound		*n.s.*		*n.s.*	0.12	0.04
	on-mound	grazed-un		*n.s.*		*n.s.*	0.17	0.07
	off-mound	grazed-un		*n.s.*		*n.s.*	0.15	-0.005
2014	grazing main	grazed-un	$2.46_{1, 61}$	0.039	0.039	*n.s.*	0.17	0.05
	grazed	on-off mound		*n.s.*		*n.s.*	0.16	0.08
	ungrazed	on-off mound		*n.s.*		*n.s.*	0.13	-0.04
	mound main	on-off mound		*n.s.*		*n.s.*	0.10	0.02
	on-mound	grazed-un		*n.s.*		*n.s.*	0.22	0.11
	off-mound	grazed-un		*n.s.*		*n.s.*	0.16	-0.12
2017	grazing main	grazed-un	$3.8_{1, 63}$	.006	0.05	*n.s.*	0.24	-0.03
	grazed	on-off mound	$5.32_{1, 31}$	0.001	0.15	0.0001	0.37	0.16
	ungrazed	on-off mound	$3.94_{1, 31}$	0.001	0.11	*n.s.*	0.36	-0.05
	mound main	on-off mound	$3.46_{1,63}$	0.001	0.05	0.026	0.34	0.09
	on-mound	grazed-un	$2.6_{1,36}$	0.013	0.069	*n.s.*	0.20	0.03
	off-mound	grazed-un	$2.09_{1, 26}$	0.026	0.07	*n.s.*	0.32	-0.08

Table S2.2. Table of species sampled in experimental plots. Nomenclature follows Baldwin and Goldman (2012).

Code	Native	Growth Habit	Full Species Name
ammein	Native	Forb	Amsinckia menziesii v intermedia
ammeme	Native	Forb	Amsinckia menziesii v menziesii
amstes	Native	Forb	Amsinckia tessellata
astdid	Native	Forb	Astragalus didymocarpus
astoxy	Native	Forb	Astragalus oxyphysus
bromad	Introduced	Grass	Bromus madritensis ssp rubens (B. rubens)
calcil	Native	Forb	Calandrinia ciliata
capbur	Introduced	Forb	Capsella bursa-pastoris
dessop	Introduced	Forb	Descurainia sophia
diccap	Native	Forb	Dichelostemma capitatum
erigra	Native	Forb	Eriogonum gracillimum
erocic	Introduced	Forb	Erodium cicutarium
guilas	Native	Forb	Guillenia lasiophylla (Thelypodium l.)
herhir	Introduced	Forb	Herniaria hirsuta ssp cineria
hormur	Introduced	Grass	Hordeum murinum
lascal	Native	Forb	Lasthenia californica (L. chrysotoma)
lasmin	Native	Forb	Lasthenia minor
lepdic	Native	Forb	Lepidium dictyotum
lepnit	Native	Forb	Lepidium nitidum
lotwra	Native	Forb	Lotus wrangelianus
lumimi	Native	Forb	Lupinus microcarpus v microcarpus (L. ruber)
malcou	Native	Forb	Malacothrix coulteri
micdou	Native	Forb	Microseris douglasii
micele	Native	Forb	Microseris elegans
pecpen	Native	Forb	Pectocarya penicillata
phacil	Native	Forb	Phacelia ciliata
phlgra	Native	Forb	Phlox gracilis (Microsteris g.)
poasec	Native	Grass	Poa secunda ssp secunda (P. scabrella)
saltra	Introduced	Forb	Salsola tragus
schara	Introduced	Grass	Schismus arabicus
sisiri	Introduced	Forb	Sisymbrium irio
trialb	Native	Forb	Trifolium albopurpureum
trigra	Native	Forb	Trifolium gracilentum
trilan	Native	Forb	Trichostema lanceolatum
trogra	Native	Forb	Tropidocarpum gracile
vulmic	Native	Grass	Vulpia microstachys vpauciflora (F. reflexa)
vulmyu	introduced	grass	Vulpia myuros v hirsuta (F. megalura)

APPENDIX B

SUPPLEMENTARY INFORMATION FOR CHAPTER III

Figure S3.1. Burn boxes are an alternative to full-pasture prescribed fire that have been successfully used across western grasslands to reproduce typical prescribed fire effects at a small scale (Sharrow & Wright 2018; White & Currie 1983). Our burn box was constructed of four 1 m by 1 m aluminum panels that bolt together using rails as seen above. The box can be disassembled for transport and has a handle on each panel.

Sharrow, S. H., & Wright, H. A. (2018). Production in the rolling plains effects of fire, ash, and litter on soil nitrate, temperature, moisture and tobosagrass production in the rolling plains. *Society for Range Management*, *30*(4), 266–270.

White, R. S., & Currie, P. O. (1983). Prescribed burning in the northern great plains: Yield and cover responses of 3 forage species in the mixed grass prairie. *Society for Range Management*, *36*(2), 179–183.

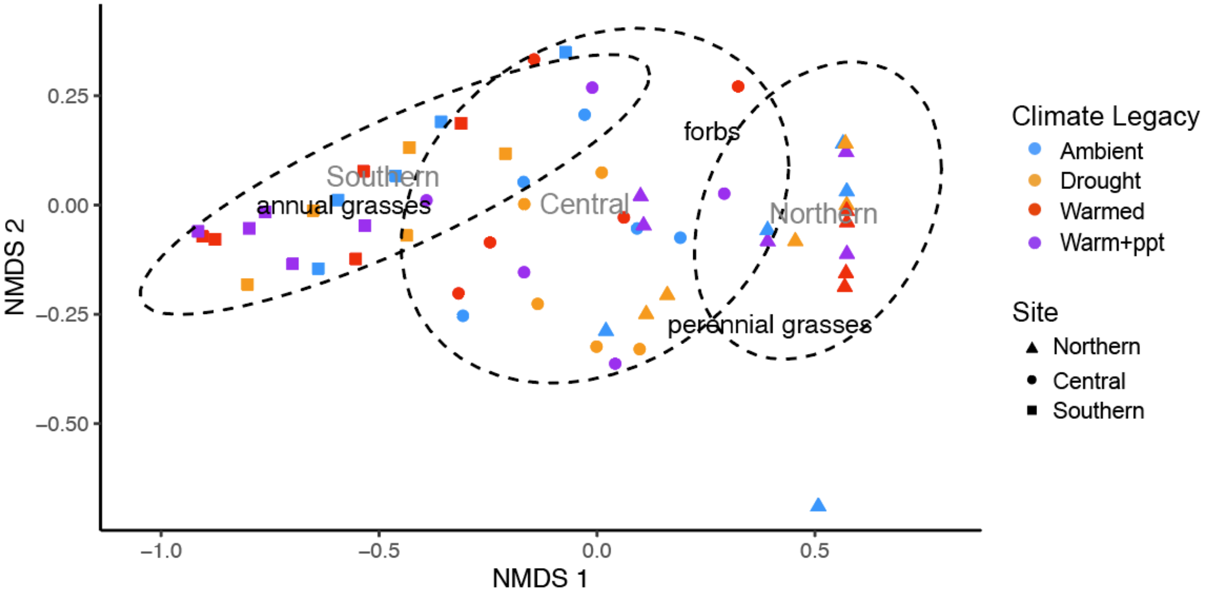


Figure S3.2. NMDS ordination of unburned subplots in 2019 by site and 2016-2018 climate legacy. Site is represented by shape and 95% confidence ellipses and climate legacy by color. While warmed and warm + precipitation treatments ended in 2018, drought structures remained in place through 2019. Black text represents functional group loading and grey text label ellipses by site. The only significant effect of climate manipulation legacy was when warmed and warm + precipitation treatments were pooled and compared against ambient and drought at the southern ($P=0.051$, $R^2=0.17$) and central ($P=0.048$, $R^2=0.16$). There was no significant effect of drought shelters at any site. For full results see Supplemental Table S4.

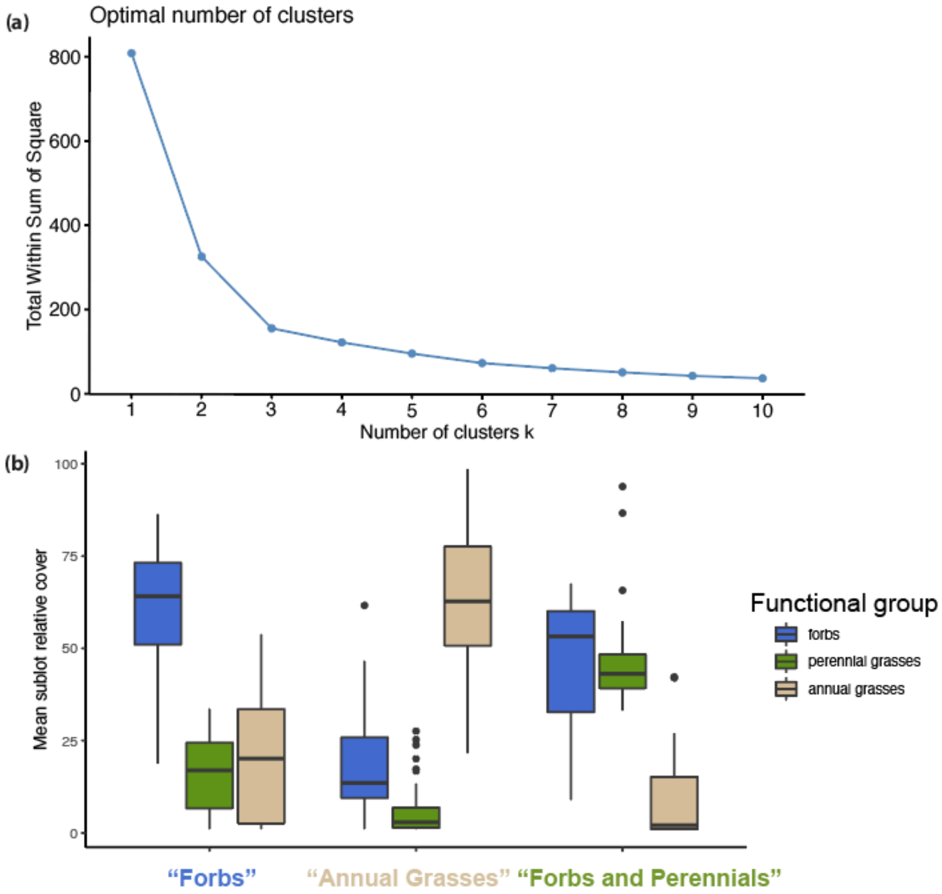


Figure S3.3. (a) Agglomerative hierarchical clustering of mean subplot functional representation by cover. Within sum of square variation declines with increasing number of clusters. Optimal number of clusters occurs at the point of inflection (k=3). **(b)** Cluster composition by functional group representation (green = forbs, blue = native and pasture perennial grasses, yellow = annual grasses) at k=3. Clusters are named "Annuals", "Forbs" and "Forbs and Perennials" based upon dominance of functional groups.

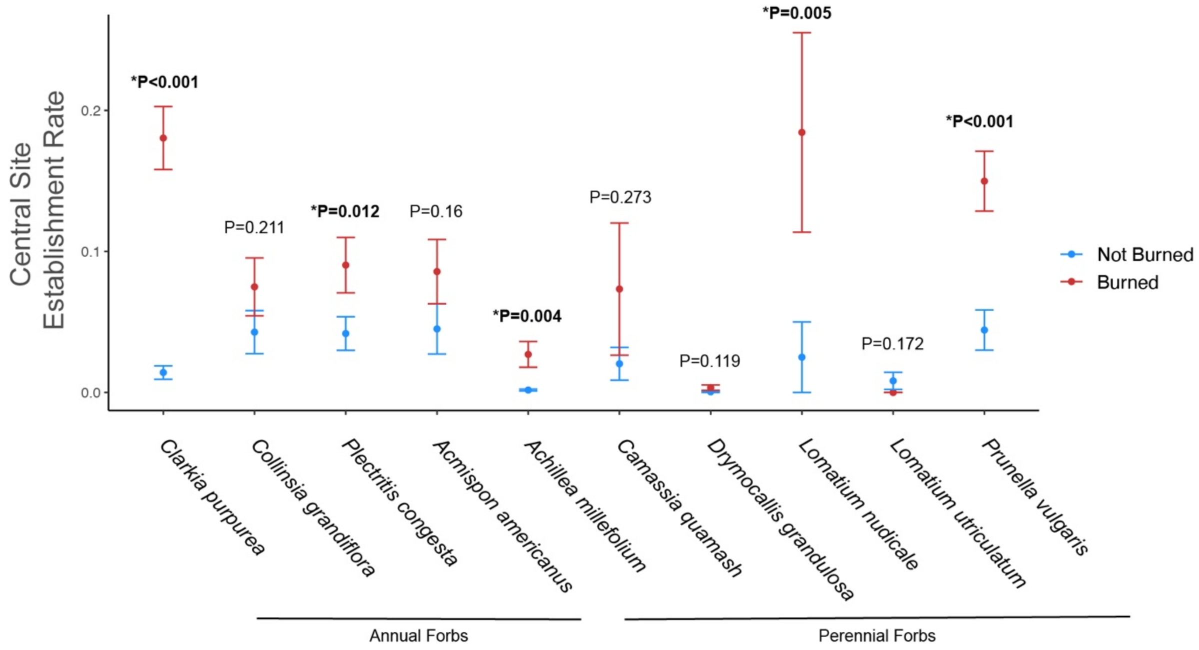


Figure S3.4. Forb species-specific establishment rates at the central site in burned (red) and unburned (blue) subplots in spring 2019. Five species were not detected. Establishment was measured as the number of individuals present in spring 2019 divided by the number of seeds introduced in fall 2018. We calculated p-values for each species (shown in black) using burn treatment as a fixed factor, and microplot nested in subplot as random.

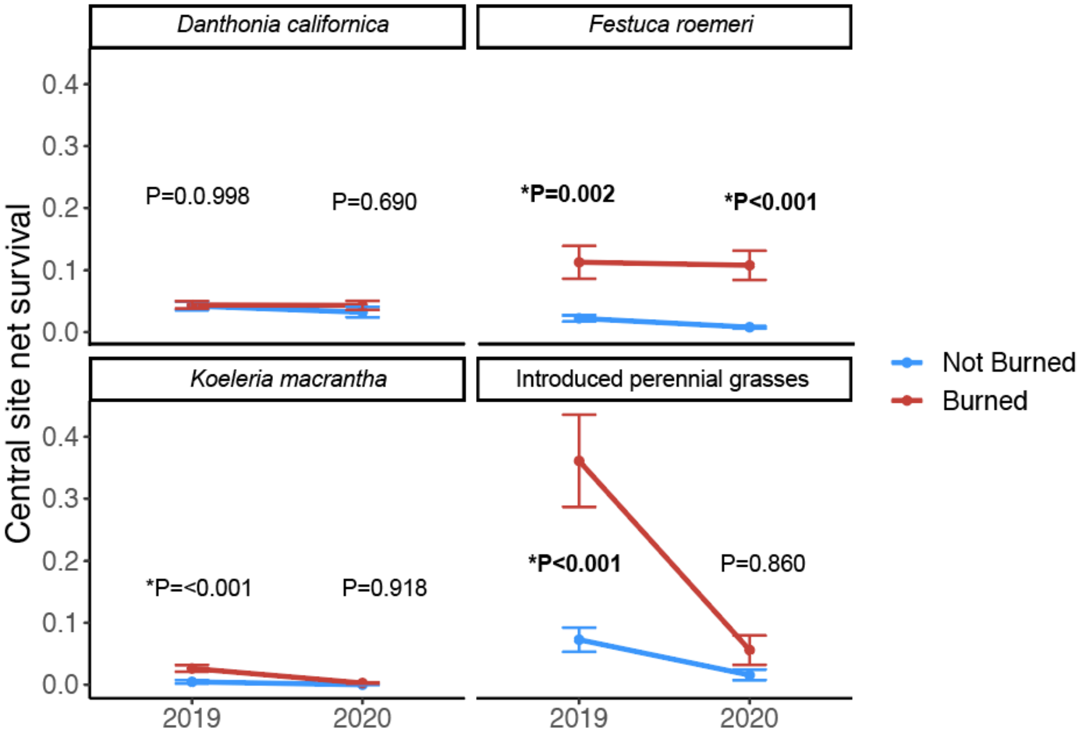


Figure S3.5. Persistence of native perennial and pasture grass seedling survival at the central site, burned (red) vs unburned (blue). All burn plots were only burned once, in 2019. While introduced perennial grasses (not differing y-axis scale) initially had much higher survival when burned than all native perennial grasses in 2019, by 2020 they were roughly at the same level as the native perennial with highest survival, *Festuca*. *Koeleria* showed a similar pattern to pasture grasses, but at much lower absolute survival; *Festuca* had the greatest stability in survival rates from 2019 to 2020 in burned subplots; and *Danthonia* was the only species where burning had no effect. We calculated p-values (shown in black) using year and burn treatment as fixed factors, and microplot nested in subplot as random.

Table S3.1: Results from PERMANOVA on unburned subplots in 2019 by site and 2016-2018 climate legacy. Climate manipulation legacies include control, drought, warming and warming + precipitation (see methods). Contrast 'fullclim' includes all four climate legacies (n=5), 'warmtrt' compares warmed and warmed + ppt against control and drought (n=10), and 'drought', 'warming' and 'warming + ppt' are compared directly against 'controls' (n=5).

Contrast	**Site**	**P**	**R2**
site	all	*<0.001	0.667
cluster	all	*<0.001	0.812
site*fullclim	all	0.503	0.033
site*warmed	all	0.248	0.016
fullclim	north	0.929	0.054
fullclim	central	0.256	0.211
fullclim	southern	0.237	0.214
warmtrt	north	0.590	0.027
warmtrt	central	0.051	0.17
warmtrt	southern	*0.048	0.165
drought	north	0.897	0.021
drought	central	0.545	0.043
drought	southern	0.572	0.07
warming	north	0.907	0.02
warming	central	0.268	0.126
warming	southern	0.241	0.15
warming + ppt	north	0.750	0.037
warming + ppt	central	0.221	0.18
warming + ppt	southern	0.389	0.103

Table S3.2: Results from Tukey post-hoc analysis of functional group relative cover across clusters (see Figure 2b). Pairwise contrasts are shown in the form cluster_functional group – cluster_functional group, with ag referring to annual grasses, pg to perennial grasses, and f to forbs. Significant contrasts have P<0.05. Groupings consist of a cluster type (i.e. "AG + Forbs") followed by a functional group type (i.e. "_f"). For example, the first row contrasts the cover of forbs vs. annual grasses in the "AG + Forbs" cluster. Clusters include "AG + Forbs" (Annual Grasses + Forbs), "Annuals Dominant", "PG + Forbs" (Perennial Grasses + Forbs), and "Forbs Dominant". Functional group types include f (forbs), ag (annual grasses) and pg (perennial grasses).

Contrast	Estimate	Std. Error	z value	Pr(>|z|)
AG + Forbs_f - AG + Forbs_ag	-18.98611	4.41846	-4.297	<0.01
AG + Forbs_pg - AG + Forbs_ag	-39.40625	4.41846	-8.919	<0.01
Annuals Dominant_ag - AG + Forbs_ag	22.99523	3.9054	5.888	<0.01
Annuals Dominant_f - AG + Forbs_ag	-39.11024	3.9054	-10.014	<0.01
Annuals Dominant_pg - AG + Forbs_ag	-45.06727	3.9054	-11.54	<0.01
Forbs Dominant_ag - AG + Forbs_ag	-28.36806	3.80922	-7.447	<0.01
Forbs Dominant_f - AG + Forbs_ag	12.68769	3.80922	3.331	0.04
Forbs Dominant_pg - AG + Forbs_ag	-32.64306	3.80922	-8.569	<0.01
PG + Forbs_ag - AG + Forbs_ag	-39.3954	3.9054	-10.087	<0.01
PG + Forbs_f - AG + Forbs_ag	-2.45092	3.9054	-0.628	1
PG + Forbs_pg - AG + Forbs_ag	-2.12754	3.9054	-0.545	1
AG + Forbs_pg - AG + Forbs_f	-20.42014	4.41846	-4.622	<0.01
Annuals Dominant_ag - AG + Forbs_f	41.98134	3.9054	10.75	<0.01
Annuals Dominant_f - AG + Forbs_f	-20.12413	3.9054	-5.153	<0.01
Annuals Dominant_pg - AG + Forbs_f	-26.08116	3.9054	-6.678	<0.01
Forbs Dominant_ag - AG + Forbs_f	-9.38194	3.80922	-2.463	0.3585
Forbs Dominant_f - AG + Forbs_f	31.6738	3.80922	8.315	<0.01
Forbs Dominant_pg - AG + Forbs_f	-13.65694	3.80922	-3.585	0.0173
PG + Forbs_ag - AG + Forbs_f	-20.40929	3.9054	-5.226	<0.01
PG + Forbs_f - AG + Forbs_f	16.53519	3.9054	4.234	<0.01
PG + Forbs_pg - AG + Forbs_f	16.85857	3.9054	4.317	<0.01
Annuals Dominant_ag - AG + Forbs_pg	62.40148	3.9054	15.978	<0.01
Annuals Dominant_f - AG + Forbs_pg	0.29601	3.9054	0.076	1
Annuals Dominant_pg - AG + Forbs_pg	-5.66102	3.9054	-1.45	0.9524
Forbs Dominant_ag - AG + Forbs_pg	11.03819	3.80922	2.898	0.1388
Forbs Dominant_f - AG + Forbs_pg	52.09394	3.80922	13.676	<0.01
Forbs Dominant_pg - AG + Forbs_pg	6.76319	3.80922	1.775	0.8283
PG + Forbs_ag - AG + Forbs_pg	0.01085	3.9054	0.003	1
PG + Forbs_f - AG + Forbs_pg	36.95533	3.9054	9.463	<0.01
PG + Forbs_pg - AG + Forbs_pg	37.27871	3.9054	9.545	<0.01
Annuals Dominant_f - Annuals Dominant_ag	-62.10547	3.31384	-18.741	<0.01
Annuals Dominant_pg - Annuals Dominant_ag	-68.0625	3.31384	-20.539	<0.01

Forbs Dominant_ag - Annuals Dominant_ag	-51.36328	3.19993	-16.051	<0.01
Forbs Dominant_f - Annuals Dominant_ag	-10.30754	3.19993	-3.221	0.0571
Forbs Dominant_pg - Annuals Dominant_ag	-55.63828	3.19993	-17.387	<0.01
PG + Forbs_ag - Annuals Dominant_ag	-62.39063	3.31384	-18.827	<0.01
PG + Forbs_f - Annuals Dominant_ag	-25.44615	3.31384	-7.679	<0.01
PG + Forbs_pg - Annuals Dominant_ag	-25.12277	3.31384	-7.581	<0.01
Annuals Dominant_pg - Annuals Dominant_f	-5.95703	3.31384	-1.798	0.8159
Forbs Dominant_ag - Annuals Dominant_f	10.74219	3.19993	3.357	0.0368
Forbs Dominant_f - Annuals Dominant_f	51.79793	3.19993	16.187	<0.01
Forbs Dominant_pg - Annuals Dominant_f	6.46719	3.19993	2.021	0.674
PG + Forbs_ag - Annuals Dominant_f	-0.28516	3.31384	-0.086	1
PG + Forbs_f - Annuals Dominant_f	36.65932	3.31384	11.062	<0.01
PG + Forbs_pg - Annuals Dominant_f	36.9827	3.31384	11.16	<0.01
Forbs Dominant_ag - Annuals Dominant_pg	16.69922	3.19993	5.219	<0.01
Forbs Dominant_f - Annuals Dominant_pg	57.75496	3.19993	18.049	<0.01
Forbs Dominant_pg - Annuals Dominant_pg	12.42422	3.19993	3.883	<0.01
PG + Forbs_ag - Annuals Dominant_pg	5.67187	3.31384	1.712	0.8604
PG + Forbs_f - Annuals Dominant_pg	42.61635	3.31384	12.86	<0.01
PG + Forbs_pg - Annuals Dominant_pg	42.93973	3.31384	12.958	<0.01
Forbs Dominant_f - Forbs Dominant_ag	41.05574	3.08181	13.322	<0.01
Forbs Dominant_pg - Forbs Dominant_ag	-4.275	3.08181	-1.387	0.9653
PG + Forbs_ag - Forbs Dominant_ag	-11.02734	3.19993	-3.446	0.0276
PG + Forbs_f - Forbs Dominant_ag	25.91713	3.19993	8.099	<0.01
PG + Forbs_pg - Forbs Dominant_ag	26.24051	3.19993	8.2	<0.01
Forbs Dominant_pg - Forbs Dominant_f	-45.33074	3.08181	-14.709	<0.01
PG + Forbs_ag - Forbs Dominant_f	-52.08309	3.19993	-16.276	<0.01
PG + Forbs_f - Forbs Dominant_f	-15.13861	3.19993	-4.731	<0.01
PG + Forbs_pg - Forbs Dominant_f	-14.81523	3.19993	-4.63	<0.01
PG + Forbs_ag - Forbs Dominant_pg	-6.75234	3.19993	-2.11	0.6097
PG + Forbs_f - Forbs Dominant_pg	30.19213	3.19993	9.435	<0.01
PG + Forbs_pg - Forbs Dominant_pg	30.51551	3.19993	9.536	<0.01
PG + Forbs_f - PG + Forbs_ag	36.94448	3.31384	11.149	<0.01
PG + Forbs_pg - PG + Forbs_ag	37.26786	3.31384	11.246	<0.01
PG + Forbs_pg - PG + Forbs_f	0.32338	3.31384	0.098	1

Table S3.3: Results from Tukey post-hoc analysis of native perennial grass establishment, introduced perennial grass establishment, forb establishment and seeded forb Shannon diversity as a function of starting community composition (cluster) in unburned plots, with site as a random effect. Clusters include “AG + Forbs” (Annual Grasses + Forbs), “Annual Grasses Dominant”, “PG + Forbs” (Perennial Grasses + Forbs), and “Forbs Dominant”.

Metric	Contrast	Estimate	Std. Error	z-value	Pr(>|z|)
Native perennial grass establishment	AG + Forbs - AG Dominant	-0.0029546	0.0036283	-0.814	0.845
	PG + Forbs - AG Dominant	0.0054812	0.0039455	1.389	0.5
	Forbs Dominant - AG Dominant	-0.0003542	0.0035457	-0.1	1
	PG + Forbs - AG + Forbs	0.0084357	0.0042482	1.986	0.189
	Forbs Dominant - AG + Forbs	0.0026004	0.0038908	0.668	0.907
	Forbs Dominant - PG + Forbs	-0.0058353	0.0030487	-1.914	0.218
Introduced perennial grass establishment	AG + Forbs - AG Dominant	0.005096	0.020548	0.248	0.99448
	PG + Forbs - AG Dominant	0.101202	0.02353	4.301	<0.001
	Forbs Dominant - AG Dominant	0.069097	0.020727	3.334	0.00466
	PG + Forbs - AG + Forbs	0.096106	0.024642	3.9	<0.001
	Forbs Dominant - AG + Forbs	0.064001	0.022173	2.886	0.01976
	Forbs Dominant - PG + Forbs	-0.032105	0.017356	-1.85	0.24427
Forb establishment	AG + Forbs - AG Dominant	0.005096	0.020548	0.248	0.99448
	PG + Forbs - AG Dominant	0.101202	0.02353	4.301	<0.001
	Forbs Dominant - AG Dominant	0.069097	0.020727	3.334	0.00466
	PG + Forbs - AG + Forbs	0.096106	0.024642	3.9	<0.001
	Forbs Dominant - AG + Forbs	0.064001	0.022173	2.886	0.01976
	Forbs Dominant - PG + Forbs	-0.032105	0.017356	-1.85	0.24427
Forb Shannon diversity	AG + Forbs - AG Dominant	0.1974	0.1792	1.102	0.68331
	PG + Forbs - AG Dominant	0.3551	0.1955	1.816	0.26072
	Forbs Dominant - AG Dominant	0.5821	0.1755	3.317	0.00493
	PG + Forbs - AG + Forbs	0.1577	0.2101	0.75	0.87398
	Forbs Dominant - AG + Forbs	0.3846	0.1922	2.001	0.18365
	Forbs Dominant - PG + Forbs	0.227	0.1506	1.507	0.42727

Table S3.4: Results from Tukey post-hoc analysis of native perennial grass establishment, introduced perennial grass establishment, forb establishment and seeded forb Shannon diversity as a function of site and burn treatment, with subplot as a random effect. Estimate of burned minus unburned.

Metric	Site	Estimate	Std. Error	z-value	Pr(>|z|)
Native perennial grass establishment	Southern	0.004767	0.005751	0.829	0.96227
	Central	0.034114	0.005772	5.91	<0.001
	Northern	0.028981	0.005873	4.934	<0.001
Introduced perennial grass establishment	Southern	0.31356	0.076377	4.105	<0.001
	Central	0.288343	0.077376	3.727	0.00274
	Northern	0.281722	0.077376	3.641	0.00376
Forb establishment	Southern	26.864	11.979	2.243	0.21824
	Central	44.909	11.869	3.784	0.00218
	Northern	101.951	11.929	8.547	<0.001
Forb Shannon diversity	Southern	0.03671	0.1101	0.333	0.99946
	Central	0.521	0.1101	4.732	<0.001
	Northern	0.42684	0.11153	3.827	0.00178

APPENDIX C

SUPPLEMENTARY INFORMATION FOR CHAPTER IV

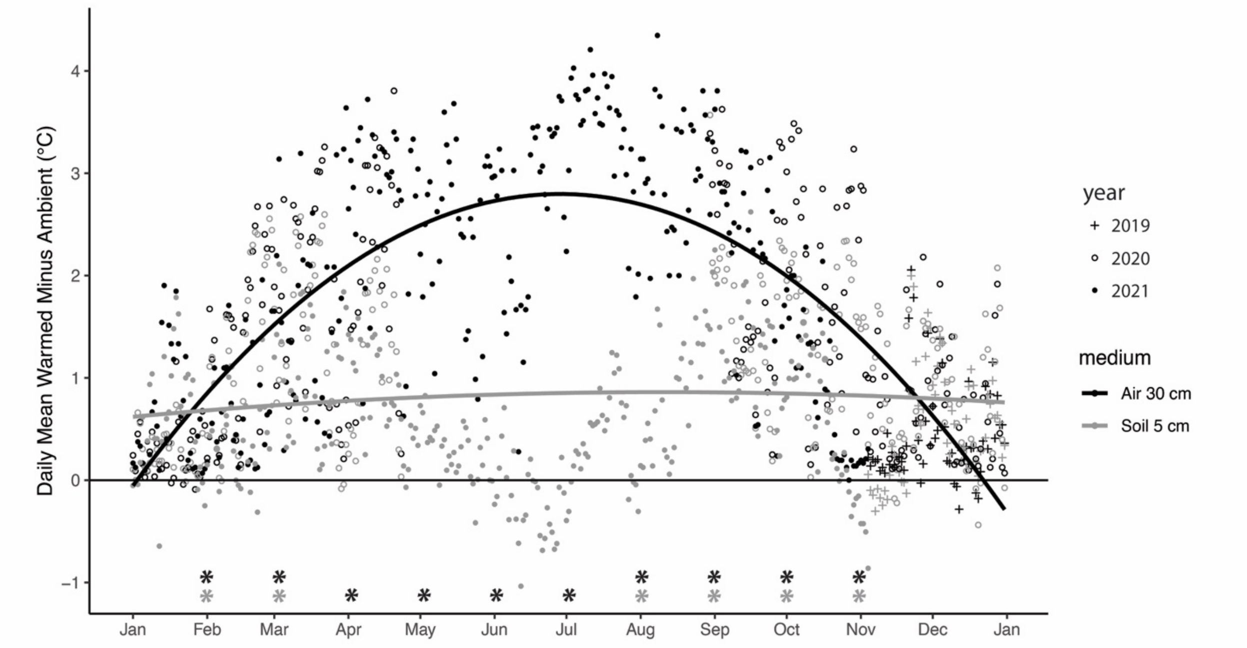


Figure S4.1: Effect of warming treatment on air and soil temperature, showing the daily deviation of the warmed plots from the ambient plots. Each point represents the difference between the mean daily warmed temperature in Celsius minus the mean daily ambient temperature. Point shape represents year and point color represents whether the measured temperature is air or soil. Months marked with asterisks (*) had significantly higher average daily air (black) or soil (grey) temperatures in the warmed treatments, using data from all three years.

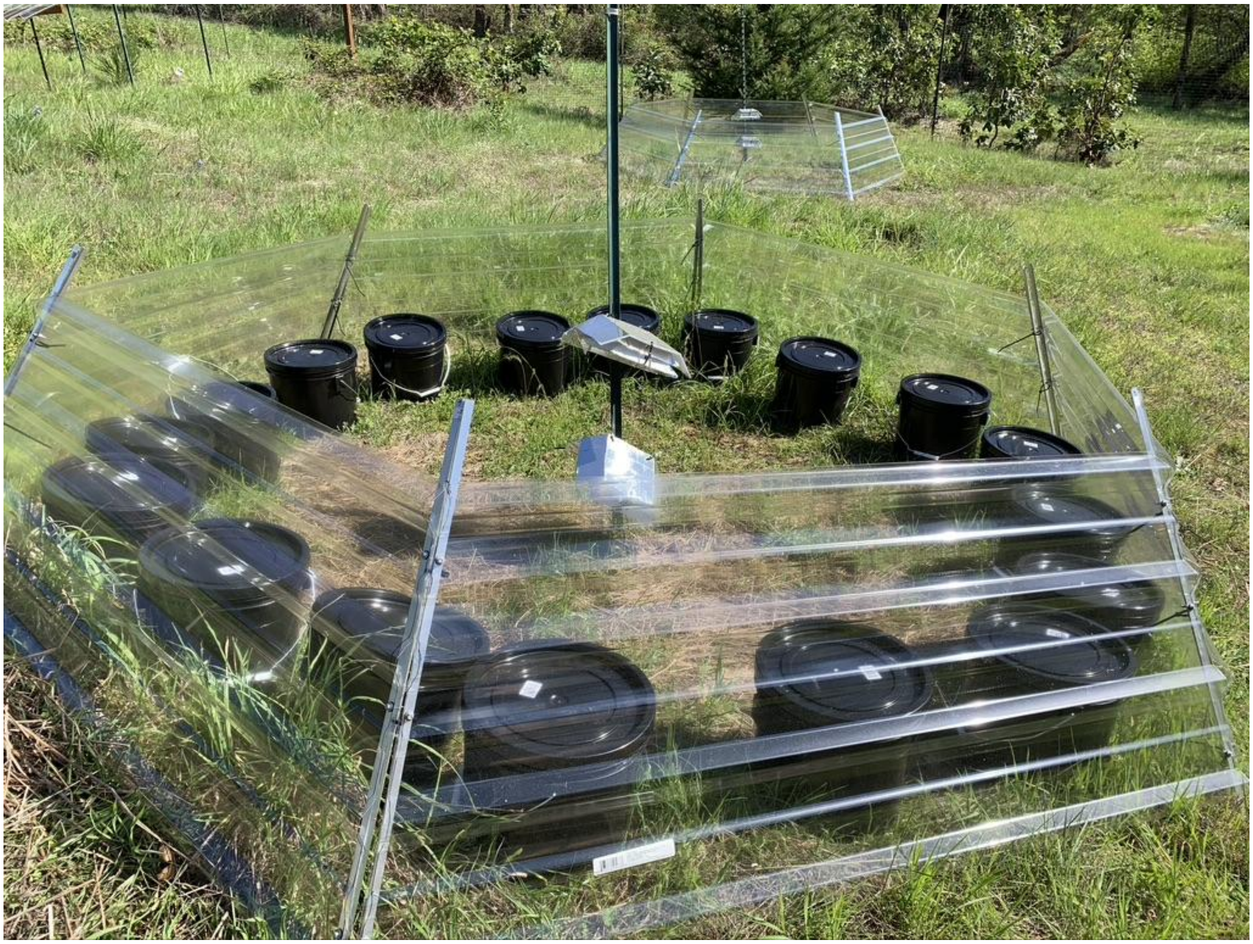


Figure S4.2. Modified passive warming chambers used to heat macroplots in this study. Design and dimensions based on (Godfree 2011). Chambers were constructed using PALRAM® polycarbonate panels, angle aluminum and zipties. We modified the original design using eighteen 3.5 gallons (63 gallons of water per chamber) buckets as thermal mass immediately inside the perimeter of each chamber.

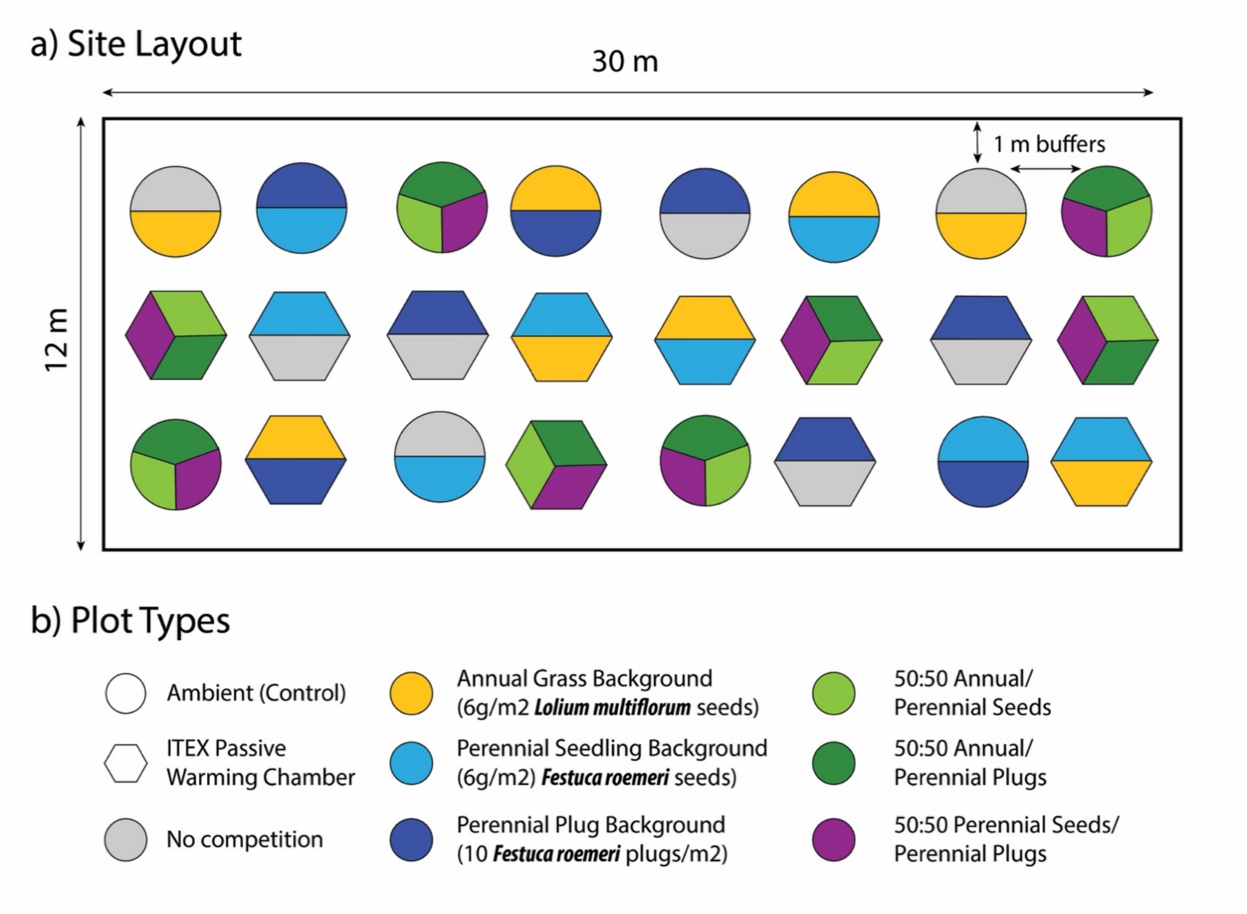


Figure S4.3. Site layout of competition subplots nested withing warming macroplots. Each combination of warming treatment and competition treatment was replicated four times. Circular plots represent ambient macroplots, while hexagonal plots represent passively warmed macroplots. Subplot color represents competition treatment. No competition and each full background treatment take up half of a macroplot (1m2), while 50:50 treatments take up one third of a macroplot (0.66m2)

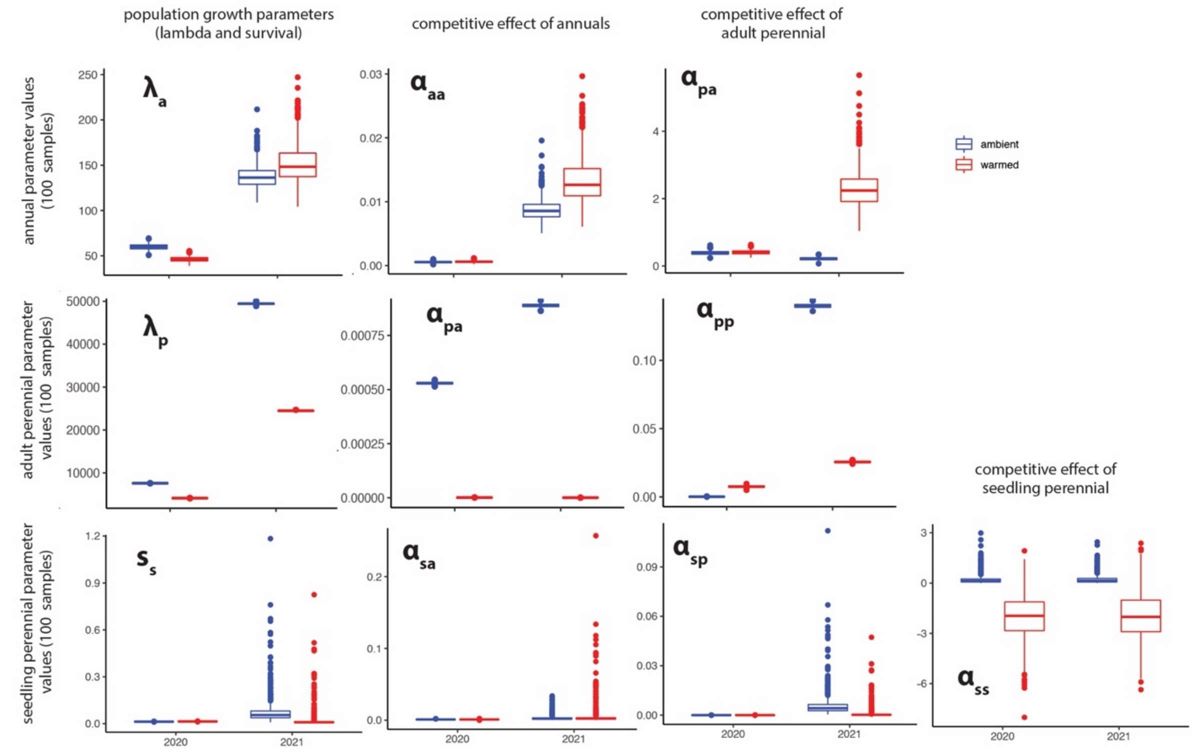
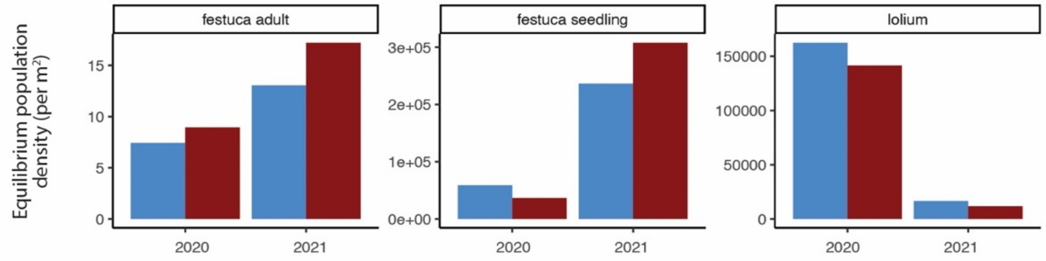
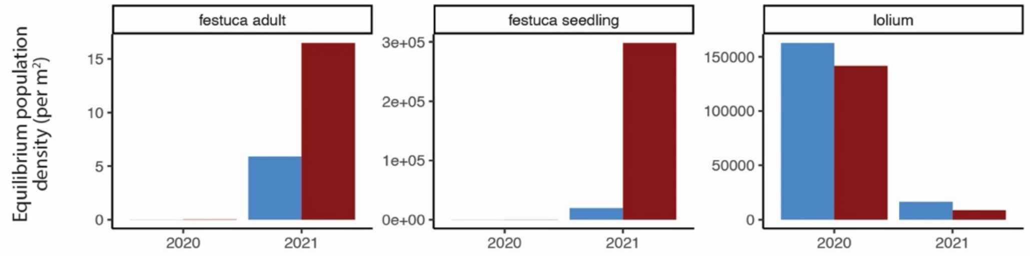


Figure S4.4. Comparison of parameter values in warmed and ambient conditions across years. Each boxplot consists of 100 posterior samples taken from model posterior distributions. Each row consists of parameters derived from one model (top: annual model, middle: adult perennial model, bottom: seedling perennial model). Each column represents a type of parameter (left: population growth parameters, middle: competitive effect of annuals on target species, right: competitive effect of adult perennial on target species, far right: competitive effect of seedling perennial on self). Blue data points represent ambient conditions and red represent warmed. Parameter labels correspond to parameters in Table S1. For simulations, only perennial fecundity, and the competitive effect of adult perennials on themselves, annuals and seedlings were allowed to vary, while all other parameters were averaged across years.

a. Equilibrium density with only interspecific competition



b. Equilibrium density with inter and intraspecific competition



c. Proportion of inter and intraspecific equilibrium density over intraspecific-only equilibrium density

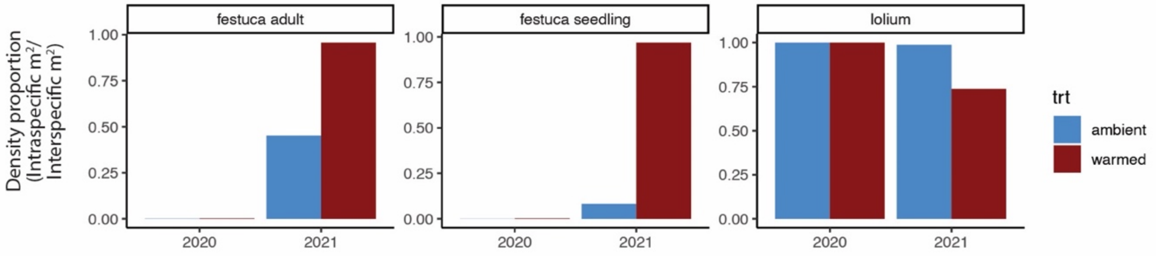


Figure S4.5. Equilibrium population size simulated using mean parameter values after 300 years of population growth in warmed and ambient conditions using data from 2020 (juvenile plugs) vs. 2021 (mature adults). a) Population in the absence of interspecific competition. b) Population with inter and intraspecific competition. c) Proportion of full intraspecific only equilibrium density under intra and interspecific competition. In contrast to Figure 2, here all parameters are allowed to vary by year (i.e. no averaging across years for seedlings and annuals).

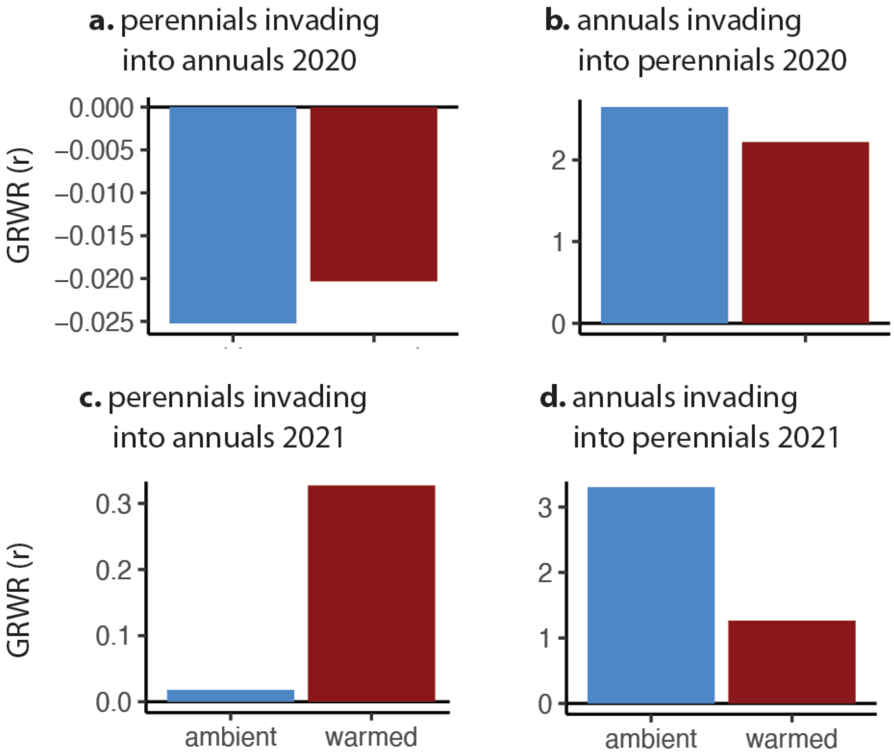


Figure S4.6. Growth rate when rare of each species in ambient (blue) and warmed (red) conditions. Warming benefits perennials at the expense of annuals. Panels a) and c) show perennial GRWR as they invade into annuals and panels b) and d) show annual GRWR as they invade into perennials. In contrast to Figure 3, here all parameters are allowed to vary by year (i.e. no averaging across years for seedlings and annuals). In 2020 juvenile perennials are competitively excluded under all climate conditions, while in 2021 mature

Table S4.1: All parameters fit or derived from literature. Germination and seed survival terms were only used to calculate seedbank survival. Because models were based on seeds in and out, competition terms, fecundity and perennial seed survival to adulthood terms all implicitly included the germination stage. All fit parameters initially varied by year for model fitting, but those marked 'no' were subsequently averaged across years. Priors were set to predict pre-log-transformed posteriors, with slope representing the effect of warming. Ambient estimates were calculated as exp(intercept), and warmed estimates as exp(intercept + slope).

Model	Model family	Parameter	Description	Fit or literature	Literature value	Vary by warming	Vary by year	prior
Annuals	Poisson	la	annual fecundity	fit	–	yes	no	intercept: normal(9, 1) slope: normal(0, 1)
		aaa	intraspecific per capita annual competition	fit	–	yes	no	intercept: normal(-2, 1) slope: normal(0, 1)
		aap	per capita competitive effect of adult perennials on annuals	fit	–	yes	yes	intercept: normal(-2, 1) slope: normal(0, 1)
		ga	annual germination (only used for seedbank)	Ghersa 1984	0.11	no	no	–
		sa	annual seed survival (only used for seedbank)	Ghersa 1984	0.89	no	no	–
Perennial seeds	Poisson	lp	adult perennial fecundity	fit	–	yes	yes	intercept: normal(4, .5) slope: normal(0, 1)
		apa	per capita competitive effect of annuals on adult perennials	fit	–	yes	yes	intercept: normal(-2, 1) slope: normal(0, 1)
		app	intraspecific per capita adult perennial competition	fit	–	yes	yes	intercept: normal(-2, 1) slope: normal(0, 1)
		gs	perennial germination (only used for seedbank)	Fiegner 2007	0.63	no	no	–
		ss	perennial seed survival (only used for seedbank)	Fiegner 2007	0.1	no	no	–
Perennial adults	Gaussian	ssp	perennial seed survival to adulthood	fit	–	yes	no	intercept: normal(-4.5, 1) slope: normal(0, 1)
		ass	intraspecific per capita seedling perennial competition	fit	–	yes	no	intercept: normal(-2, 1) slope: normal(0, 1)
		asa	per capita competitive effect of annuals on seedling perennials	fit	–	yes	no	intercept: normal(-2, 1) slope: normal(0, 1)
		asp	per capita competitive effect of adult on seedling perennials	fit	–	yes	yes	intercept: normal(-2, 1) slope: normal(0, 1)
		sp	adult perennial interannual survival	Fiegner 2007	0.975	no	no	–

APPENDIX D

SUPPLEMENTARY INFORMATION FOR CHAPTER V

Figure S5.1: Orchard and block locations. a) Orchards are located at two sites north of Salem, Oregon. At location b1) is the 60-year-old orchard. At location b2) is the 40-year-old orchard as well as the 15-year-old orchard. Blocks are represented by red triangles, and in the 40 and 60-year-old orchards they are at least two rows of trees away from the orchard edge. The 15-year-old orchard is made up of only two rows of trees, so blocks have variable edge conditions. To the North, an open road leads to no additional shading. To the south of blocks 1-3, the 40-year-old orchard affects approximately 60% of the conventional cover crop and control subplots. To the south of blocks 4-6, a Douglas-fir plantation affects the same area. Canopy cover in the Douglas-fir plantation is approximately 90%.

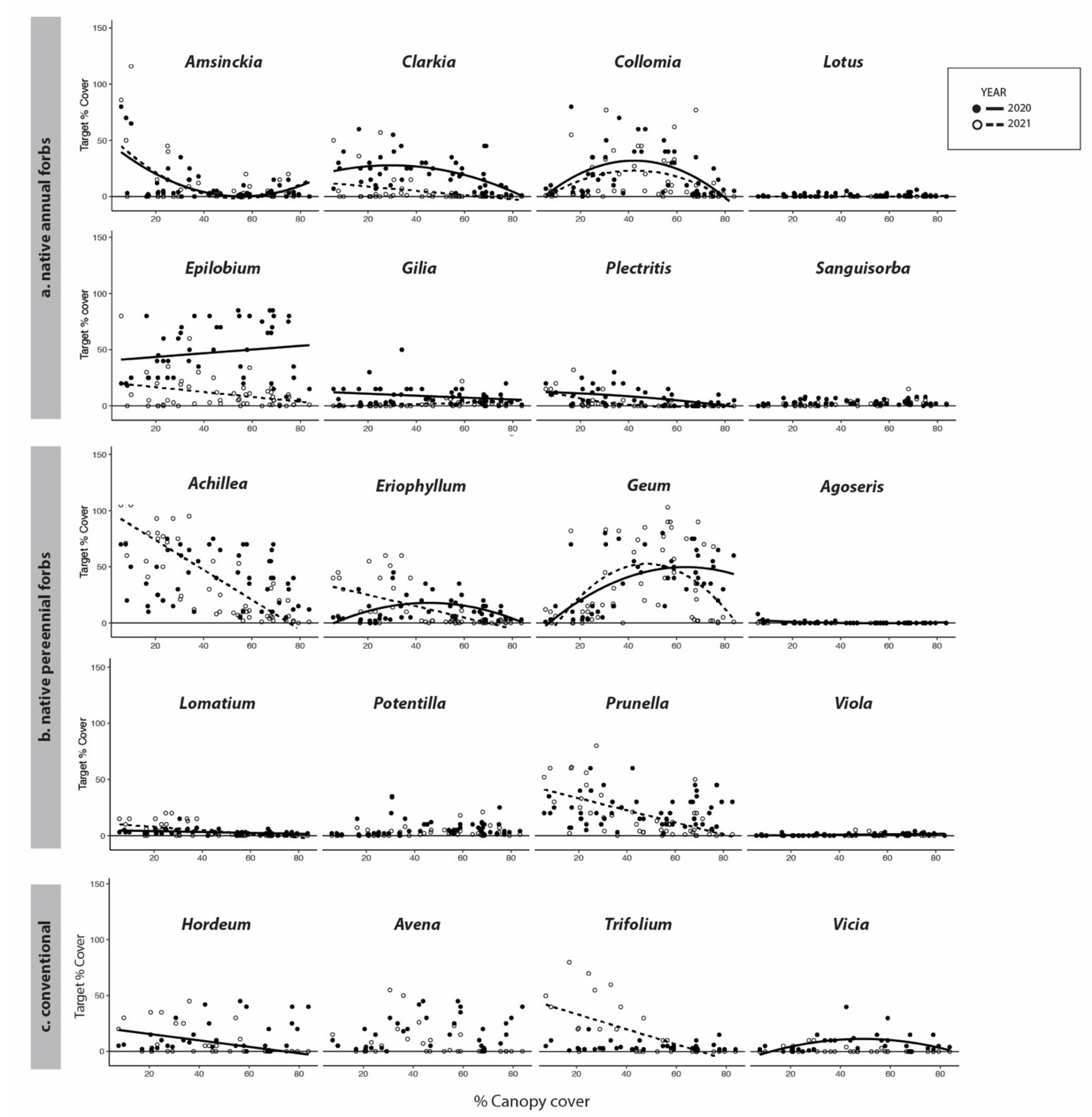


Figure S5.2. Individual species vegetation cover responses to hazelnut canopy cover each year across all three orchards. Data from 2020 is shown with closed circles and solid lines, data from 2021 as open circles and dashed lines. Regression lines are drawn for significant polynomial or linear correlations only (p<.05). If the quadratic term was significant, a quadratic relationship was plotted, otherwise significant linear relationships are shown. Species demonstrate a wide variety of cover and survival responses, with a few very successful species in each seed mix. Species also demonstrate a wide range of responses to canopy cover, with many performing best at low or intermediate canopy cover.

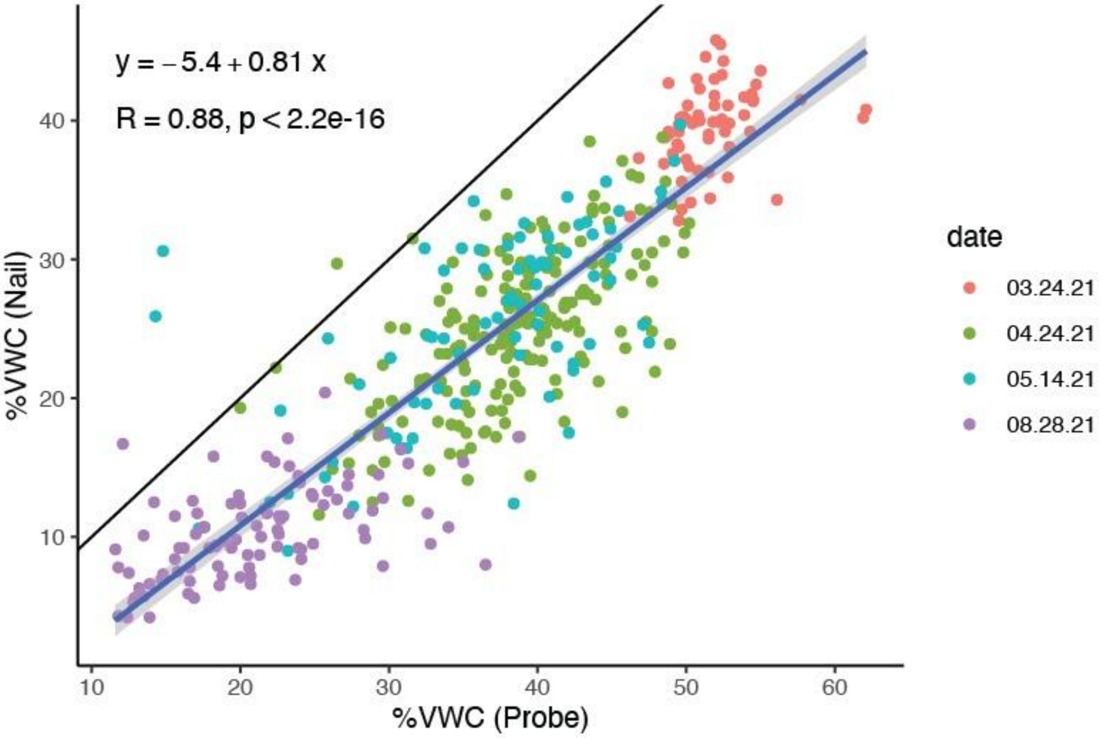


Figure S5.3: Linear regression calibration (blue line) between nail and probe readings for soil moisture data compared to a to one fit line (black line). Point color represents the date moisture readings were taken. Nails were used when available, otherwise probe data filled in gaps. Nail readings were adjusted given the fit line drawn here.

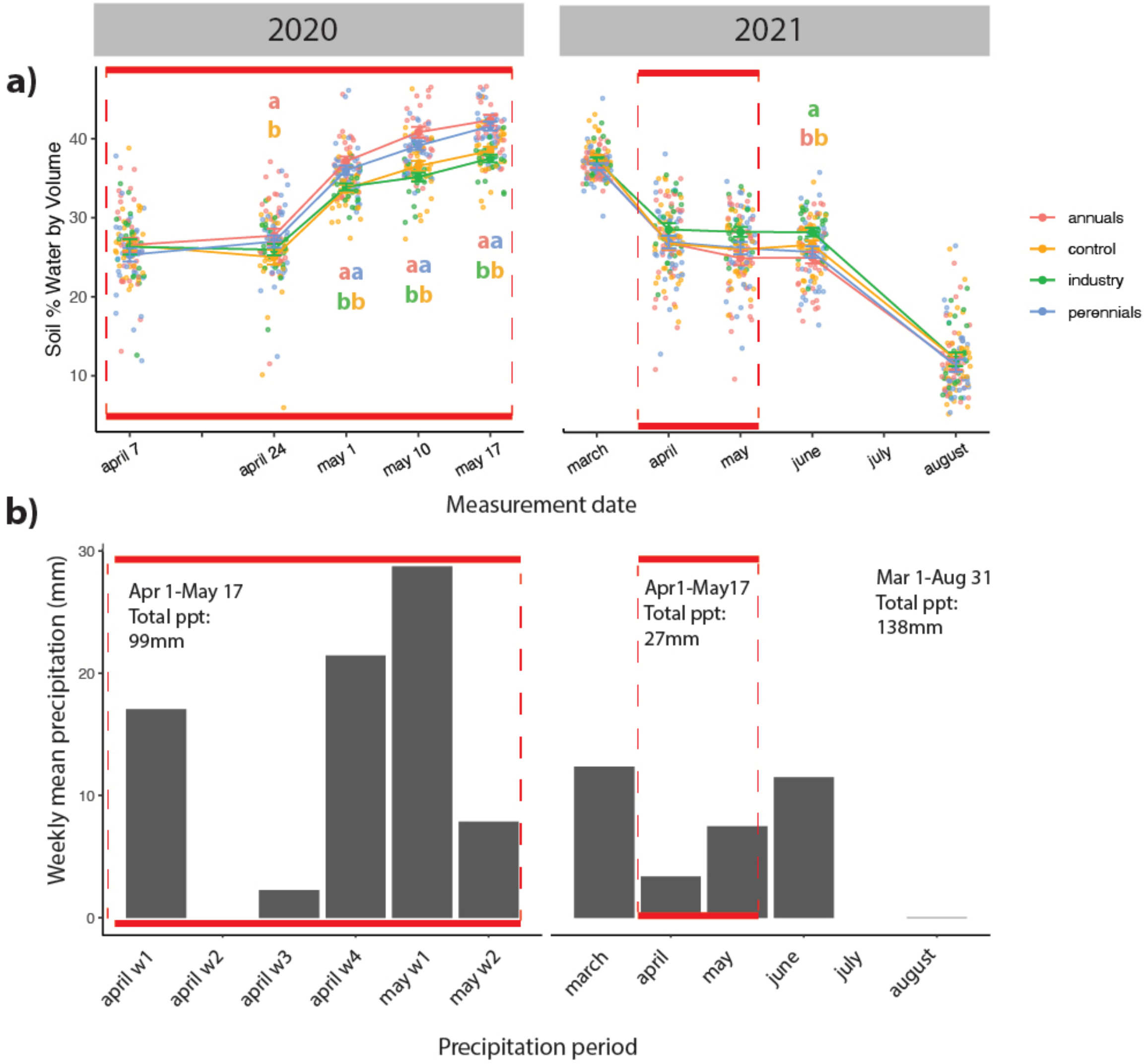


Figure S5.4: Cover crop seed mix type can have small effects on soil moisture, but these vary across years. a) Soil volumetric water content (VWC) in 2020 and 2021. In 2020 VWC was monitored in subplots weekly from April 7 to May 17. In 2021, VWC was monitored monthly from March through August. Transparent points represent individual seeding plots, and solid points and lines represent means with error bars of one standard error. Point and line color represents seed mix. Red boxes represent equivalent time periods in 2020 and 2021. Letters represent statistically significant different groups of soil moisture by seed mix within, but not across, months and are colored by seed mix. b) Mean weekly precipitation modeled by PRISM during time periods that correspond to VWC monitoring above. Total precipitation from corresponding time periods of April 1 through May 17 is shown inside red boxes, while the total precipitation over the 2021 monitoring period of March 1 through August 31 is shown outside the box.

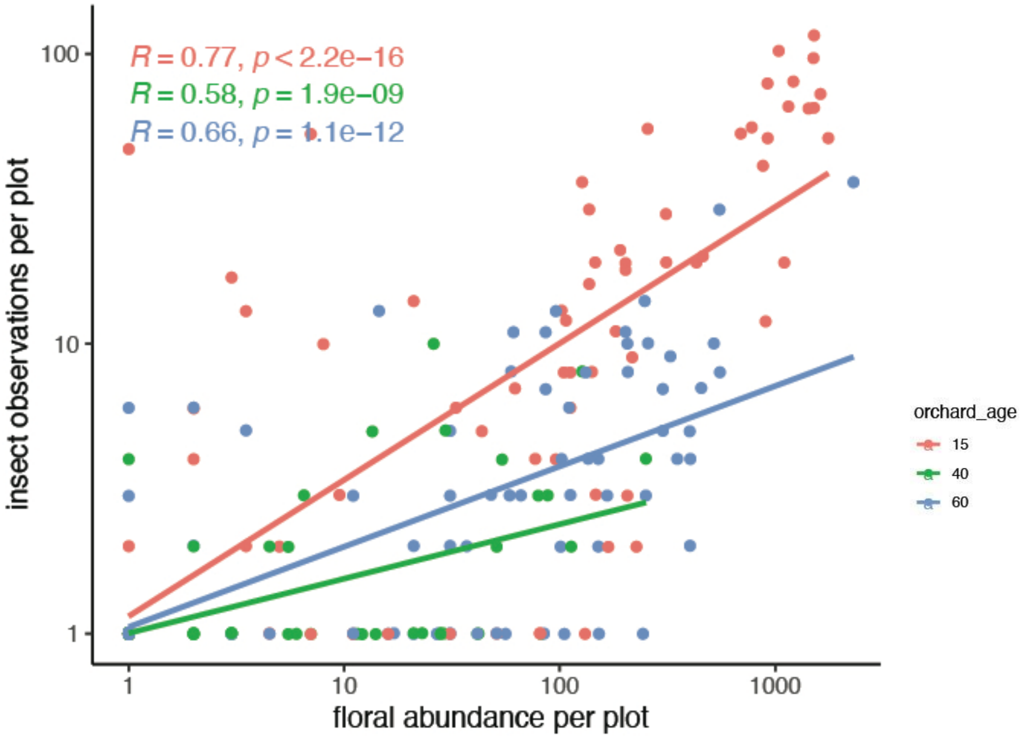


Figure S5.5: Insect observations (visitations) are positively correlated with floral abundance across all three orchard ages. The slope and R value of this relationship declines from the most open (15-year-old) to the most shaded (40-year-old) orchard.

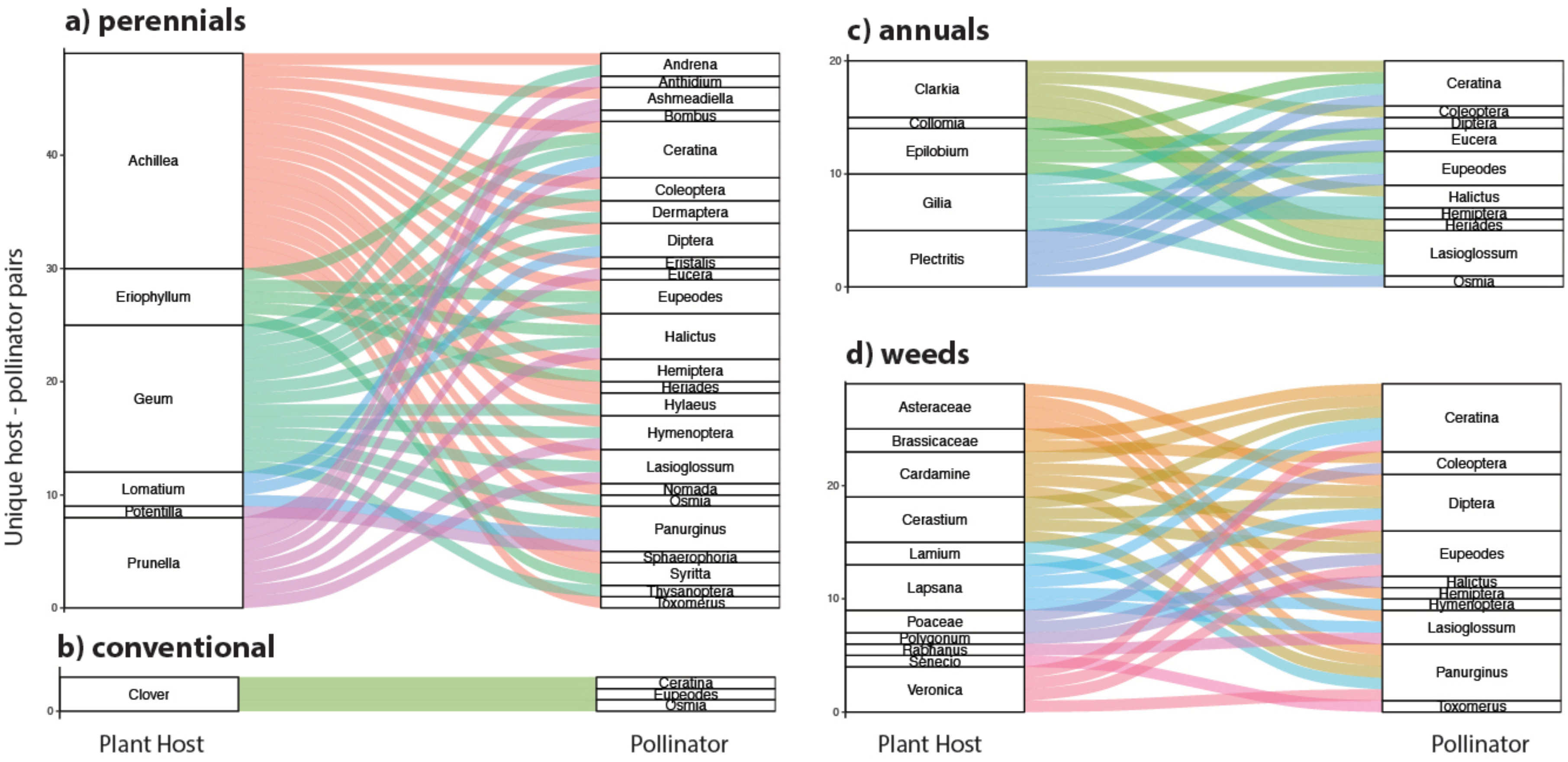


Figure S5.6: Number of unique pollinators collected from flowers of individual plant species in annual, industry, perennial and weeds. Height of taxa labels and width of rivers correspond to total of visitations.

Table S5.1: Standard Willamette Valley hazelnut orchard management activities and timing, as practiced by Lane-Massee Farms. Typical timeframe refers to the range of dates or conditions during which an activity normally takes place. The allowable timeframe represents the broader period or conditions which an activity could take place without having negative impacts to production. Year 1 and 2 dates completed refer to when these activities took place at the farms during our experiment. * These activities were excluded from all of our plots. **Limitation of these activities defined our management treatments. i.e. The second and third flail were excluded from unmanaged plots, and the scraping was excluded from flailed plots.

Orchard activities in order of typical completion	Description	Typical timeframe for activity completion	Allowable timeframe for activity completion	Year 1 dates completed	Year 2 dates completed	Notes
Pruning	Removed diseased wood and shape trees	12/1 - 2/20	11/1 - 3/1	12/15/19 - 1/31/20	12/28/21 - 2/28/21	Ice storm in 2021 extended pruning, and shredding season, damage cleanup.
Shredding	Chip pruned materials, remove logs from orchard	1/1/ - 3/31	11/1 - 4/1	2/1/20- 2/20/20	2/12/21 - 3/15/21	
Hazelnut leaf emergence	Leaves emerge from bud	2/15 - 3/15	n/a	2/21/20	3/1/21	
Spray suckers (herbicide)*	Paraquat	3/31 - 7/20	2/15 - 8/31	2/26/20 - 2/28/20 & 5/1/20 & 5/13/20	6/30	Requires leaf emergence, excluded from experimental plots to allow cover crops to persist.
First blight spray (fungicide)	Chlorothalonil	3/1 - 3/20	bud break - 4/30	3/9/20 - 3/10/20	3/11/21 - 3/12/21	Not lethal to adult bees, but larval side effects have been studied.
Apply fertilizer	Fertilizer Blend (40-0-0-6S) ground broadcast pellets	Between blight sprays	Any time besides nut fall	3/20	3/20	Optional.
Second blight spray (fungicide)	Flint	3/15 - 4/15	<2 weeks after first blight spray	3/21/20 - 3/22/20	3/26/21 - 3/27/21	As needed. Not lethal to adult bees, but potential larval effects.

Spray for oblique banded leaf rollers (insecticide)	Lorsban Advanced (LA), Javalin (J)	3/25 - 4/25	3/15 - 5/15	5/14/20 - 5/15/20 (LA)	3/26/21 - 3/27/21 (J) 4/23/21 - 4/24/21 (J)	Lorsban Advanced (LA, a.k.a Chlorpyrifos) is a non-selective insecticide last used on site in 2020. Will be banned in Oregon in 2023. Javalin is only lethal to Leptodoptera larvae.
Third & fourth blight spray (fungicide)	Aproach and Propicon applied as "Stratigo"	4/10 - 4/15	<2 weeks after second blight spray	n/a	4/23/21 - 4/24/21	As needed. Propicon and Aproach not listed to have effects on pollinators.
Full canopy	Approximate max canopy cover achieved	5/15 - 6/15	n/a	~5/10/20	~5/10/21	
Apply Boron (fertilizer)	Ground spray, liquid	5/15 - 6/1	5/1 - 6/25	5/15/20 - 5/20/20	5/22/21 - 5/23/21	Optional.
First flail*	Chip shredded materials into fine mulch and terminate vegetation	6/20 - 9/1	4/1 - 9/10	6/20/20 - 7/20/20	5/1/21 - 8/25/21	Excluded from plots to extend our ability to evaluate phenology and pollinator visitations to later flowering species
Scrape orchard**	Level orchard floor surface	7/1 - 7/31	6/1 - 9/10	7/10/20 - 7/31/20	7/1/21 - 7/20/21	Approximately concurrent with second flail.
Spray for filbert worm (insecticide)	Guardian & Asana XL (AXL)	7/5 - 8/10	6/15 - 8/15 (pre-harvest interval)	7/10/20(G) 7/13/20 - 7/14/20 (AXL)	7/2 - 7/7 (G) & 7/27 - 8/1 (AXL)	Asana XL is highly toxic to bees exposed to direct treatment or residues on forage.
Spray for aphids (insecticide)	Transform	7/5 - 8/10	6/15 - 8/15 (pre-harvest interval)	n/a	7/2/21 - 7/7/21	Toxic to bees within 3 hrs of application.
Spray for stink bug (insecticide)	Brigade 2EC	7/5 - 8/10	6/15 - 8/15 (pre-harvest interval)	n/a	7/2/21 - 7/7/21	Toxic to bees, direct and forage residue.
Second flail**	Chip shredded materials into fine mulch and terminate vegetation	7/1 - 7/31	6/1 - 9/10	8/25/20 - 8/27/20	7/22/21 - 8/5/21	Delayed beyond typical to allowable timeframe in 2020.
Final flail**	Break down blank nuts and any remaining vegetation	8/20 - 9/1	8/10 - 9/10	8/15/20 - 9/1/20	8/25/21 - 8/30/21	Depends on nut-crack blank-count method (when three good nuts are present).

Nut fall	Orchard activities stop	9/1 - 10/20	n/a	9/1/20 - 10/15/20	9/1/21 - 10/10/21	
Harvest	Harvest nuts	9/20 - 10/20	when >90% nuts fall, good weather window	9/26/20 - 10/10/20	9/24/21 - 10/3/21	Immediately before harvest, any remaining vegetation (i.e. in unmanaged plots) was clipped to 15cm.
Foliar fertilizer application	Apply when majority of leaves are still on trees. Fertilizer Blend (5-11-11, 0.2 UD, 1.3 B)	10/15 - 11/15	after harvest, before majority leaf fall	10/23/20 - 10/24/20	11/1/21 - 11/3/21	Application optional, though highly recommended.
Leaf drop	Estimate of leaf drop duration	9/25 - first hard freeze	n/a	9/25/20 - 12/31/20	10/1/21 - 12/26/21	
Push out dead trees	Push out dead trees, usually from blight or rot	10/20 - 11/20	after harvest - pruning starts	10/30	11/6	

Table S5.2: Individual cover crop mixed model responses to canopy cover.

Seed mix	Species	Year	Linear coefficient	Linear p-val	Quadratic coefficient	Quadratic p-val	Regression
Native annuals	Amsinckia	2020	-52.6	**<0.001**	31.9	**0.028**	Polynomial
		2021	-60.7	**0.001**	45.5	**0.017**	Polynomial
	Clarkia	2020	-39.4	**0.002**	-43.2	**0.001**	Polynomial
		2021	-26.4	**0.019**	-0.368	0.97	Linear
	Collomia	2020	-7.59	**0.612**	-98.8	**<0.001**	Polynomial
		2021	6.30	0.690	-86.3	**<0.001**	Polynomial
	Acmispon	2020	0.967	0.537	-2.35	0.137	None
		2021	0.917	0.054	-0.40	0.386	None
	Epilobium	2020	40.1	0.093	-76.6	**0.002**	Polynomial
		2021	-31.1	**0.046**	-4.57	0.764	Linear
	Gilia	2020	-18.8	**0.013**	-6.30	0.402	Linear
		2021	11.1	**0.001**	0.228	0.946	Linear
	Plectritis	2020	-30.4	**<0.001**	-2.23	-2.23	Linear
		2021	-21.7	**<0.001**	12.9	**0.015**	Polynomial
	Sanguisorba	2020	-1.65	0.475	-4.04	0.084	None
		2021	8.82	**<0.001**	-0.937	0.685	Linear
Native perennials	Achillea	2020	-16.7	0.454	-42.8	**0.060**	Polynomial
		2021	-229.9	**<0.001**	16.2	0.506	Linear
	Eriophyllum	2020	12.8	0.146	-48.7	**<0.001**	Polynomial
		2021	-83.4	**<0.001**	7.97	0.584	Linear
	Geum	2020	115.7	**<0.001**	-62.7	**<0.001**	Polynomial
		2021	59.7	**0.024**	-143.4	**<0.001**	Polynomial
	Agoseris	2020	-3.402	**0.003**	1.86	0.103	Linear

		2021	-	-	-	-	NA (no data)
	Lomatium	2020	-5.34	**0.027**	-4.44	0.066	Linear
		2021	-28.23	**<0.001**	7.018	0.122	Linear
	Potentilla	2020	13.7	**0.024**	-19.6	**0.001**	Polynomial
		2021	8.95	0.117	-16.6	**0.005**	Polynomial
	Prunella	2020	-3.81	0.772	14.4	0.286	None
		2021	-97.7	**<0.001**	49.9	**<0.001**	Polynomial
	Viola	2020	3.48	**<0.001**	-0.31	0.737	Linear
		2021	1.032	0.075	-0.185	0.748	None
Conventional cover crops	Hordeum	2020	19.6	0.109	12.8	0.296	None
		2021	-37	**<0.001**	-7.65	0.43	Linear
	Avena	2020	20.4	0.117	-22.9	0.085	None
		2021	-21.5	0.069	-25.0	**0.039**	Polynomial
	Trifolium	2020	-1.09	0.802	1.66	0.702	None
		2021	-87.0	**<0.001**	20.1	0.255	Linear
	Vicia	2020	3.88	0.589	-22.0	**0.005**	Polynomial
		2021	-5.41	**0.025**	0.072	0.975	Linear

Table S5.3: Tukey-adjusted contrasts of seed mix effects on soil moisture from mixed modeling approach.Contrasts are given for each time period in each year.

Year	Time Period	Contrast	Estimate	SE	df	t-ratio	p-value
2020	Week 1	annuals - control	0.0455	0.993	107	0.046	1
		annuals - industry	0.2333	1.11	107	0.21	0.9967
		annuals - perennials	1.2455	0.993	107	1.254	0.5941
		control - industry	0.1879	1.11	107	0.169	0.9983
		control - perennials	1.2	0.993	107	1.208	0.623
		industry - perennials	1.0121	1.11	107	0.911	0.7988
	Week 3	**annuals - control**	**2.704**	**0.965**	**107**	**2.802**	**0.0303**
		annuals - industry	1.763	1.079	107	1.634	0.3643
		annuals - perennials	0.742	0.965	107	0.769	0.8684
		control - industry	-0.942	1.079	107	-0.872	0.8191
		control - perennials	-1.962	0.965	107	-2.033	0.1824
		industry - perennials	-1.021	1.079	107	-0.946	0.7801
	Week 4	**annuals - control**	**3.445**	**0.604**	**107**	**5.7**	**<.0001**
		annuals - industry	**3.223**	**0.676**	**107**	**4.769**	**<.0001**
		annuals - perennials	1.121	0.604	107	1.855	0.2538
		control - industry	-0.223	0.676	107	-0.33	0.9876
		control - perennials	**-2.324**	**0.604**	**107**	**-3.845**	**0.0012**
		industry - perennials	**-2.102**	**0.676**	**107**	**-3.11**	**0.0126**
	Week 5	**annuals - control**	**4.27**	**0.711**	**107**	**6.002**	**<.0001**
		annuals - industry	**5.66**	**0.795**	**107**	**7.118**	**<.0001**

		annuals - perennials	1.69	0.711	107	2.379	0.0874
		control - industry	1.39	0.795	107	1.75	0.3033
		control - perennials	**-2.58**	**0.711**	**107**	**-3.623**	**0.0025**
		industry - perennials	**-3.97**	**0.795**	**107**	**-4.991**	**<.0001**
	Week 6	**annuals - control**	**3.879**	**0.605**	**107**	**6.407**	**<.0001**
		annuals - industry	**4.842**	**0.677**	**107**	**7.154**	**<.0001**
		annuals - perennials	0.761	0.605	107	1.256	0.5926
		control - industry	0.964	0.677	107	1.424	0.4875
		control - perennials	**-3.118**	**0.605**	**107**	**-5.151**	**<.0001**
		industry - perennials	**-4.082**	**0.677**	**107**	**-6.03**	**<.0001**
2021	March	annuals - control	-1.002	0.456	117	-2.197	0.1301
		annuals - industry	-0.635	0.51	117	-1.245	0.5995
		annuals - perennials	0.127	0.456	117	0.279	0.9923
		control - industry	0.367	0.51	117	0.72	0.889
		control - perennials	1.129	0.456	117	2.476	0.069
		industry - perennials	0.762	0.51	117	1.495	0.4437
	April	annuals - control	0.0436	0.788	117	0.055	0.9999
		annuals - industry	-1.6947	0.881	117	-1.923	0.224
		annuals - perennials	-0.1268	0.788	117	-0.161	0.9985
		control - industry	-1.7383	0.881	117	-1.973	0.2043
		control - perennials	-0.1704	0.788	117	-0.216	0.9964
		industry - perennials	1.5679	0.881	117	1.779	0.2885

May	annuals - control	0.0436	0.788	117	0.055	0.9999
	annuals - industry	-1.6947	0.881	117	-1.923	0.224
	annuals - perennials	-0.1268	0.788	117	-0.161	0.9985
	control - industry	-1.7383	0.881	117	-1.973	0.2043
	control - perennials	-0.1704	0.788	117	-0.216	0.9964
	industry - perennials	1.5679	0.881	117	1.779	0.2885
June	annuals - control	-1.636	0.71	117	-2.303	0.1032
	annuals - industry	**-3.221**	**0.794**	**117**	**-4.055**	**0.0005**
	annuals - perennials	-0.73	0.71	117	-1.028	0.7336
	control - industry	-1.585	0.794	117	-1.996	0.1955
	control - perennials	0.906	0.71	117	1.275	0.5804
	industry - perennials	**2.491**	**0.794**	**117**	**3.136**	**0.0115**
August	annuals - control	-0.57336	0.91	117	-0.63	0.9221
	annuals - industry	-0.58292	1.02	117	-0.573	0.9399
	annuals - perennials	0.22125	0.91	117	0.243	0.9949
	control - industry	-0.00956	1.02	117	-0.009	1
	control - perennials	0.79461	0.91	117	0.874	0.8185
	industry - perennials	0.80417	1.02	117	0.791	0.8585

Table S5.4: Tukey-adjusted contrasts of estimated floral abundance by seed mix, month, and orchard from mixed modeling approach.

Treatment	Data Subset	Contrast	Estimate	SE	df	t-ratio	p-value
Seedmix*Orchard age	15 year old orchard	annuals_15 - industry_15	49.99	37.3	457	1.341	0.9185
		annuals_15 - perennials_15	-217.84	31.2	457	-6.992	**<.0001**
		industry_15 - perennials_15	-267.83	37.3	457	-7.183	**<.0001**
	40 year old orchard	annuals_40 - industry_40	11.07	38.7	457	0.286	1
		annuals_40 - perennials_40	-6.42	31.9	457	-0.201	1
		industry_40 - perennials_40	-17.49	38.7	457	-0.452	1
	60 year old orchard	annuals_60 - industry_60	43.93	37.3	457	1.178	0.9608
		annuals_60 - perennials_60	-76.05	31.2	457	-2.441	0.2643
		industry_60 - perennials_60	-119.99	37.3	457	-3.218	**0.037**
	native annuals	annuals_15 - annuals_60	24.25	31.2	457	0.778	0.9974
		annuals_15 - annuals_40	58.22	31.5	457	1.846	0.6511
		annuals_60 - annuals_40	33.97	31.5	457	1.077	0.9772
	industry (conventional cover crops)	industry_15 industry_60	18.19	42.2	457	0.431	1
		industry_15 - industry_40	19.29	43.2	457	0.447	1
		industry_60 - industry_40	1.1	43.2	457	0.025	1
	native perennials	**perennials_15 - perennials_60**	166.04	31.2	457	5.33	**<.0001**
		perennials_15 - perennials_40	269.64	31.5	457	8.551	**<.0001**
		perennials_60 - perennials_40	103.6	31.5	457	3.286	**0.03**

Month*Orchard age (note: only significant month by orchard age interactions shown)	annuals, 15 year old orchard	**4 - 8**	-351.53	55.5	56	-6.333	**<.0001**
		4 - 5	-322.06	55.5	56	-5.802	**<.0001**
		6 - 8	-300.61	55.5	56	-5.416	**<.0001**
		7 - 8	-324.67	68	56	-4.776	**0.0001**
	annuals, 40 year old orchard	**4 - 6**	-21.359	3.12	53	-6.856	**<.0001**
		5 - 6	-20.947	3.12	53	-6.723	**<.0001**
		6 - 7	18.942	4.31	53	4.392	**0.0005**
		6 - 8	20.275	4.31	53	4.701	**0.0002**
	annuals, 60 year old orchard	**4 - 6**	-124.861	40.2	56	-3.109	**0.0236**
		5 - 6	-124.278	40.2	56	-3.095	**0.0246**
	perennials, 15 year old orchard	**4 - 6**	-844.64	70.2	56	-12.037	**<.0001**
		5 - 6	-785.67	70.2	56	-11.197	**<.0001**
		6 - 7	791.7	99.2	56	7.978	**<.0001**
		6 - 8	804.37	99.2	56	8.106	**<.0001**
	industry, 15 year old orchard	**4 - 6**	-60.96	15.1	28	-4.037	**0.0011**
		5 - 6	-56.79	15.1	28	-3.761	**0.0022**
	industry 60 year old orchard	**4 - 6**	-10.333	3.67	28	-2.814	**0.0233**
		5 - 6	-10.125	3.67	28	-2.757	**0.0266**

Table S5.5: Tukey-adjusted contrasts of pollinator visitation by seed mix, month, and orchard from mixed modeling approach.

Treatment	**Data Subset**	**Contrast**	**Estimate**	**SE**	**df**	**t-ratio**	**p-value**
Seedmix	all data	annuals - industry	1.059	1.01	669	1.048	0.7212
		annuals - perennials	-3.768	0.84	669	-4.487	**0.0001**
		annuals - control	1.894	0.84	669	2.255	0.1097
		industry - perennials	-4.827	1.01	669	-4.776	**<.0001**
		industry - control	0.835	1.01	669	0.826	0.8421
		perennials - control	5.662	0.84	669	6.742	**<.0001**
Orchard age	all data	**15 - 60**	5.269	0.758	670	6.952	**<.0001**
		15 - 40	6.218	0.758	670	8.204	**<.0001**
		60 - 40	0.949	0.758	670	1.252	0.4232
Seedmix*Orchard age	15 year old orchard	**annuals_15 - control_15**	4.3636	1.31	661	3.325	**0.0435**
		annuals_15 - industry_15	1.346	1.57	661	0.858	0.9994
		annuals_15 - perennials_15	-9.8485	1.31	661	-7.505	**<.0001**
		control_15 - industry_15	-3.0177	1.57	661	-1.925	0.7434
		control_15 - perennials_15	-14.2121	1.31	661	-10.83	**<.0001**
		industry_15 - perennials_15	-11.1945	1.57	661	-7.14	**<.0001**
	40 year old orchard	annuals_40 - industry_40	0.3535	1.57	661	0.225	1
		annuals_40 - perennials_40	-0.3939	1.31	661	-0.3	1
		control_40 - industry_40	0.2626	1.57	661	0.168	1
		control_40 - perennials_40	-0.4848	1.31	661	-0.369	1
		industry_40 - perennials_40	-0.7475	1.57	661	-0.477	1
		annuals_40 - control_40	0.0909	1.31	661	0.069	1

	60 year old orchard	annuals_60 - control_60	1.2273	1.31	661	0.935	0.9987
		annuals_60 - industry_60	1.5	1.57	661	0.957	0.9984
		annuals_60 - perennials_60	-1.0606	1.31	661	-0.808	0.9997
		control_60 - industry_60	0.2727	1.57	661	0.174	1
		control_60 - perennials_60	-2.2879	1.31	661	-1.743	0.8473
		industry_60 - perennials_60	-2.5606	1.57	661	-1.633	0.8964
	native annuals	annuals_15 - annuals_60	3.6515	1.31	661	2.783	0.1898
		annuals_15 - annuals_40	4.9091	1.31	661	3.741	**0.0107**
		annuals_60 - annuals_40	1.2576	1.31	661	0.958	0.9984
	industry (conventional cover crops)	industry_15 - industry_60	3.8056	1.78	661	2.142	0.5927
		industry_15 - industry_40	3.9167	1.78	661	2.204	0.5471
		industry_60 - industry_40	0.1111	1.78	661	0.063	1
	control	control_15 - control_60	0.5152	1.31	661	0.393	1
		control_15 - control_40	0.6364	1.31	661	0.485	1
		control_60 - control_40	0.1212	1.31	661	0.092	1
	native perennials	**perennials_15 - perennials_60**	12.4394	1.31	661	9.479	**<.0001**
		perennials_15 - perennials_40	14.3636	1.31	661	10.946	**<.0001**
		perennials_60 - perennials_40	1.9242	1.31	661	1.466	0.9491
Month*Orchard age (note: only significant month by orchard age interactions shown)	industry, 15 year old orchard	**4 - 6**	-10.333	2.08	28	-4.963	**0.0001**

		5 - 6	-10.667	2.08	28	-5.124	**0.0001**
	perennial, 15 year old orchard	**4 - 6**	-45.389	3.84	56	-11.822	**<.0001**
		5 - 6	-46	3.84	56	-11.981	**<.0001**
		6 - 7	38.167	5.43	56	7.029	**<.0001**
		6 - 8	46.833	5.43	56	8.625	**<.0001**
	perennial, 60 year old orchard	**4 - 5**	-4	1.06	56	-3.758	**0.0036**
		5 - 8	4.444	1.51	56	2.952	**0.0357**
	annual, 60 year old orchard	**4 - 6**	-4.5	0.973	56	-4.626	**0.0002**
		5 - 6	-4.5556	0.973	56	-4.683	**0.0002**
		6 - 8	4.3889	1.376	56	3.19	**0.019**

Table S5.6: Tukey-adjusted contrasts of pollinator diversity by seed mix, month, and orchard from mixed modeling approach.

Treatment	Data Subset	Contrast	Estimate	SE	df	t-ratio	p-value
Seedmix	all data	annuals - industry	0.1369	0.122	669	1.118	0.6784
		annuals - perennials	-0.4444	0.102	669	-4.367	**0.0001**
		annuals - control	0.0707	0.102	669	0.695	0.8991
		industry - perennials	-0.5813	0.122	669	-4.748	**<.0001**
		industry - control	-0.0662	0.122	669	-0.541	0.949
		perennials - control	0.5152	0.102	669	5.062	**<.0001**
Orchard age	all data	**15 - 60**	0.607	0.0892	670	6.807	**<.0001**
		15 - 40	0.91	0.0892	670	10.21	**<.0001**
		60 - 40	0.303	0.0892	670	3.403	**0.002**
Seedmix*Orchard age	15 year old orchard	annuals_15 - industry_15	0.19063	0.194	661	0.984	0.998
		annuals_15 - perennials_15	-0.72727	0.162	661	-4.485	**0.0005**
		annuals_15 - control_15	0.19697	0.162	661	1.215	0.9877
		industry_15 - perennials_15	-0.9179	0.194	661	-4.738	**0.0002**
		industry_15 - control_15	0.00634	0.194	661	0.033	1
		perennials_15 - control_15	0.92424	0.162	661	5.7	**<.0001**
	40 year old orchard	annuals_40 - industry_40	0.03912	0.194	661	0.202	1
		annuals_40 - perennials_40	-0.13636	0.162	661	-0.841	0.9995
		annuals_40 - control_40	0.01515	0.162	661	0.093	1
		industry_40 - perennials_40	-0.17548	0.194	661	-0.906	0.9991
		industry_40 - control_40	-0.02396	0.194	661	-0.124	1

	perennials_40 - control_40	0.15152	0.162	661	0.934	0.9987
60 year old orchard	annuals_60 - industry_60	0.18306	0.194	661	0.945	0.9986
	annuals_60 - perennials_60	-0.4697	0.162	661	-2.897	0.1445
	annuals_60 - control_60	0	0.162	661	0	1
	industry_60 - perennials_60	-0.65275	0.194	661	-3.37	**0.0379**
	industry_60 - control_60	-0.18306	0.194	661	-0.945	0.9986
	perennials_60 - control_60	0.4697	0.162	661	2.897	0.1445
native annuals	**annuals_15 - annuals_60**	0.59091	0.162	661	3.644	**0.0151**
	annuals_15 - annuals_40	0.81818	0.162	661	5.046	**<.0001**
	annuals_60 - annuals_40	0.22727	0.162	661	1.402	0.9631
industry (conventional cover crops)	industry_60 - industry_40	0.08333	0.22	661	0.38	1
	industry_15 - industry_60	0.58333	0.22	661	2.657	0.2506
	industry_15 - industry_40	0.66667	0.22	661	3.036	0.1006
control	control_60 - control_40	0.24242	0.162	661	1.495	0.9418
	control_15 - control_60	0.39394	0.162	661	2.429	0.3876
	control_15 - control_40	0.63636	0.162	661	3.924	**0.0054**
native perennials	**perennials_15 - perennials_40**	1.40909	0.162	661	8.69	**<.0001**
	perennials_15 - perennials 60	0.84848	0.162	661	5.232	**<.0001**
	perennials_60 - perennials_40	0.56061	0.162	661	3.457	**0.0286**

Month*Orchard age (note: only significant month by orchard age interactions shown)	control, 15 year old orchard	**5 - 6**	-1.167	0.353	56	-3.302	**0.0139**
		4 - 6	-1.167	0.336	28	-3.469	**0.0047**
	industry, 15 year old orchard	**5 - 6**	-0.833	0.336	28	-2.478	**0.0496**
	perennial, 15 year old orchard	**4 - 6**	-2.722	0.51	56	-5.341	**<.0001**
		5 - 6	-3.167	0.51	56	-6.212	**<.0001**
		6 - 7	2.389	0.721	56	3.314	**0.0135**

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