


Introduced annuals mediate climate-driven community change in Mediterranean prairies of the Pacific Northwest, USA

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Abstract

Aim: How climate change will alter plant functional group composition is a critical question given the well-recognized effects of plant functional groups on ecosystem services. While climate can have direct effects on different functional groups, indirect effects mediated through changes in biotic interactions have the potential to amplify or counteract direct climatic effects. As a result, identifying the underlying causes for climate effects on plant communities is important to conservation and restoration initiatives.

Location: Western Pacific Northwest (Oregon and Washington), USA.

Methods: Utilizing a 3-year experiment in three prairie sites across a 520-km latitudinal climate gradient, we manipulated temperature and precipitation and recorded plant cover at the peak of each growing season. We used structural equation models to examine how abiotic drivers (i.e. temperature, moisture and soil nitrogen) controlled functional group cover, and how these groups in turn determined overall plant diversity.

Results: Warming increased the cover of introduced annual species, causing subsequent declines in other functional groups and diversity. While we found direct effects of temperature and moisture on extant vegetation (i.e. native annuals, native perennials and introduced perennials), these effects were typically amplified by introduced annuals. Competition for moisture and light or space, rather than nitrogen, were critical mechanisms of community change in this seasonally water-limited Mediterranean-climate system. Diversity declines were driven by reductions in native annual cover and increasing dominance by introduced annuals.

Main conclusions: A shift towards increasing introduced annual dominance in this system may be akin to that previously experienced in California grasslands, resulting in the “Californication” of Pacific Northwest prairies. Such a phenomenon may challenge local land managers in their efforts to maintain species-rich and functionally diverse prairie ecosystems in the future.

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KEYWORDS

climate manipulations, diversity, evenness, functional groups, invasion, plant community, richness, soil moisture, structural equation modelling, warming

1 | INTRODUCTION

Climate change is altering plant communities by promoting widespread invasions (Thuiller et al., 2008), reshuffling compositional assemblages (Pecl et al., 2017) and contributing to the loss of species diversity (Harrison et al., 2015). These changes play out through direct effects of temperature and moisture on individual species, as well as indirect effects of temperature and moisture on interspecific interactions such as competition. A major challenge to effectively managing plant communities under climate change is identifying the direct and/or indirect pathways by which these changes occur (Avolio et al., 2015; Gornish & Tylianakis, 2013). For example, moisture, rather than temperature, could be the primary influence on plant community responses (Franklin et al., 2016), or vice versa. Biotic interactions can act as important intermediaries (Brooker, 2006). Nutrient availability may be the driver of change but be dependent on climate (Brooks, 2003). In many cases, the underlying mechanisms by which temperature, moisture, nutrients and biotic interactions influence change in plant communities remain a black box.

There is debate whether direct or indirect effects dominate climate-driven plant community change. Theoretical evidence suggests that direct climatic effects are more important in some grassland plant communities (Chu et al., 2016), which has been corroborated in some empirical studies. For example, in a Kansas prairie, the direct effects of temperature had greater influence than species interactions on the population dynamics of ten forb species (Adler & HilleRisLambers, 2008). However, alternative evidence highlights the important roles of indirect effects, given their potential to amplify or counteract direct effects (Adler et al., 2009).

Studies in California grasslands with Mediterranean-climate systems support both direct and indirect effects of climate on plant communities. For example, Levine et al. (2010) found that the precipitation responses of native annual forbs were minimally affected by the responses of their competitors. However, LaForgia et al. (2020) found that drought effects on native annual forbs (especially resource-acquisitive ones) were exacerbated when invasive winter-annual grasses were present, suggesting a strong mediation of climate through competition. Suttle et al. (2007) found that while extending the wet season initially boosted plant species richness, these effects were reversed once increased nutrient availability prompted a shift from forbs to winter-annual grasses, which suppressed other species through their litter accumulation. In prairie and grassland systems such as this, winter-annual invasives may amplify or counteract direct climatic effects on other functional groups by altering soil resources such as moisture or nitrogen (Prevéy & Seastedt, 2014), potentially shifting competitive hierarchies in their favour (Everard et al., 2010).

The Pacific Northwest (PNW) of the United States is a Mediterranean-climate region defined by its mild, wet winters and warm-to-hot, dry summers (Kottek et al., 2006). Like many other Mediterranean-climate ecosystems across the globe, PNW prairies are critically endangered (Klausmeyer & Shaw, 2009; Noss et al., 1995; Sala et al., 2000). Following Euro-American settlement, most of these prairies have been lost to land use change or considerably altered by non-native plant invasions (Dunwiddie & Bakker, 2011). While introduced winter-annual species achieved dominance in the hotter, drier California grasslands (Clary, 2012), introduced perennial grasses were the primary invaders in the cooler, moister PNW (Sinclair et al., 2006). Looking towards the future, how climate change will alter these (and other Mediterranean climate) plant communities is an important conservation question.

Models for the PNW project a temperature increase of at least 2.5°C by the 2080s (compared to 1970–1999), with changes in precipitation being less certain (Dalton & Fleishman, 2021; Mote & Salathé, 2010). In general, the seasonality of the Mediterranean-climate system is expected to become more extreme, with winters becoming wetter and summers becoming longer and drier. Increased precipitation variability and extreme events are likely (Pendergrass et al., 2017). Drought potential may rise due to increasing evaporative demands, particularly in the valley lowlands (Jung & Chang, 2012), where many of these prairies occur.

Previous research by our group suggested that future climate change will alter plant community composition and decrease diversity in PNW prairies. Population-level studies of native annual and perennial species revealed declining demographic performance under experimental warming (Pfeifer-Meister et al., 2013; Reed, Bridgham, et al., 2021; Reed, Peterson, et al., 2021). At the community level, warming increased the cover of introduced annual species, causing a “Californication” phenomenon in which communities became more similar to invaded grasslands further south in California (Pfeifer-Meister et al., 2016). Although this was hypothesized to be due to a reduction in soil moisture, temperature and moisture were confounded: adding +20% precipitation to warming did little to alleviate the warming-induced drying effects. Additionally, the role of introduced annuals in mediating climatic effects, or whether nutrient availability played any role, was unexplored. Thus, it is difficult to ascertain whether these climate-driven community changes can be primarily attributed to temperature, moisture, nutrients or other factors.

Here, we built upon this previous research with 3 years of new data, decoupling the direct warming effects from their drying effect. We used structural equation modelling to examine the extent to which abiotic drivers (i.e. temperature, moisture and nitrogen) controlled functional group cover, and how these groups in turn determined diversity, richness and evenness. Utilizing a climate

manipulation experiment embedded at three sites across a latitudinal gradient, our overarching question was: How does climate change cause shifts in plant functional group dominance and diversity in a Mediterranean-climate prairie ecosystem? More specifically, we asked: What are the direct and indirect effects of climate on the cover and diversity of PNW prairie plant communities? And, to what extent are warming effects driven by introduced annuals, either directly or indirectly through their control over soil moisture and nitrogen?

We hypothesized that warming would favour introduced annual species at the expense of other functional groups and would thus negatively affect diversity. In particular, we expected a direct positive effect of temperature on introduced annual cover, as many of these species in this system are winter annuals (Dennehy et al., 2011) that may benefit from more favourable early growing season conditions (Dunwiddie et al., 2014; Pfeifer-Meister et al., 2016). Concurrently, we expected increasing temperatures to reduce soil moisture, augmented by feedback from introduced annuals, whose rapid growth draws down available soil water (Prevéy & Seastedt, 2014). We also expected a decline in nitrogen (N) availability due to reduced soil moisture and greater uptake by introduced annuals, shifting the competitive hierarchy in their favour (Everard et al., 2010; Prévéy & Seastedt, 2014). As a result, we expected the cover of later-growing functional groups (i.e. introduced perennials, native perennials and native annuals) to decline with warming and drying, and for this to be primarily mediated through increasing competitive pressure by

introduced annuals. Finally, we expected these changes to result in a decline in diversity, induced by losses in both richness and evenness.

2 | METHODS

2.1 | Experimental design

We conducted this study at three prairie sites spanning a 520-km latitudinal gradient across the western PNW (Figure 1a). Sites were selected to reflect the Mediterranean-climate gradient of increasing temperature and summer drought severity from north to south. Each site contained 20 circular 7.1-m² plots (Figure 1b). The southern and central site plots had legacies dating back to 2009–2012 in a previous experiment (Pfeifer-Meister et al., 2013, 2016), while the northern site plots were established in late 2014. Prior to plot establishment, all three sites were dominated by introduced perennial grasses.

All plots were initially established for native plant demography experiments (Pfeifer-Meister et al., 2013; Reed, Bridgman, et al., 2021; Reed, Peterson, et al., 2021). In 2009, the southern and central plots were treated with herbicide (2% Glyphosate (RoundUp) and 0.75% grass-specific Fusilade) and then sown with identical mixtures of 31 native prairie species to establish the first demography experiment (Pfeifer-Meister et al., 2013). These plots then had additional sowings of 12 focal native species in fall 2010 and 2011. Between late

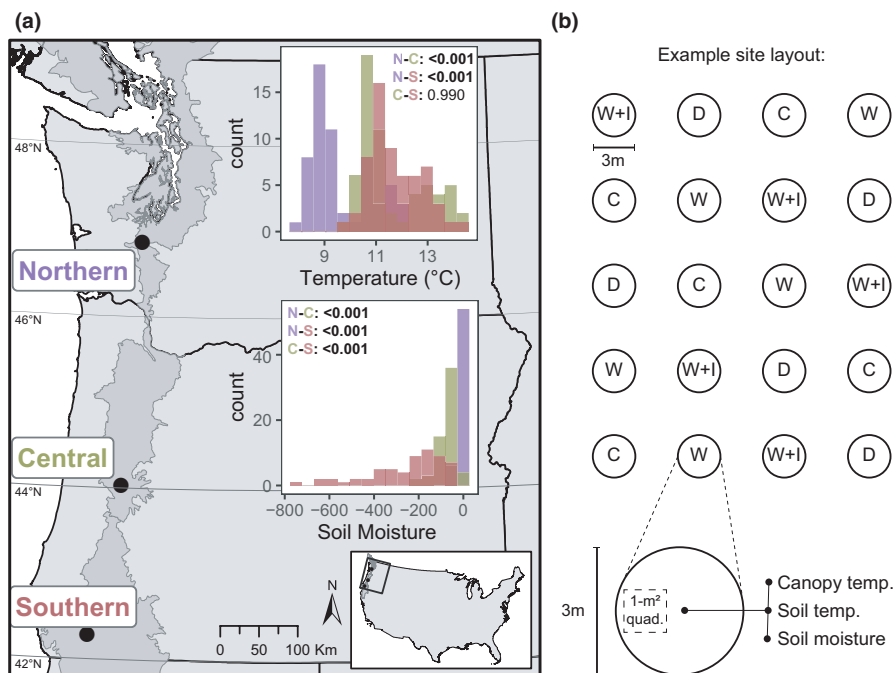


FIGURE 1 (a) The southern, central and northern experimental sites occur across a 520 km latitudinal climate gradient in the western Pacific Northwest, USA. Site significantly affects mean growing season soil temperature (top histograms) and moisture (soil matric potential (kPa); bottom histograms). *p*-values of Tukey's post hoc comparisons provided within histograms. Soil moisture was transformed prior to analyses (see Methods). (b) Schematic of experimental design. Each climate treatment is replicated five times at each site for a total of 60 plots. C = control, D = drought, W = warming, W + I = warming + irrigation. Plant cover was measured in a fixed 1-m² quadrat within each plot. Canopy temperature, soil temperature and soil moisture were continuously logged in the centre of each plot

2012 and early 2014, these plots were left fallow with no treatments or maintenance. In late 2014, all 60 plots (the southern, central and new northern plots) were treated with herbicide and then sown with identical mixtures of 29 native prairie species to establish the subsequent demography experiments (Reed, Bridgman, et al., 2021; Reed, Peterson, et al., 2021). Finally, all 60 plots had additional sowings of 14 focal native species in fall 2015, 2016 and 2017.

By September 2016, we initiated four climate treatments: control, drought, warming and warming + irrigation (five plots per treatment per site; Figure 1b). Controls experienced ambient temperature and precipitation, the drought treatment reduced annual precipitation by ~40% using fixed rainout shelters, and the warming treatments increased canopy temperature by approximately +2.5°C with infrared lamps. The warming + irrigation plots were irrigated with additional rainfall such that their soil volumetric water content matched the control plot average. Both the warming and warming + irrigation treatments ceased in July 2018 at the conclusion of the demography experiments, while the drought treatment continued through the 2019 growing season (see Supplemental Methods for additional details).

2.2 | Climate and nitrogen data

Between fall 2016 and summer 2019, we continuously logged plot canopy and soil temperatures and soil volumetric water content aggregated to daily averages. Missing values due to equipment malfunction were interpolated (see Appendix S1). To compare moisture across sites with different soil characteristics, we calculated soil matric potential from volumetric water content, soil texture and soil carbon (Saxton & Rawls, 2006; see Appendix S1). Matric potentials are negative values where 0 kPa indicates saturation and -1500 kPa indicates permanent wilting point. In the Mediterranean climate of the PNW, active vegetation growth occurs mainly in the wet season (October–June), followed by several months of dormancy during the summer drought (July–September). Therefore, we aggregated soil temperature and moisture data to the growing season from October 1 to June 30 (Reed et al., 2019). We also investigated annual, winter and spring seasonal values, but only report growing season here because trends were consistent.

We collected data on total inorganic nitrogen (N) availability ($\mu\text{g}/10 \text{ cm}^2$ strip/burial period) using Plant Root Simulator (PRS[®]) Probes (Western Ag, Saskatoon, SK, CAN). We buried four anion and four cation probes in each plot for 4-month periods (fall, winter and spring) between August 2016 and July 2018. We calculated the mean growing season N availability by averaging values across the three burial periods for 2017 (August 2016–July 2017) and 2018 (August 2017–July 2018) but lacked these data for 2019.

2.3 | Plant community data

In each spring 2017–2019, we measured plant cover at peak standing biomass (approximately mid-May, late-May and mid-June at the

southern, central and northern sites, respectively) using the point intercept method (Elzinga et al., 1998). Using a 1-m² quadrat in a fixed location within each plot, we dropped 25 equally spaced pins (4.8 mm diameter) through the plant canopy. We counted each plant contact with a pin (hit) to the species level and multiplied hits by four (to scale to 100). Due to canopy layering, >100% cover occurred. The same four researchers counted pin hits during all 3 years of the study and calibrated pin-hit counting techniques together to ensure consistency across researchers. We assigned a cover of 0.4% to species, which were present in the quadrat but not hit by a pin. Because pin diameter affects counts, the method is more precisely described as a cover index than an absolute cover measure, and pin size can be adjusted for a given study without introducing bias (Jonasson, 1988). Point-intercept methods have proved effective and accurate across a wide range of grassland productivity and diversity (Barkaoui et al., 2013).

To determine the functional group covers, we assigned each species to an origin (native/introduced), duration (annual/perennial, with the few biennials assigned as annuals), and growth form (grass/forb, with forbs further classified as legume/non-legume) by referring to the Consortium of Pacific Northwest Herbaria (<https://www.pnwherbaria.org/data/search.php>) and the USDA Plant Profiles (<https://plants.usda.gov/>) databases. While we included growth form to identify species to finer-scale functional groups (i.e. origin/duration/growth form), we focused specifically on coarser origin/duration groups in our analyses to reduce complexity and because preliminary analyses revealed we could capture the overwhelming patterns at this resolution. Using the *vegan* package in R (Oksanen et al., 2019), we calculated Simpson's index of diversity as:

$$1 - D = 1 - \sum_i^s p_i^2$$

where p_i is the relative cover of species i and s is the richness, or total number of species. Lastly, we calculated Simpson's evenness (Morris et al., 2014; Simpson, 1949) as:

$$E = \frac{1}{\sum_i^s p_i^2}$$

2.4 | Analyses

We conducted analyses using R version 4.0.2 (R Core Team, 2020). Due to repeated sampling of the plots, we ran all analyses using mixed models (lme4 package; Bates et al., 2015) with plot as a random effect. Marginal and conditional R^2 values were calculated based on Nakagawa et al. (2017), with R_m^2 providing the variance explained by the fixed effect(s) alone and R_c^2 providing the variance explained by both fixed and random effects. Because heaters and irrigation were turned off after July 2018, we excluded data from the warming and warming + irrigation plots in 2019 to prevent any legacy treatment effects from obscuring patterns.

To improve the normality of distributions for several variables, we used the following transformations. We transformed soil

moisture using $-\log(1 - \text{matric potential})$ so that the transformed values stayed consistent with raw values (more negative = drier, less negative = moister). We used square root transformations for N availability and the cover of both introduced annuals and introduced perennials. For native perennial and native annual cover, we used a log transformation after adding a constant of 0.4% as these functional groups had 0% cover in some plots. Lastly, because diversity and evenness were proportional data, we used logit transformations (Warton & Hui, 2011).

Differences in the abiotic variables (temperature, moisture and N availability) were examined with ANOVA with site as a fixed effect followed by Tukey's post hoc comparisons if site was significant ($p < .05$). We explicitly left site out as a predictor from all subsequent analyses because sites were chosen to represent a climate gradient and would obscure the continuous-data climate signals.

Using the *piecewiseSEM* package (Lefcheck, 2016), we examined our a priori hypothesized causal pathways with structural equation models (SEM), which linked together a series of multiple regressions fitted using *lme4* with plot as a random effect. In SEMs, overall model fit is determined by testing the significance of unspecified causal pathways (i.e. a well-supported model has a high goodness-of-fit p -value). We investigated Pearson's correlation coefficients and checked for multicollinearity using variance inflation factors (VIFs). Concerns over multicollinearity were minimal as the greatest VIF was 3.4 (Table S1) and, in general, VIFs >5 may indicate multicollinearity (James et al., 2013). We ran separate SEMs for diversity, richness and evenness. Although we hypothesized that biotic effects would primarily occur through introduced annuals, we also accounted for the possibility of introduced perennials affecting the two native functional groups, as introduced perennials are already widely prevalent throughout this system and have strong competitive effects on native prairie species (Sinclair et al., 2006; Stanley et al., 2011).

We initially restricted SEMs to 2017 and 2018 as we lacked N availability data in 2019. After discovering minimal effects of N availability on functional group cover (see Results), we reran SEMs without this variable to include the 30 additional 2019 data points. The richness and evenness SEMs had poor model fit when only including the four functional groups as their predictors (see Results), so we also added direct effects of temperature and soil moisture on richness and evenness. To calculate indirect effects, we multiplied the standardized coefficients of the significant paths that constituted the effect. Finally, we also ran independent bivariate regressions for visualization.

3 | RESULTS

3.1 | Abiotic variables

Across all treatments, mean growing season soil temperature, moisture and N availability differed by site ($p < .001$). From north to south, average plot conditions became warmer (northern: $9.8 \pm 1.1^\circ\text{C}$

(mean \pm s.d.), central: $11.8 \pm 1.4^\circ\text{C}$, southern: $11.9 \pm 0.9^\circ\text{C}$) and drier (northern: -11.4 ± 10.8 kPa, central: -66.3 ± 44.7 kPa, southern: -239.0 ± 172.6 kPa), although the central and southern plots were not significantly different for temperature (Figure 1). Treatment-specific means in temperature and moisture differed by site and year (Figures S1 and S2). Mean N availability was lowest in the central plots, while the northern and southern plots did not significantly differ (Figure S3). There was a significant positive correlation between temperature and introduced annual cover, and significant negative correlations between temperature and soil moisture, introduced annual cover and soil moisture, and soil moisture and N availability (Figure S4).

Using SEM, we found that temperature significantly reduced soil moisture regardless of restricting to 2017 and 2018 data (-0.65 standardized estimated, $p < .001$, Figure S6, Table S2) or including 2019 data (-0.40 std. est., $p < .001$, Figure 2, Table S3). Introduced annual cover also contributed to a reduction in soil moisture (2017–2018: -0.20 std. est., $p = .011$, Figure S6; 2017–2019: -0.18 std. est., $p = .022$, Figure 2). N availability was negatively affected by soil moisture (-0.34 std. est., $p = .024$, Figure S6), but not directly by either temperature (0.09 std. est., $p = .519$) or introduced annual cover (-0.22 , $p = .146$, Figure S6, Table S2).

3.2 | Functional group cover

Overall, introduced annuals had the greatest average cover (505.4%, range: 0%–1596.4%), followed by introduced perennials (228.3%, range: 0%–900.8%), native perennials (121.0%, range: 0%–564.8%) and native annuals (30.0%, range: 0%–328.4%). Native annual, native perennial and introduced perennial cover all had significant, positive correlations with one another but significant, negative correlations with introduced annual cover (Figure S5). Introduced annuals increased with temperature and had a negative relationship with soil moisture (Figure 3a,e; Table S4), while the other three functional groups all decreased with increasing temperature and increased with soil moisture (Figure 3b–d,f,g; Table S4). Functional group cover was not related to N availability (Figure S7a–d; Table S4), nor did N availability ever act as a significant mediator in the SEMs (Figure S6; Table S2). Therefore, we focus on the SEMs, which include 2019 data (and exclude N availability).

We found the effects of temperature on introduced perennials and native perennials to be primarily mediated through its effects on introduced annuals and soil moisture (Figure 2). In particular, soil moisture had a positive effect on introduced perennials (0.49 std. est.), while introduced annuals had a negative effect (-0.27 std. est.), as well as an indirect effect (-0.09 std. est.) mediated through their effect on soil moisture. For native perennials, the only significant effect was a negative effect from introduced annuals (-0.35 std. est.). For native annuals, temperature and moisture had direct negative (-0.33 std. est.) and positive (0.31 std. est.) effects, respectively, while the effects of introduced annuals on native annuals were mediated indirectly (-0.06 std. est.) through soil moisture (Figure 2).

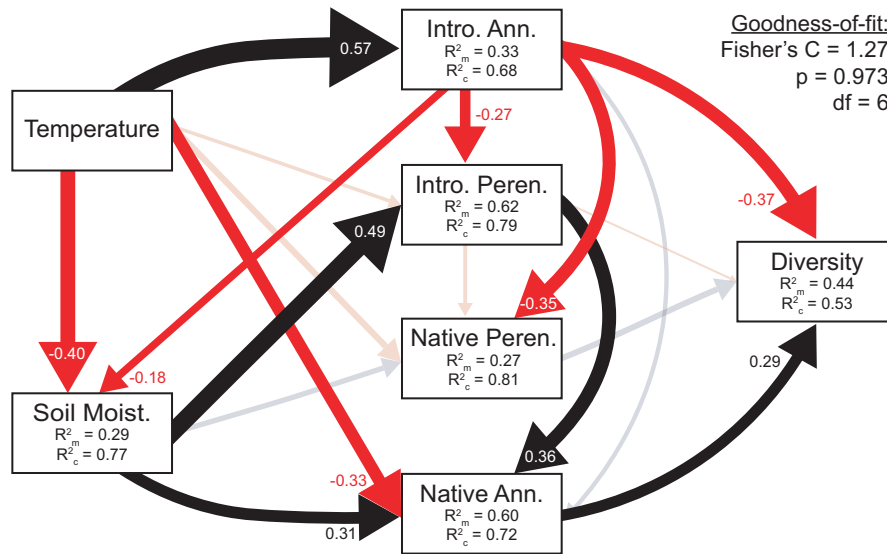


FIGURE 2 Structural equation model using 2017–2019 data to determine how climate controls functional groups and how functional groups control diversity. Values within/next to arrows (direct effects) are standardized estimates of coefficients, and arrow thickness is scaled to their magnitude. Red = negative effects, black = positive effects, semi-transparent = non-significant effects ($p > .05$; Table S3). Within each response variable box (those at the receiving end of arrows), R_m^2 provides the variance explained by the fixed effect(s) alone (boxes at the starting end of the arrows) and R_c^2 provides the variance explained by both fixed and random effects (plot = random). “Moist.” = Moisture, “Intro.” = Introduced, “Peren.” = “Perennials,” “Ann.” = Annuals. Introduced annuals had indirect effects mediated through their effect on soil moisture for introduced perennials ($-0.18 \times 0.49 = -0.09$) and native annuals ($-0.18 \times 0.31 = -0.06$)

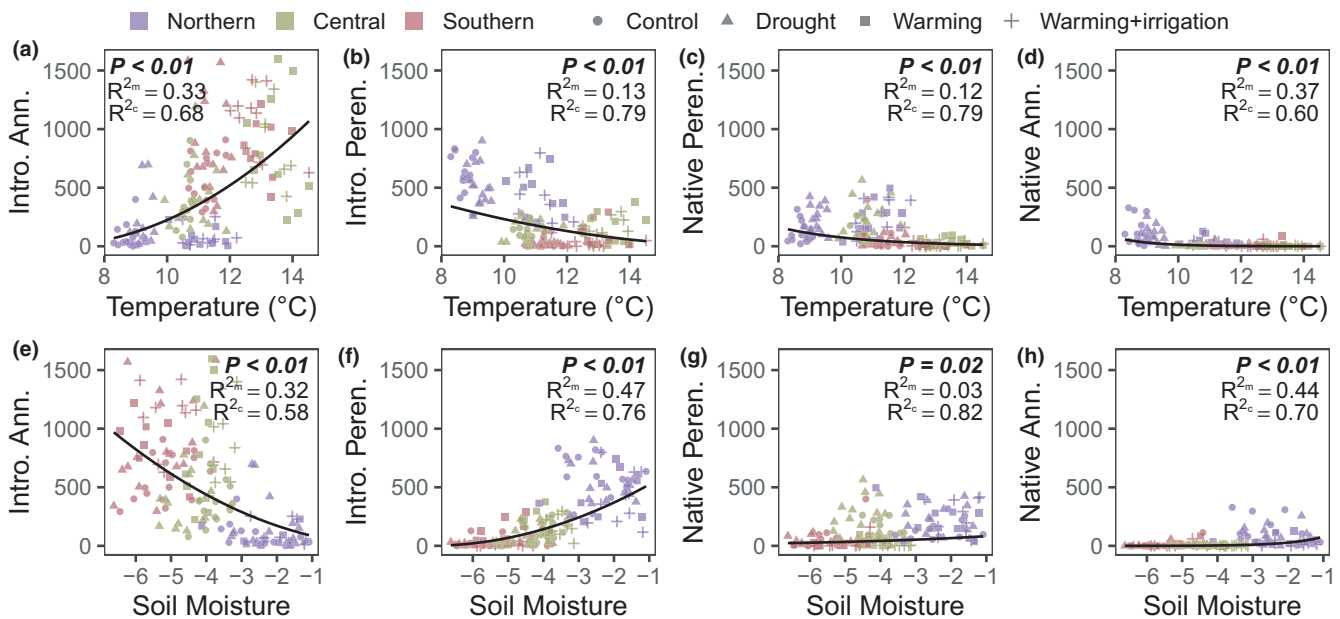


FIGURE 3 Bivariate regressions showing functional group cover against mean growing season soil temperature (a–d) and moisture (e–h), with plot as a random effect. Soil moisture = $-\log(1-\text{matric potential})$. R_m^2 (above) provides the variance explained by the fixed effect(s) alone and R_c^2 (below) provides the variance explained by both fixed and random effects (plot = random)

3.3 | Diversity, richness and evenness

Diversity declined with increasing temperature and increased with soil moisture (Figure 4a,d; Table S4). It also declined with increasing

introduced annual cover but increased with cover for the three other functional groups (Figure S8a–d; Table S4). Using SEM, we found that introduced annual cover had a negative effect (-0.37 std. est.) and native annual cover a positive effect (0.29 std. est.)

on diversity, while introduced perennial and native perennial cover had negligible effects (Figure 2; Table S3). There was a 45% reduction in predicted diversity from minimum to maximum introduced annual cover and a 31% increase from minimum to maximum native annual cover. The SEM for diversity had good model fit (goodness-of-fit: $p = .973$).

Like diversity, richness also declined with increasing temperature and increased with moisture (Figure 4b,e; Table S4), whereas evenness was not affected by temperature and weakly declined with moisture (Figure 4c,f; Table S4). Additionally, richness declined with increasing introduced annual cover but increased with cover for the three other functional groups (Figure S8e–h; Table S4), whereas evenness only declined with increasing introduced annual cover (Figure S8i–l; Table S4). Both richness and evenness SEMs had poor model fit when only including functional group cover as their predictors (goodness-of-fit: $p \leq .057$), so we added direct effects of temperature and moisture. For richness, soil moisture, native annual cover and native perennial cover had positive effects (0.51, 0.54 and 0.20 std. est., respectively; Figure S9a). Predicted richness increased from 6.5 to 24.5 species from minimum to maximum soil moisture. For evenness, introduced annual cover and soil moisture had negative effects (–0.65 and –0.35 std. est., respectively; Figure S9b).

4 | DISCUSSION

A major challenge in community ecology is to tease apart the complex relationships behind climate-driven community change. This challenge may be best-achieved using large-scale, multisite experiments analysed with path-analytic approaches (Brooker, 2006; Gornish & Tylianakis, 2013). Using a climate manipulation experiment embedded in three Mediterranean-prairie sites across a latitudinal gradient in the PNW, we used SEM and found that warmer conditions resulted in increasing cover of introduced annuals, along

with subsequent declines in other functional groups and diversity. Our data not only confirm results from our previous study (Pfeifer-Meister et al., 2016), but identify the causal pathways underlying the observed climate–community relationships.

Our first hypothesis, that warmer conditions favour introduced annuals, was strongly supported. Indeed, we found a direct positive effect of temperature on introduced annual cover, which we suspect was due to the early winter-growth habits common to this group. The most abundant introduced annuals in our study, *Vulpia* spp. (*V. myuros* and *V. bromoides*), *Bromus* spp. (*B. hordeaceus* and *B. tectorum*) and *Trifolium subterraneum*, were orders of magnitude more common than other annuals (Figure S10) and are characterized as winter-growing, early-maturing species (Friddle, 2018; USDA-Natural Resources Conservation Service, 2012; USDA-NRCS, 2014). Warming could be advantageous to such species by promoting growth during the early growing season (Blumenthal et al., 2016; Cleland et al., 2006), at a time when temperature is most limiting and the rest of the community is still largely dormant.

Whether this favouring of introduced annuals came at the expense of other functional groups (i.e. through competition for limiting resources) was partially supported. Invasive annual grasses such as *Bromus* can rapidly exploit and draw down soil water resources (Dyer & Rice, 1999; Melgoza et al., 1990). These grasses generally reached peak flowering in our study by mid-April, whereas most other functional groups peaked around mid-May to mid-June (P. Reed, pers. obs.), when soil moisture became a critically limiting resource (Figure S2). As corroborated by our SEMs, introduced annuals negatively affected soil moisture and soil moisture had strong effects on introduced perennials and native annuals. Thus, one major mechanism of climate-driven community change in this system is through increasing competition for soil moisture. The most abundant introduced annuals, *Vulpia* and *Bromus*, are relatively drought-tolerant (USDA-Natural Resources Conservation Service, 2012; USDA-NRCS, 2014) and avoid the detriments of reducing soil moisture by

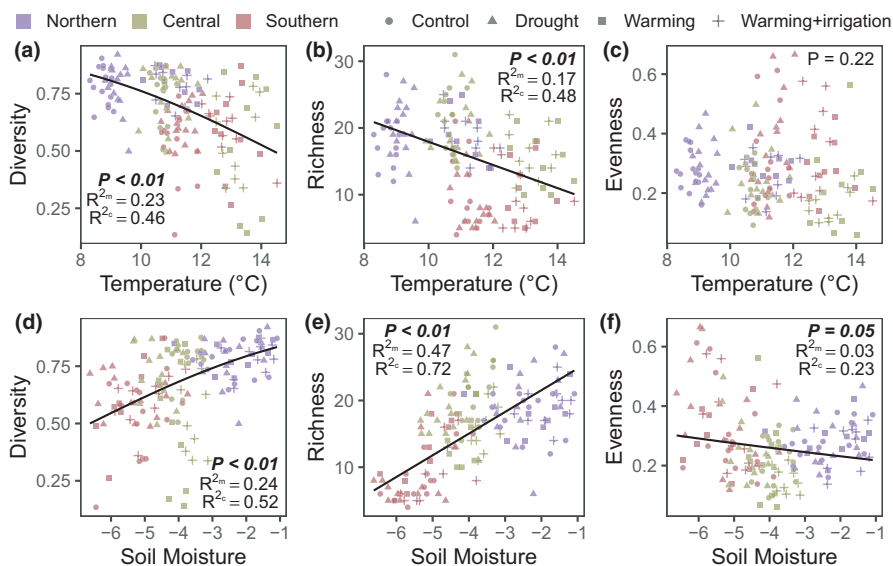


FIGURE 4 Bivariate regressions showing Simpson's index of diversity, richness and evenness against mean growing season soil temperature (a–c) and moisture (d–f), with plot as a random effect. Soil moisture = $-\log(1-\text{matric potential})$. R_m^2 (above) provides the variance explained by the fixed effect(s) alone and R_c^2 (below) provides the variance explained by both fixed and random effects (plot = random)

completing their entire life cycle prior the onset of extreme summer drought. However, it is important to note that the direct negative effect of temperature on soil moisture was greater than that from introduced annuals, indicating that competition from this functional group amplifies, but does not entirely control, moisture limitation for the rest of the community.

We found minimal support for N limitation acting as an important intermediary in these community dynamics. Soil moisture is the transport medium for plant-available N (Everard et al., 2010), but we actually found a slightly negative relationship between N availability and soil moisture (Figure S4), driven by relatively high N availability at our driest (southern) site (Figure S3). Legumes (e.g. *Trifolium* and *Vicia* spp.) were among the most common introduced annuals in this study (Figure S10), and *Trifolium subterraneum* was especially common at the southern site in 2017. Thus, increases in N-fixation may have offset decreases in N availability due to drier conditions. Alternatively, N availability could be controlled by other site-specific factors. Regardless, N availability did not affect the cover of introduced perennials, native perennials or native annuals, and was poorly predicted by temperature, soil moisture and introduced annual cover ($R_m^2 = 0.07$, $R_c^2 = 0.27$, Figure S6).

The direct effects of introduced annuals on the two perennial functional groups suggest that an additional competition mechanism is at play. In our parallel demography experiment, we speculated that poor recruitment among native perennials was driven by competition from introduced annual grasses (Reed, Peterson, et al., 2021). Poor recruitment ultimately led to fewer adult-stage individuals, hence the lower cover observed here. In a similar California grassland system, litter accumulation positively reinforces the biomass of introduced annual grasses to suppress native recruitment (Mariotte et al., 2017). Likewise, seedling establishment for both native and introduced perennials declined with increasing litter depth in our plots (Brambila et al., unpublished data). Given that existing vegetation was initially removed from our plots, introduced perennials had to re-establish through the seedbank, while native perennials came in via our seed additions. As warmer conditions promoted the rapid biomass growth of introduced annuals, they formed a dense cover early in the season (*Vulpia* and *Bromus* spp. often reaching 20+ hits per pin) coupled by a thick litter layer that remained the following season. Such conditions shade out young seedlings of slower-growing perennials during their critical establishment phase. Thus, an additional mechanism mediated by introduced annuals seems to be through increasing competition for space and light.

There was also a strong direct effect of moisture on introduced perennials. In California, introduced perennial grass cover is strongly correlated with proximity to the moist coastline (Clary, 2012). Likewise, in PNW prairies, this functional group was highly successful at invading cool, moist sites (Sinclair et al., 2006). Although the land surrounding our plots at the driest (southern) site is dominated by introduced perennial grasses, the property is regularly irrigated from spring to summer (P. Reed, pers. obs.). The strong effect of moisture on introduced perennials implies that, even in the absence of competitive pressure by introduced annuals, future moisture

limitation may prove detrimental for this group. From a management perspective, any decline in a non-native functional group may appear desirable on the surface. However, some non-natives can play an important role relative to management objectives (Dunwiddie & Rogers, 2017). For example, in PNW prairies, the introduced perennial forb *Plantago lanceolata* serves as a critical host for the endangered Taylor's checkerspot butterfly (Dunwiddie & Rogers, 2017), and several other introduced perennial forbs provide important nectar resources for a variety of pollinators (Lindh, 2018). Introduced perennial grasses provide important forage value for livestock throughout the region. Given the potential undesirability of a perennial-to-annual state transition (D'Antonio & Vitousek, 1992), any perennial cover (whether native or introduced) may be worth preserving to some degree.

As for native annuals, the direct effects of temperature and moisture strongly support our parallel demography study, which suggests that climate change will cause many native annuals to decline, regardless of competition (Reed, Bridgham, et al., 2021). Although several species in that study were strongly disturbance-dependent, population growth rates rapidly deteriorated with warming even under favourable disturbance regimes (i.e. low competition). Importantly, the two most abundant native annuals in this study (*Collinsia grandiflora* and *Plectritis congesta*; Figure S10) were also the two least affected by disturbance in that demography study (Reed, Bridgham, et al., 2021). Thus, their relatively high abundances may have influenced the negligible direct effect from introduced annuals.

Surprisingly, there was a positive effect from introduced perennials to native annuals (0.36 std. est., Figure 2). We included this pathway as introduced perennials have long been directly out-competing native species in this system (Sinclair et al., 2006; Stanley et al., 2011). However, the positive relationships that we found between native annual, native perennial and introduced perennial cover suggest that these three functional groups can coexist under common favourable conditions without inherent competitive exclusion (Figure S5). Therefore, we suspect that the significant positive arrow from introduced perennials to native annuals is correlative, rather than causative, as both functional groups were most common at the northern site, where cooler and moister conditions are the true underlying causes. Throughout PNW prairies, native annuals have already declined to an alarming degree (Dunwiddie et al., 2014). Our results suggest that this trend may continue with climate change, whether introduced annuals are present or not.

We found support for the hypothesis that diversity will decline with warmer and drier conditions (Harrison, 2020). This result was driven mostly by changes in the two annual functional groups. Similar to California annual grasslands (Harrison et al., 2018), native annual cover was a strong factor contributing to richness. Soil moisture was also a strong driver of richness (Figure S9b), consistent with several grassland studies that find positive relationships between moisture and richness (Adler & Levine, 2007; Hallett et al., 2014; Harrison et al., 2018). If soil water availability declines in the future (due to more frequent droughts, higher evaporative demand, and/or

greater competition), native annuals may drop out of these communities, thereby reducing overall diversity through a decline in species richness.

Intriguingly, introduced annuals played a large role in affecting diversity not by their effects on richness, but by their strong negative effects on evenness (Figure S9). This result is consistent with a study conducted in a more arid sagebrush-grassland ecosystem, in which communities with more introduced annuals (e.g. *Bromus tectorum*) had lower evenness (despite higher richness) as only a few species dominated (Allen & Knight, 1984). This finding is also consistent with the idea of the “invasion paradox,” in which native and non-native species richness can have both a negative or positive relationship, depending on spatial scale (Fridley et al., 2007). With plant communities, complete local extinctions resulting from invasive competitors are generally rare (Gurevitch & Padilla, 2004), especially when the natives and invaders are of different functional groups. Consequently, it is possible that a time-lag to local extinction could explain why the effects of the introduced annuals on diversity are driven by evenness rather than richness (Fridley et al., 2007).

In our study, this phenomenon seems to be driven by fundamental differences between the central and southern sites. Introduced annuals were the most species-rich functional group (Figure S10), and most of their richness occurred at the central site. *Vulpia* spp. and *Bromus hordeaceus* tended to dominate in these plots (hence low evenness; Figure S8i), but the central plots were moist enough to maintain relatively high richness (Figure 4e). Richness plummeted under the driest conditions of the southern plots (Figure 4e). These conditions so highly favoured *Vulpia* spp. and *Bromus hordeaceus* that there actually became a tipping point for evenness: cover was almost exclusively these two species, often in a roughly equal split. This may explain why evenness was actually highest in the driest (southern) plots (Figure 4f). However, we caution that this evenness-moisture bivariate relationship was weak ($R_m^2 = 0.03$; $R_c^2 = 0.23$), and the total proportion of variance explained for evenness in its SEM remained relatively low ($R_m^2 = 0.22$; $R_c^2 = 0.41$). Overall, diversity appears poised to decline with climate change due to an increasing dominance by only a handful of introduced annuals.

While our large-scale experiment and SEM approach were powerful ways to identify the pathways by which climate alters plant communities, there are a few caveats. Separate from its effects on the aboveground community, climate change can also directly and/or indirectly affect the soil seed bank (Ma et al., 2020), which we do not consider in this study. However, seedbank responses to climate change may parallel or even amplify aboveground responses, despite being independent (Basto et al., 2018). Additionally, there are likely bidirectional, causative relationships between variables (i.e. feedback loops) and missing pathways not considered in these models. However, given our previous evidence (Pfeifer-Meister et al., 2016), we feel our hypothesized model structure represents the most likely reality. Finally, our plots were relatively early-successional, “restored”

communities that were established following a clearing disturbance. It is quite possible that effects would be different in established, undisturbed communities, where priority effects exist (Corbin & D'Antonio, 2004). However, this makes our results highly relevant for local prairie restoration efforts, which must consider the complex relationships between disturbance, invasives and climate if they are to be successful.

In conclusion, while we found direct negative effects of warming and drying on extant vegetation (i.e. native annuals, native perennials and introduced perennials), we also found that these effects were commonly amplified by increasing introduced annuals. These invaders directly benefit from warmer temperatures and seem to out-compete other functional groups for limiting resources such as moisture, space and light. Thus, introduced annuals appear to be the only functional group in this system that are poised to prosper under warmer and drier conditions. Other groups and overall diversity will decline because of this shift in dominance and/or due to direct negative effects of climate change. This shift towards increasing introduced annual dominance may be akin to that previously experienced in California grasslands, resulting in the “Californication” of PNW prairies. Such changes will challenge local land managers in their efforts to maintain species-rich and functionally diverse prairie ecosystems in the future.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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DATA AVAILABILITY STATEMENT

Data are archived at the Dryad digital data repository: <https://doi.org/10.5061/dryad.n5tb2rbwf>.

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REFERENCES

- Adler, P. B., & HilleRisLambers, J. (2008). The influence of climate and species composition on the population dynamics of ten prairie forbs. *Ecology*, 89, 3049–3060. <https://doi.org/10.1890/07-1569.1>

- Adler, P. B., Leiker, J., & Levine, J. M. (2009). Direct and indirect effects of climate change on a prairie plant community. *PLoS One*, 4, 1–6. <https://doi.org/10.1371/journal.pone.0006887>
- Adler, P. B., & Levine, J. M. (2007). Contrasting relationships between precipitation and species richness in space and time. *Oikos*, 116, 221–232. <https://doi.org/10.1111/j.0030-1299.2007.15327.x>
- Allen, E. B., & Knight, D. H. (1984). The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. *The Southwestern Naturalist*, 29, 407–421. <https://doi.org/10.2307/3670993>
- Avolio, M. L., Pierre, K. J. L., Houseman, G. R., Koerner, S. E., Grman, E., Isbell, F., Johnson, D. S., & Wilcox, K. R. (2015). A framework for quantifying the magnitude and variability of community responses to global change drivers. *Ecosphere*, 6, 1–14. <https://doi.org/10.1890/ES15-00317.1>
- Barkaoui, K., Bernard-Verdier, M., & Navas, M. L. (2013). Questioning the reliability of the point intercept method for assessing community functional structure in low-productive and highly diverse Mediterranean grasslands. *Folia Geobotanica*, 48, 393–414. <https://doi.org/10.1007/s12224-013-9172-2>
- Basto, S., Thompson, K., Grime, J. P., Fridley, J. D., Calhim, S., Askew, A. P., & Rees, M. (2018). Severe effects of long-term drought on calcareous grassland seed banks. *Npj Climate and Atmospheric Science*, 1, 1–7. <https://doi.org/10.1038/s41612-017-0007-3>
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Blumenthal, D. M., Kray, J. A., Ortman, W., Ziska, L. H., & Pendall, E. (2016). Cheatgrass is favored by warming but not CO₂ enrichment in a semi-arid grassland. *Global Change Biology*, 22, 3026–3038.
- Brooker, R. W. (2006). Plant-plant interactions and environmental change. *New Phytologist*, 171, 271–284. <https://doi.org/10.1111/j.1469-8137.2006.01752.x>
- Brooks, M. L. (2003). Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology*, 40, 344–353. <https://doi.org/10.1046/j.1365-2664.2003.00789.x>
- Chu, C., Kleinhesselink, A. R., Havstad, K. M., McClaran, M. P., Peters, D. P., Vermeire, L. T., Wei, H., & Adler, P. B. (2016). Direct effects dominate responses to climate perturbations in grassland plant communities. *Nature Communications*, 7, 1–10. <https://doi.org/10.1038/ncomms11766>
- Clary, J. (2012). Determinants of perennial and annual grass distribution in Mediterranean-climate California. *Plant Ecology*, 213, 1203–1208. <https://doi.org/10.1007/s11258-012-0076-7>
- Cleland, E. E., Chiariello, N. R., Loarie, S. R., Mooney, H. A., & Field, C. B. (2006). Diverse responses of phenology to global changes in a grassland ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 13740–13744. <https://doi.org/10.1073/pnas.0600815103>
- Corbin, J. D., & D'Antonio, C. M. (2004). Competition between native perennial and exotic annual grasses: Implications for an historical invasion. *Ecology*, 85, 1273–1283.
- D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, 23, 63–87. <https://doi.org/10.1146/annurev.es.23.110192.000431>
- Dalton, M., & Fleishman, E. (2021). *Fifth Oregon Climate Assessment*. Oregon Climate Change Research Institute, Oregon State University. Retrieved from <https://blogs.oregonstate.edu/occri/oregon-climate-assessments/>
- Dennehy, C., Alverson, E. R., Anderson, H. E., Clements, D. R., Gilbert, R., & Kaye, T. N. (2011). Management strategies for invasive plants in Pacific Northwest prairies, savannas, and oak woodlands. *Northwest Science*, 85, 329–351. <https://doi.org/10.3955/046.085.0219>
- Dunwiddie, P. W., Alverson, E. R., Martin, R. A., & Gilbert, R. (2014). Annual species in native prairies of South Puget Sound, Washington. *Northwest Science*, 88, 94–105. <https://doi.org/10.3955/046.088.0205>
- Dunwiddie, P. W., & Bakker, J. D. (2011). The future of restoration and management of prairie-oak ecosystems in the Pacific Northwest. *Northwest Science*, 85, 83–92. <https://doi.org/10.3955/046.085.0201>
- Dunwiddie, P. W., & Rogers, D. L. (2017). Rare species and aliens: Reconsidering non-native plants in the management of natural areas. *Restoration Ecology*, 25, S164–S169.
- Dyer, A. R., & Rice, K. J. (1999). Effects of competition on resource availability and growth of a California bunchgrass. *Ecology*, 80, 2697–2710. [https://doi.org/10.1890/0012-9658\(1999\)080\[2697:EOCOR A\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2697:EOCOR A]2.0.CO;2)
- Elzinga, C. L., Salzer, D. W., & Willoughby, J. W. (1998). *Measuring & monitoring plant populations*. U.S. Dep. Inter. Bur. L. Manag.
- Everard, K., Seabloom, E. W., Harpole, W. S., & De Mazancourt, C. (2010). Plant water use affects competition for nitrogen: Why drought favors invasive species in California. *American Naturalist*, 175, 85–97. <https://doi.org/10.1086/648557>
- Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 3725–3734. <https://doi.org/10.1073/pnas.1519911113>
- Friddle, M. (2018). *Plant guide for subterranean clover (Trifolium subterraneum)*. USDA-Natural Resources Conservation Service, Corvallis Plant Materials Center.
- Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D. F., Seabloom, E. W., Smith, M. D., Stohlgren, T. J., Tilman, D., & Holle, B. V. (2007). The invasion paradox: Reconciling pattern and process in species invasions. *Ecology*, 88, 3–17. [https://doi.org/10.1890/0012-9658\(2007\)88\[3:TIPRPA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2)
- Gornish, E. S., & Tylianakis, J. M. (2013). Community shifts under climate change: Mechanisms at multiple scales. *American Journal of Botany*, 100, 1422–1434. <https://doi.org/10.3732/ajb.1300046>
- Gurevitch, J., & Padilla, D. K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution*, 19, 470–474.
- Hallett, L. M., Hsu, J. S., Cleland, E. E., Collins, S. L., Dickson, T. L., Farrer, E. C., Gherardi, L. A., Gross, K. L., Hobbs, R. J., Turnbull, L., & Suding, K. N. (2014). Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology*, 95, 1693–1700. <https://doi.org/10.1890/13-0895.1>
- Harrison, S. (2020). Plant community diversity will decline more than increase under climatic warming. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1794), 20190106. <https://doi.org/10.1098/rstb.2019.0106>
- Harrison, S. P., Gornish, E. S., Copeland, S., & Levine, J. M. (2015). Climate-driven diversity loss in a grassland community. *Proceedings of the National Academy of Sciences*, 112, 1–6. <https://doi.org/10.1073/pnas.1502074112>
- Harrison, S. P., LaForgia, M. L., & Latimer, A. M. (2018). Climate-driven diversity change in annual grasslands: Drought plus deluge does not equal normal. *Global Change Biology*, 24, 1782–1792. <https://doi.org/10.1111/gcb.14018>
- James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). *An introduction to statistical learning with applications in R* (1st ed.). Springer.
- Jonasson, S. (1988). Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, 52, 101–106. <https://doi.org/10.2307/3565988>
- Jung, I. W., & Chang, H. (2012). Climate change impacts on spatial patterns in drought risk in the Willamette River Basin, Oregon, USA. *Theoretical and Applied Climatology*, 108, 355–371. <https://doi.org/10.1007/s00704-011-0531-8>

- Klausmeyer, K. R., & Shaw, M. R. (2009). Climate change, habitat loss, protected areas and the climate adaptation potential of species in mediterranean ecosystems worldwide. *PLoS One*, *4*, e6392. <https://doi.org/10.1371/journal.pone.0006392>
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, *15*, 259–263. <https://doi.org/10.1127/0941-2948/2006/0130>
- LaForgia, M. L., Harrison, S. P., & Latimer, A. M. (2020). Invasive species interact with climatic variability to reduce success of natives. *Ecology*, *101*, 1–10. <https://doi.org/10.1002/ecy.3022>
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.
- Levine, J. M., McEachern, A. K., & Cowan, C. (2010). Do competitors modulate rare plant response to precipitation change? *Ecology*, *91*, 130–140. <https://doi.org/10.1890/08-2039.1>
- Lindh, B. C. (2018). Tipping the native-exotic balance: Succession in restored upland prairies in Oregon's Willamette valley. *Ecological Restoration*, *36*, 28–40. <https://doi.org/10.3368/er.36.1.28>
- Ma, M., Collins, S. L., & Du, G. (2020). Direct and indirect effects of temperature and precipitation on alpine seed banks in the Tibetan Plateau. *Ecological Applications*, *30*, 1–13. <https://doi.org/10.1002/eap.2096>
- Mariotte, P., Spotswood, E. N., Farrer, E. C., & Suding, K. N. (2017). Positive litter feedbacks of an introduced species reduce native diversity and promote invasion in Californian grasslands. *Applied Vegetation Science*, *20*, 28–39. <https://doi.org/10.1111/avsc.12291>
- Melgoza, G., Nowak, R. S., & Tausch, R. J. (1990). Soil water exploitation after fire: Competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia*, *83*, 7–13. <https://doi.org/10.1007/BF00324626>
- Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S. A., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S., & Rillig, M. C. (2014). Choosing and using diversity indices: Insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*, *4*, 3514–3524. <https://doi.org/10.1002/ece3.1155>
- Mote, P. W., & Salathé, E. P. (2010). Future climate in the Pacific Northwest. *Climatic Change*, *102*, 29–50. <https://doi.org/10.1007/s10584-010-9848-z>
- Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R² and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society, Interface*, *14*, 1–11.
- Noss, R. F., LaRoe, E. T., & Scott, J. M. (1995). *Endangered ecosystems of the United States: A preliminary assessment of loss and degradation*.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D. et al (2019). *vegan: Community Ecology Package*. R package version 2.5-6. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., ... Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*, eaai9214. <https://doi.org/10.1126/science.aai9214>
- Pendergrass, A. G., Knutti, R., Lehner, F., Deser, C., & Sanderson, B. M. (2017). Precipitation variability increases in a warmer climate. *Scientific Reports*, *7*, 1–9. <https://doi.org/10.1038/s41598-017-17966-y>
- Pfeifer-Meister, L., Bridgman, S. D., Little, C. J., Reynolds, L. L., Goklany, M. E., & Johnson, B. R. (2013). Pushing the limit: Experimental evidence of climate effects on plant range distributions. *Ecology*, *94*, 2131–2137. <https://doi.org/10.1890/13-0284.1>
- Pfeifer-Meister, L., Bridgman, S. D., Reynolds, L. L., Goklany, M. E., Wilson, H. E., Little, C. J., Ferguson, A., & Johnson, B. R. (2016). Climate change alters plant biogeography in Mediterranean prairies along the West Coast, USA. *Global Change Biology*, *22*, 845–855.
- Prevéy, J. S., & Seastedt, T. R. (2014). Seasonality of precipitation interacts with exotic species to alter composition and phenology of a semi-arid grassland. *Journal of Ecology*, *102*, 1549–1561. <https://doi.org/10.1111/1365-2745.12320>
- R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Reed, P. B., Bridgman, S. D., Pfeifer-Meister, L. E., Peterson, M. L., Johnson, B. R., Roy, B. A., Bailes, G. T., Nelson, A. A., Morris, W. F., & Doak, D. F. (2021). Climate warming threatens the persistence of a community of disturbance-adapted native annual plants. *Ecology*, *1–13*. <https://doi.org/10.1002/ecy.3464>
- Reed, P. B., Peterson, M. L., Pfeifer-Meister, L. E., Morris, W. F., Doak, D. F., Roy, B. A., Johnson, B. R., Bailes, G. T., Nelson, A. A., & Bridgman, S. D. (2021). Climate manipulations differentially affect plant population dynamics within versus beyond northern range limits. *Journal of Ecology*, *109*, 664–675. <https://doi.org/10.1111/1365-2745.13494>
- Reed, P. B., Pfeifer-Meister, L. E., Roy, B. A., Johnson, B. R., Bailes, G. T., Nelson, A. A., Boulay, M. C., Hamman, S. T., & Bridgman, S. D. (2019). Prairie plant phenology driven more by temperature than moisture in climate manipulations across a latitudinal gradient in the Pacific Northwest, USA. *Ecology and Evolution*, *9*, 3637–3650. <https://doi.org/10.1002/ece3.4995>
- Sala, O. E., Chapin Iii, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774.
- Saxton, K. E., & Rawls, W. J. (2006). Soil water characteristic estimates by texture and organic matter for hydrologic solutions. *Soil Science Society of America Journal*, *1578*, 1569–1578. <https://doi.org/10.2136/sssaj2005.0117>
- Simpson, E. H. (1949). Measurement of diversity. *Nature*, *163*, 688. <https://doi.org/10.1038/163688a0>
- Sinclair, M., Alverson, E., Dunn, P., Dunwiddie, P., & Gray, E. (2006). Bunchgrass prairies. In D. Apostol, M. Sinclair, & E. Higgs (Eds.), *Restoring the Pacific Northwest: The art and science of ecological restoration in Cascadia* (pp. 22–62). Island Press.
- Stanley, A. G., Kaye, T. N., & Dunwiddie, P. W. (2011). Multiple treatment combinations and seed addition increase abundance and diversity of native plants in Pacific Northwest prairies. *Ecological Restoration*, *29*, 35–44. <https://doi.org/10.3368/er.29.1-2.35>
- Suttle, K. B., Thomsen, M. A., & Power, M. E. (2007). Species interactions reverse grassland responses to changing climate. *Science*, *315*, 640–642.
- Thuiller, W., Richardson, D. M., & Midgley, G. F. (2008). Will climate change promote alien plant invasions? In W. Nentwig (Ed.), *Biological invasions* (pp. 197–211). Springer.
- USDA-Natural Resources Conservation Service (2012). *'Zorro' annual fescue (Vulpia myuros)*. California Plant Materials Center.
- USDA-Natural Resources Conservation Service. (2014). *Conservation Plant Release Brochure for 'Blando' brome (Bromus hordeaceus subsp. hordeaceus)*. California Plant Materials Center.
- Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: The analysis of proportions in ecology. *Ecology*, *92*, 3–10. <https://doi.org/10.1890/10-0340.1>

BIOSKETCH

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Author contributions: All authors designed the study and collected the data. PR analysed the data and wrote the manuscript, and all authors contributed to revisions and gave final approval for publication.

SUPPORTING INFORMATION

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