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Year effects drive beta diversity, but unevenly across plant community types

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Abstract

Year of establishment can be a critical driver of plant communities with the establishment stage of community development particularly susceptible to factors including ambient rain, temperature, and other temporally variable drivers (e.g., seed and seedling predators). However, while year effects have been shown to drive community structure at local (patch) scales, it is yet unexplored how these within-patch effects scale up to drive landscape-level patterns of biodiversity. These dynamics are likely to be critical but are overlooked in many systems including those with high-frequency disturbance regimes or active management. Here we leveraged a series of field-based grassland mesocosms established identically at three sites across 5 years, and each monitored for 4–8 years. We compared the strength of these temporal and spatial drivers (year effects and site effects) on consequent patterns of spatial and temporal variability (beta diversity and turnover) between plots seeded with native perennial species versus those seeded with nonnative annual species. The composition of plots seeded with perennial species showed strong effects of planting year and consequently exhibited higher beta diversity within sites (across mesocosms established in five different years within sites), while plots seeded with annual species had higher between-site variation but low beta diversity within sites. Plots with annual species were also more temporally variable than plots with perennial species. These findings have important implications for our understanding of key drivers of biodiversity across landscapes. Specifically, we showed that variable trajectories in community composition generated by site and year effects during establishment can promote beta diversity across landscapes dominated by perennial species, but are considerably less impactful in annual-dominated systems. These findings further our understanding of the importance of assembly dynamics on landscape-scale patterns of diversity, and have important management implications for restoration efforts.

KEYWORDS
assembly, beta diversity, heterogeneity, turnover, year effects

INTRODUCTION

Year of establishment can be a critical driver of plant community composition, with the establishment stage of community development particularly susceptible to factors including ambient rain, temperature, and other temporally variable drivers (e.g., seed and seedling predators) (Groves et al., 2020; MacDougall et al., 2008; Stuble, Fick, & Young, 2017; Werner et al., 2020). While it is now accepted that these "year effects" can drive community trajectories within a site, our understanding of how these dynamics may influence biodiversity across a landscape is limited (Werner et al., 2020). Landscapes are composed of a patchwork of sites of variable ages, each with a unique community assemblage influenced by the nuances associated with the year of establishment, for example, areas burned, flooded, abandoned, or restored in different years (Turner et al., 2013; Turner & Gardner, 2015). Across a patchwork landscape, the variation in communities associated with year effects could consequently be assumed to impact patterns of biodiversity across the landscape. Specifically, variability among sites across the landscape would likely increase beta diversity, an aspect of landscape-level diversity driven by differences between community assemblages across individual sites (Socolar et al., 2016). However, our understanding of the temporal mechanisms structuring beta diversity is limited (Hu et al., 2022; Khattar et al., 2021) and, in particular, the potential for year effects to scale up to influence landscape-level beta diversity has not been directly investigated.

Not all plant communities are likely to experience year effects in the same ways, and certain systems or species could be more prone to exhibiting strong and/or lasting year effects. For example, annual-dominated and perennial-dominated communities are likely to differ in the mechanism, magnitude, and duration of their responses to year effects during establishment. We could expect that initial establishment success would be particularly important for long-lived species (Chu & Adler, 2015), which, once established, typically persist on the landscape for years, decades, or longer. For such long-lived species, an initial favorable or, inversely, unfavorable establishment year could have persistent consequences through age-asymmetric competition dynamics (Connolly & Wayne, 1996; Mordecai et al., 2015). For example, in California grasslands, cooler, wetter years tend to promote native grasses, while warmer, drier years promote native forbs (Hallett et al., 2019; Pitt & Heady, 1978), and the weather conditions experienced in the year of initiation can drive the balance of grasses and forbs within a community for years following initiation (Stuble, Fick, & Young, 2017; Werner et al., 2020).

While there has been some experimental research exploring year effects in perennial communities, much of the theoretical and empirical literature on historical contingency in plant communities has focused on annual species (likely for practical reasons), in which there are also persistent legacies of year effects and other historical contingencies (Levine & Rees, 2004; Miller et al., 2021; Song et al., 2020). However, direct comparisons of the relative importance of year effects between annual-dominated and perennial-dominated plant communities are lacking, and how these year effects may scale up to landscape patterns of diversity in these communities is unknown.

When year effects have stronger and longer lasting impacts on community dynamics, they are likely to contribute to beta diversity in patchy landscapes. In contrast, when year effects are weaker or less persistent, even landscapes with patchwork disturbances may experience a lower contribution of year effects to beta diversity. While year effects seem likely to be a potentially important, yet rarely considered, driver of beta diversity, beta diversity is itself an emergent property of multiple interacting abiotic and biotic factors, many of which drive variation among sites. Beta diversity has been used to measure the strength of stochasticity in communities (Chase & Myers, 2011), although the drivers of beta diversity can themselves be site dependent and scale dependent (Segre et al., 2014). The heterogeneous patchwork represented by high beta diversity can be an important driver of temporal dynamics, as compensatory dynamics of different species increase community stability (De Mazancourt et al., 2013; Isbell et al., 2009; Wilcox et al., 2017). In systems with strong and persistent effects of establishment year, we might expect more stable communities, that is, less temporal variability within each plot (hereafter referred to as "turnover"). This would be consistent with an expectation that perennial-dominated communities, once established, vary less year to year than do annual-dominated communities. Indeed, a broad meta-analysis found that turnover was generally higher in communities with short-lived species than in perennial-dominated communities (Collins et al., 2018).

Here, we analyzed an 8-year field-based grassland mesocosm experiment that generated a patchwork of plots of varying years of initiation to explore long-term patterns of beta diversity and stability associated with perennial-dominated versus annual-dominated plant communities. Sown communities were either composed of annual nonnative grasses or perennial native grasses, and were established identically across 5 years of initiation and three sites. We calculated spatial beta diversity at two levels—within site and across sites—each considered within each sampling year (year of data collection). We also calculated one temporal metric of variation:

annual turnover. We hypothesized that within sites (within a given sampling year), spatial beta diversity would be higher among plots seeded with native perennial grasses than among those seeded with nonnative annual grasses (H_{1a}). We expected that this higher spatial beta diversity among native perennial-seeded plots would result from a combination of planting year effects and additional within-planting year and within-site stochasticity (H_{1b}). We additionally hypothesized that spatial beta diversity on a coarser, among-site scale would also be higher in native perennial-seeded plots than nonnative annual-seeded plots (H_{1c}). Conversely, we hypothesized that temporal variability (annual turnover) would be higher for plots seeded with nonnative annual grasses than for plots seeded with native perennial grasses, with higher annual turnover within nonnative annual plots than within native perennial plots (H_2).

METHODS

Study system

California Valley grasslands are widely distributed in California. Today, these grasslands are largely dominated by nonnative annual grasses including *Avena* spp., *Bromus* spp., and *Hordeum* spp. (Bartolome et al., 2007; Keeley, 1990). Native flora commonly includes perennial bunchgrasses and a mix of annual and perennial forbs (Lulow & Young, 2009; Stromberg et al., 2007). These grasslands are characterized by a Mediterranean climate with hot, dry summers and cool wet winters.

We established mesocosms at three grassland sites in Northern California: (1) the University of California, Davis Agricultural Experiment Station in Davis, California, (2) the Donald and Sylvia McLaughlin Natural Reserve near Lower Lake, California, and (3) the Hopland Research and Extension Center in Hopland, California (Table 1). Research plots were situated in areas that were flat, characterized by clay loam soils. All three research areas were used for crop agriculture in the years prior to the initiation of this experiment and were dominated by nonnative grasses at the start of this study.

Experimental design

We established mesocosms identically in 2011, 2012, 2013, 2014, and 2015. 1.56-m^2 (1.25 m × 1.25 m) plots were established by sowing plots with one of two seed mixes: four native perennial grass species (*Bromus carinatus*, *Elymus glaucus*, *Hordeum brachyantherum*, *Stipa pulchra*) or four nonnative annual grasses (*Avena barbata/fatua*, *Bromus hordeaceus*, *Hordeum murinum*, *Vulpia myuros/bromoides*). Due to site-level differences in dominant nonnatives, *A. fatua* was sown at Davis and *A. barbata* was sown at Hopland and McLaughlin. Similarly, *Vulpia myuros* was sown at Davis and McLaughlin, while *V. bromoides* was sown at Hopland. These species pairs were lumped at the genus level for the diversity analyses. *Bromus carinatus*, *Elymus glaucus*, *Hordeum brachyantherum*, *Stipa pulchra*, *Avena barbata/fatua*, and *Hordeum murinum* were sown at 100 seeds per square meter. *Bromus hordeaceus* and *Vulpia myuros/bromoides* were sown at 400 seeds per square meter. Seeding rates for native grasses were based on common restoration practices locally and seeding rates of nonnative grasses were estimated to have the potential to generate complete cover by the species in the absence of competition (Vaughn & Young, 2015). Seeds of local provenance were collected in the vicinity of each of the three sites. When local seed collection was not feasible for native grasses, seeds were purchased from Hedgerow Farms, using the closest provenance available for each site.

Plots were arranged in blocks with each block containing one plot representing each treatment type (sown with native perennials, sown with nonnative annuals). Five blocks were established at each site in each of the 5 planting years. Within blocks, plots were separated from neighboring plots by 1 m and blocks were separated from neighboring blocks by 4 m. Note that additional planting treatments were represented within the blocks that were not used in this analysis (c.f. Stuble, Zefferman, et al., 2017) and so these treatment mesocosms were typically separated by more than 1 m. Plots were prepared for planting by two rounds of tilling. The first round of tilling was timed shortly before the first

TABLE 1 Site conditions.

Site	Elevation (m)	Coordinates	Mean annual temperature (°C)	Mean annual rainfall (cm)
Hopland Research and Extension Center	150	39°00′ N, 123°04′ W	14	92
McLaughlin Natural Reserve	650	38°87′ N, 122°42′ W	15	75
UC Davis Agricultural Station	15	38°32′ N, 121°51′ W	16	45

Note: Temperature and rainfall averages represent historic means from 1986 through 2010.

germinating rain of the wet season, while the second round occurred 1–2 weeks following the first germinating rain. Because this was part of a larger experiment on priority effects (Stuble, Zefferman, et al., 2017), the sowing of annual and perennial seeds was slightly offset. Specifically, planting of native perennials occurred ~1 week following the second round of tilling and planting of nonnative annuals occurred ~3 weeks following the second round of tilling. At planting, sites were lightly raked, seeds were sown by hand, and then plots were lightly raked again to increase seed-soil contact. For the first growing season after planting, plots with serious (nonseeded) forb recruitment were weeded of forbs.

Aerial cover of seeded species was estimated visually by T. Young from May through June in 2012, 2013, 2014, 2015, 2016, 2018, and 2019 (Appendix S1: Figure S1), estimating cover to the nearest 1% for 1%–15% cover, and to the nearest 5% for higher covers. The total cover of unseeded species was also visually estimated for all grasses combined and all forbs combined, but this was not included in our analyses. Because of the extensive number of plots to be sampled in the broader experiment, not every plot was surveyed every year (Table 2).

Statistical analysis

To test H_{1a}, that within-site spatial beta diversity would be higher for plots seeded with native perennial grasses compared with plots seeded with nonnative annual grasses, we computed spatial variance using the multivariate homogeneity of group dispersions metric (Anderson et al., 2011). Specifically, we calculated (within site, within year) variance as the distance of each individual plot to the centroid of its respective treatment group (native perennial or nonnative annual) using the "betadisper()" function in the *vegan* package (Oksanen et al., 2019). Differences in beta diversity

(distance to centroid) among planting treatments (perennial vs. annual) were explored across all sampling years using linear mixed-effects models with planting treatment (perennial vs. annual) as a fixed effect and sampling year as a random effect. We did this calculation separately within each of our three sites and eight sampling years. Satterthwaite's degrees of freedom method was used to calculate significance (Bates et al., 2015; Kuznetsova et al., 2017). In addition to the general results presented across sampling years, we also individually analyzed the data collected in 2018, which was the year with the most complete sampling of all the planting years (Table 2). Distance to centroid within sites for just the 2018 sampling year was analyzed using ANOVA with planting treatment (perennial vs. annual) included as the explanatory variable.

To investigate the relative contributions of planting year effects, site effects, and sampling year to overall variability (H_{1b} and H_{1c}), we used PERMANOVA to partition variance in all plots' community composition separately for the native perennial plots and for the nonnative annual plots, and compared the proportion of variance explained by each variable (R^2).

To measure the turnover of each plot through time, we calculated the Bray–Curtis distance of each plot compared with itself in consecutive sampling years. We began these comparisons with the transition between the second and third growing years for each plot (not calculating turnover between the first and second growing seasons), as past work in this experiment has demonstrated that plots undergo strong changes in community composition in the first growing year as initial communities establish (Stuble, Fick, & Young, 2017). Because not all plots were sampled annually, sometimes a gap of more than 1 year was present between data points. For example, a plot planted in 2011 and sampled in 2012, 2013, 2014, 2015, and 2018 would have three turnover calculations: 2013–2014 (1-year interval), 2014–2015 (1-year interval),

TABLE 2 Years in which plots were sampled (columns), by year in which plots were planted (rows).

Year planted	Years sampled							
	2012	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**
2011	1	2	3	4	…	…	7	8
2012		1	2	3	…	…	6	…
2013			1	2	…	…	5	…
2014				1	2	…	4	5
2015					1	…	3	4
Total	1	2	3	4	2	0	5	3

Note: Numbers show plot age in years of plots that were sampled, "…" indicates that plots from those planting years were not sampled in a given year, and blank cells are plots that had not yet been planted in the given sampling year. All plots were sampled in 2018 (all 5 planting years), and all plots planted up to that point were sampled in 2015 (four planting years).

and 2015–2018 (3-year interval). We used a linear regression of turnover by time interval to calculate a conversion factor for community turnover over multiyear intervals (Appendix S1: Figure S2). This approach allowed us to include all seeded plots in the analysis while accounting for irregular sampling intervals. After applying this conversion factor, we used an ANOVA to compare the temporal variability of native perennial plots versus nonnative annual plots (H_2). All analyses and visualizations were done in R version 4.0.2 using *tidyverse* and *ggplot2* packages (Wickham, 2016, 2017), code and data (Werner et al., 2022) are archived in Figshare at https://doi.org/10.6084/m9.figshare.21505203.

RESULTS

Across all sampling years, beta diversity within sites was higher for perennial plots than for annual plots, with overall average distances to the centroid of 0.40 versus 0.33, respectively (Figure 1A; $t = -5.0$,

$p < 0.001$). Within sites, average distances to centroid across all sampling years were 0.39 versus 0.27 at the Davis site, 0.42 versus 0.31 at the Hopland site, and 0.37 versus 0.38 at the McLaughlin site. These differences can be clearly visualized in 2018, the year with a complete sampling of all seeded plots, with an overall average distance to the centroid of 0.42 for perennial-seeded plots versus 0.32 for annual-seeded plots (Figure 1B; $F = 10.9$, $p = 0.0012$).

Planting year, site, number of growing seasons, and data collection year all contributed significantly to the total variance among plots for both perennial and annual treatments (Figure 2, all $p < 0.001$ except data collection year for the perennial treatment with $p = 0.002$). The contribution of planting year to total variance was higher for perennial plots relative to annual plots (R^2 perennial 0.11 vs. annual 0.03), as was the contribution of number of growing seasons since the plot was planted (R^2 perennial 0.09 vs. annual 0.05; Figure 2). In contrast, the contributions of site and data collection year to total variance were lower for perennial plots relative to annual plots
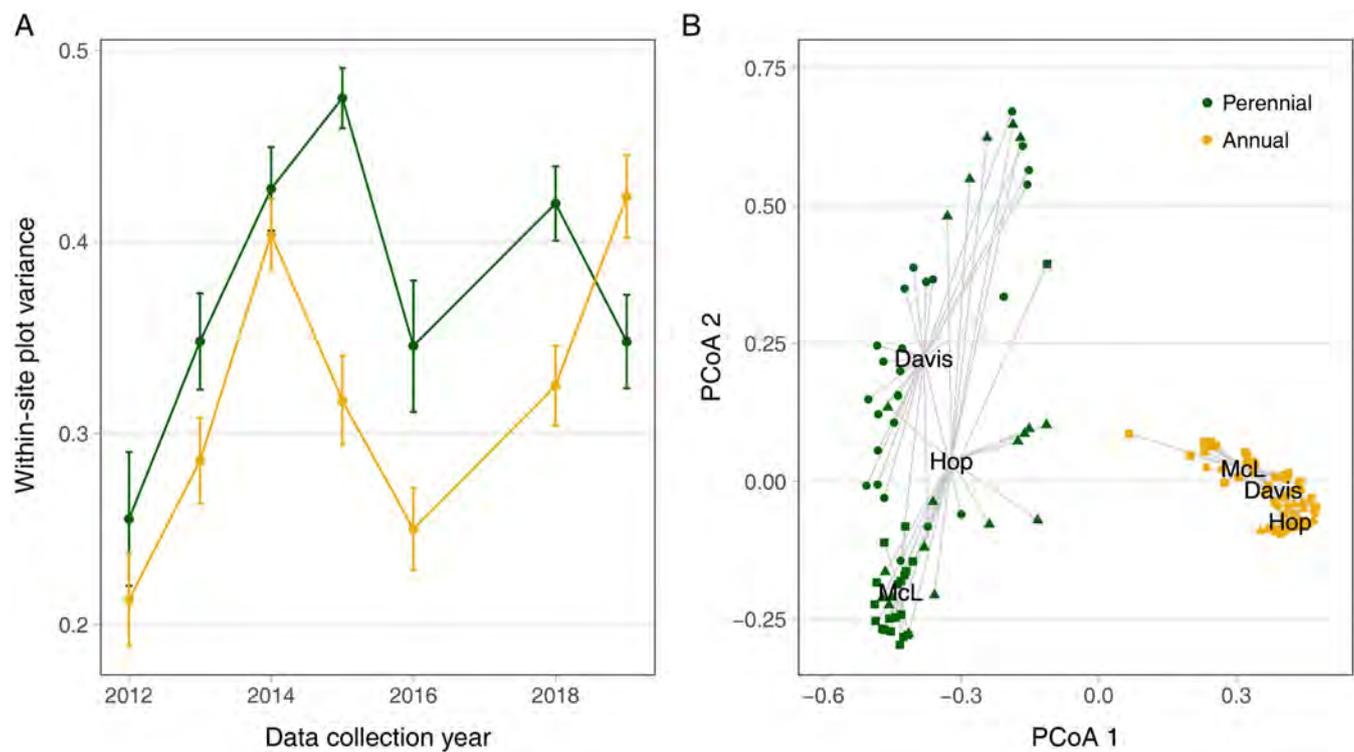

FIGURE 1 Spatial variance (beta diversity) within sites by treatment (A) across all survey years and (B) a visual depiction of the variance metric for all plots surveyed in 2018. Variance was calculated as the average distance to group median within each site across all 1 × 1 m plots. (A) Average variance within each of the three sites for each treatment, for each sampling year. Note that different data collection years sampled different subsets of plots, as enumerated in Table 2, with 2018 and 2015 being the most complete sampling years. Bars represent ±1 standard error (N = number of plots surveyed in each year, varying from 15 to 73). (B) Visualizing this variance calculation: a depiction in two-dimensional space of the distances from each plot to the group medians, for plots surveyed in 2018. Plots are marked with points, in green for perennial communities and yellow for annual communities, with shapes representing sites, site medians written with labels of site names, and gray lines showing the distance. Hop, Hopland; McL, McLaughlin.
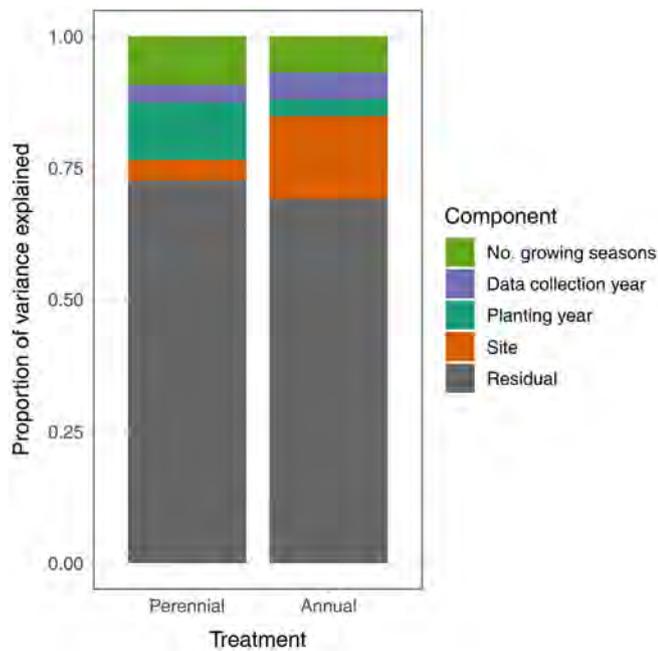
FIGURE 2 Proportion of plot variance in species composition explained by site, planting year, data collection year, and number of growing seasons (PERMANOVA, R^2 values, calculated separately for each treatment and shown side-by-side for comparison). All listed values are significant with all $p < 0.001$, except data collection year in the perennial treatment with $p = 0.002$.

(site R^2 perennial 0.04 vs. annual 0.16; data collection year R^2 perennial 0.03 vs. annual 0.05).

Temporal turnover of annual plots was higher than turnover of perennial plots across all three sites, and in particular at McLaughlin (Figure 3, $F = 5.1$, $p = 0.024$). The average Bray–Curtis distance for per-year turnover in perennial plots was 0.39, compared with a distance of 0.44 for annual plots.

DISCUSSION

Beta diversity within sites was higher among perennial-seeded plots than among annual-seeded plots. Higher beta diversity among perennial plots was driven, in part, by strong year effects (the effects of the year in which plots were established on resulting community composition). In contrast, the composition of annual plots was largely independent of the establishment year. Instead, these annual plots exhibited high levels of turnover from year to year, probably reassembling in response to the environmental conditions each year. Interestingly, these annual-seeded communities showed much higher sensitivity to site effects, with a greater proportion of variance among these communities explained by site than was the case for perennial-seeded
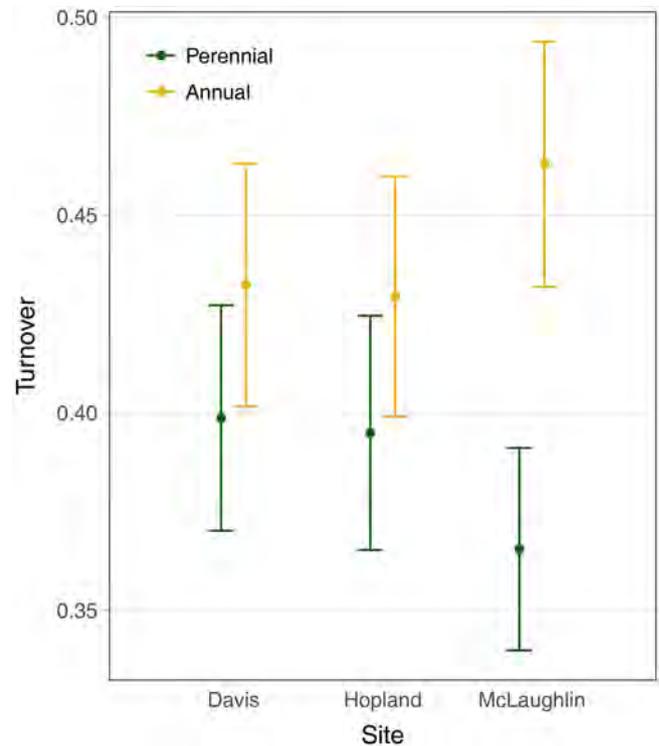

FIGURE 3 Community change through time within each plot, by site and treatment (mean $\pm$ SE). Turnover was calculated as Bray–Curtis distance within plots from one data collection time point to the next consecutive data collection time point. Because not all plots were sampled every year, sampling intervals ranged from 1 to 3 years; for time intervals longer than 1 year we used a conversion factor to estimate annual turnover (see Appendix S1: Figure S2 for more details).

communities. The year of data collection drove similar proportions of variance in both community types. Both site effects and year of establishment effects have the potential to drive species diversity across multiple spatial scales, but the differential responses of perennial-dominated and annual-dominated communities to these factors may play divergent roles in determining beta diversity across the landscape.

Fine-scale environmental variability among microsites is an important driver of beta diversity (Jiang et al., 2021); however, our findings suggest that, while much less recognized, temporal factors driving dissimilarity in communities established in different years can also be important drivers of beta diversity. It is increasingly understood that community composition can be shaped by conditions specific to the year of establishment (year effects) in ways that are often persistent through time (Groves et al., 2020; MacDougall et al., 2008; Stuble, Fick, & Young, 2017; Werner et al., 2020). Prior research in this study system and other grassland restoration systems has revealed annual rainfall and

mean annual temperature to be key drivers of community composition during assembly, along with other, yet unidentified, factors that vary interannually (Groves & Brudvig, 2018; Stuble, Fick, & Young, 2017; Stuble, Zefferman, et al., 2017). Here we emphasized how this variation, regardless of mechanism, can contribute to beta diversity as disturbance or restoration events occurring at relatively small spatial scales generate a patchwork of community ages across the landscape (Turner et al., 1993).

Site-to-site compositional dissimilarity, when driven by year effects in such landscapes, has the potential to drive higher levels of beta diversity in areas composed of multiple patch ages relative to even-aged landscapes. Higher within-site beta diversity can be associated with increased ecosystem functioning including higher or more stable biomass, soil carbon storage, litter decomposition rates, and resistance to invasion (Hautier et al., 2018; Mori, 2018; Reu et al., 2022; but see Van der Plas et al., 2023). Spatial heterogeneity in community composition across landscapes can also support wildlife diversity and stability (Hovick et al., 2015), which in turn can increase plant community diversity and heterogeneity (Knapp et al., 1999). This heterogeneity can also promote resilience to current and future global change impacts such as high-severity fire and new invasions (Hautier et al., 2018; Koontz et al., 2020) and can be important in maintaining ecosystem function in the face of climate change drivers, including drought (Yan et al., 2020).

We found that communities dominated by longer lived species exhibited a stronger signature of planting year effects over the long term, with the result that beta diversity in these communities was elevated in systems expressing a patchwork of community ages. In contrast, beta diversity was relatively insensitive to variation in patch ages in annual communities that exhibited weaker year effects. However, it is important to note that perennial species' sensitivity to year effects could be limited by seed availability, and in naturally regenerating systems without a robust seed bank, could be driven more by site-specific legacies (Young et al., 2019). Communities dominated by annual plants instead exhibited increased annual turnover, with weather conditions each year likely to have played an important role in determining community structure. This was in agreement with other studies finding relatively high interannual turnover in annual-dominated plant communities (Cleland et al., 2013; Collins et al., 2018). High turnover in annual-dominated communities can stabilize total community biomass through compensatory mechanisms, leading to more productive, if not necessarily more desirable, communities (Allan et al., 2011; Grman et al., 2010).

Assembly dynamics driven by year effects may interact with species invasions to drive landscape-level patterns of biodiversity. While nonnative species are known to suppress biodiversity by monopolizing space and resources, their unique assembly dynamics may couple with year effects to drive larger-scale losses in biodiversity. For example, many grasslands in the United States are dominated by nonnative annual grasses, including the sites in our study. While native-dominated communities (also containing native perennial bunchgrasses) have been found to be highly respondent to year effects during their year of initiation (Groves & Brudvig, 2018; Stuble, Fick, & Young, 2017), their nonnative annual counterparts may be less likely to set up lasting trajectories based on weather conditions during initiation; instead shifting in relative abundance every year based on conditions, as found in our study. If beta diversity within these nonnative annual-dominated communities is less influenced by year effects, this may limit beta diversity at the landscape scale, providing an additional mechanism via which nonnative species can impact biodiversity within ecosystems. This can compound with other homogenizing impacts nonnative species have on communities (Petsch et al., 2022), including the loss of rare species (Mollot et al., 2017) and spatial homogenization of soil nutrients (Dickens et al., 2013). In conjunction with this lower spatial diversity, nonnative annual-dominated communities may be more sensitive to year-to-year variation after establishment, and consequently exhibit higher turnover compared to native-dominated communities.

It is important to note that alpha diversity was consistent across our plots, each of which was seeded with four species of either annual or perennial grasses. This approach allowed us to disentangle patterns of alpha and beta diversity. That said, in naturally assembling and particularly more species-rich systems, these two factors are often interlinked (Jost, 2007). In addition, most natural systems are not entirely composed of perennial or annual species, but a combination of multiple life history strategies. In naturally assembling California grasslands nonnative-dominated grasslands have lower alpha diversity and lower within-site beta diversity than native-dominated grasslands, but patterns of beta diversity at higher scales are location dependent and scale dependent (Martin & Wilsey, 2015). Further extensions of our approach to higher diversity or mixed annual–perennial experiments might help to disentangle the interacting components of alpha and beta diversity in these systems.

The potential for year effects to drive levels of beta diversity across the landscape has clear implications for restoration work. Restoration outcomes are notoriously difficult to predict (Brudvig et al., 2017; Stuble, Fick, & Young, 2017) and can be susceptible to strong year

effects, with the year of initiation setting up alternative trajectories for a restored system (Baeten et al., 2010). As a result, it can be difficult to predict the outcome of restoration in a particular year (Stuble, Zefferman, et al., 2017) and identical restorations conducted in different years would probably yield differing results, sometimes dramatically so (Bakker et al., 2003; Stuble, Fick, & Young, 2017). This dynamic might be harnessed to promote beta diversity in restored landscapes by purposefully initiating restoration efforts at multiple time points (across the landscape), promoting distinct community trajectories across the restored landscapes, and ultimately increasing beta diversity. Increased beta diversity in the restored landscape can serve to promote resiliency and ecosystem function.

Year effects are known to influence community composition in ways that make the timing of events, including disturbance and restoration, critical in many systems. But while we understand these dynamics to be an important driver of community dynamics at small spatial scales, less is known about how these dynamics may shape levels of diversity across landscapes. Here we show that year effects—and specifically variable years of community initiation across patches of land—can be important drivers of diversity across the landscape. Specifically, variable initiation years in patches across the landscape can promote higher levels of beta diversity. While year effects are likely to be a key but underappreciated driver of biodiversity across landscapes, they can have far-reaching consequences for our understanding of potential threats to biodiversity and best practices in restoration and conservation. For example, the invasion of nonnative annual grasses into perennial-dominated native grassland systems has the potential to mute the influence of year effects beta diversity, potentially reducing biodiversity across the landscape via this novel pathway. Restoration practices, however, could be shaped to harness this knowledge, developing multiyear restoration practices specifically aimed at increasing beta diversity across the landscape.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Werner et al., 2022) are available in Figshare: https://doi.org/10.6084/m9.figshare.21505203.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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