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OPINION ARTICLE

Homogenizing biodiversity in restoration: the "perennialization" of California prairies

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Restoration frequently aims to improve native species biodiversity at a site, but practitioners have limited resources. In diverse ecosystems, the selective use of certain guilds or species can come at the cost of species that are more challenging to incorporate, resulting in the overall homogenization of the ecosystem and a relative loss of biodiversity. We surveyed practitioners who restore California prairies to understand their use of native annual forbs, an important component of the biodiversity in this ecosystem. We found that practitioners preferentially planted native perennial species, mainly grasses. Despite practitioners' recognition of the high conservation value of native annual forbs, they were hesitant to include this guild in their planting palettes because of high costs, low and unpredictable establishment, and lack of seed. We recommend that California annual prairie forbs be seeded in multiple years to enhance establishment, and that monitoring targets be designed to better reflect the high variability in interannual abundance of native annual forbs. These issues are not unique to California prairie, and more broadly, restoration objectives and research across a range of ecosystems should prioritize guilds that are more challenging to establish but are of high conservation concern.

Key words: biotic homogenization, grassland, native annual forbs, perennial species, prairie diversity, restoration goals, species palette

Implications for Practice

- Restoration goals, practices, and research should incorporate a fuller suite of species, including those that are more challenging to propagate and establish, such as annual forbs in California prairies.
- Restoration objectives and monitoring should be tailored to reflect differences in life histories across plant guilds.
- Practitioners can employ several techniques to reduce the cost and risk associated with planting native annual forbs, such as seeding or planting in subportions of larger restoration projects, in years with high expected precipitation, or over multiple years.

Biotic Homogenization in Restoration

Restoration projects have various goals, but often seek to restore a similar species composition to that of a reference ecosystem (McDonald et al. 2016). Restoration activities frequently aim to increase the diversity of native species present at a site; however, species are often selected based on ease and cost of collection and propagation (Elliott et al. 2003; Meli et al. 2014), which in turn can result in the planting of the same suite of relatively few readily available, quick-to-grow, and easily established species in many restoration projects (Hughes et al. 2017), eventually homogenizing a site or system relative to the desired reference communities, if not the prerestoration state. Native species that are patchily distributed, slow growing, or difficult to establish are less likely included in restoration species palettes. In other words, restoration has tended to focus on dominant species and site-level (α) diversity rather than restoring the full suite of species across the landscape (β-diversity) (Holl 2002; Polley et al. 2005). We contend that this narrowing of the pool of locally present species homogenizes the ecosystem, and in some cases, could shift the life-history composition of a community by favoring plant guilds or species that are better studied and easier to establish, or better at outcompeting non-native species.

The homogenization of communities through restoration is particularly problematic in biodiversity hotspots that host many endemic species and have exceptionally high species richness over a small area. Here, we highlight the challenge of restoring ecosystems in which annual plant species contribute substantially to overall biodiversity, such as in some Mediterranean ecosystems, where the seasonal timing of precipitation and high interannual rainfall variability have contributed to the evolution of many annual species (Cowling et al. 2005; Clary 2008, 2012). Our informal observations suggest that annual species are often neglected in restoration efforts due

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to the financial and labor costs associated with collecting and germinating seed and specifically the unpredictability of establishing consistent populations. We focus our argument on restoration efforts in California's historically diverse prairies, where we work.

Like all Mediterranean regions, California experiences hot, dry summers and mild, wet winters, and has high interannual variability in the timing and quantity of precipitation (Cowling et al. 2005). These climate factors and the isolated geologic history of California led to the exceptionally diverse California floristic province, which includes large numbers of annual species, forbs in particular, making California a biodiversity hotspot (Myers et al. 2000; Calsbeek et al. 2003). However, human population growth and habitat conversion also make it an area of critical concern for conservation and habitat restoration (Hoekstra et al. 2004). In California, 75 prairie-associated species are listed under the federal Endangered Species Act, and 580 prairie-associated species have some form of state protection (Bartolome et al. 2014).

Though heavily debated, there is evidence that the historical composition of California's prairies was a matrix of perennial bunchgrasses, perennial forbs, and annual forbs (Hamilton 1997; Bartolome et al. 2007; Minnich 2008; Lulow & Young 2011; Fick & Evett 2018). California's prairies are home to an unusually high richness of native annual forbs, especially in northern coastal prairies. Annual forbs represent between 25 and 60% of recorded species richness in California prairies based on prior survey work (Stromberg et al. 2002; Hayes & Holl 2003; Ford & Hayes 2007; Lulow & Young 2009), though interannual and spatial variation in site-level richness can be dramatic. Furthermore, native annual forbs make up approximately 40% of endangered plant species listed statewide. Among the threats to this group of species are anthropogenic climate change (Harrison et al. 2015), invasive non-native plant species (Carlsen et al. 2000; Brandt & Seabloom 2012), habitat loss and urban development (Hoekstra et al. 2004; Ford & Hayes 2007), and changes to management regimes (Hayes & Holl 2003; Satterthwaite et al. 2007).

The recognition of how little remaining "natural" or remnant prairie exists in California and the addition of multiple prairie species to state and federal endangered species lists has driven a dramatic increase in prairie restoration and mitigation projects over the last 20–30 years. Nonetheless, our observations of practices where we work along the central coast of California suggest that prairie restoration has concentrated on perennial grasses and forbs, and the published research has focused largely on perennial grasses, in particular *Stipa* (*Nassella*) *pulchra* (Menke 1992; Hamilton et al. 1999; Buisson et al. 2008), that can be better competitors with non-native invaders (e.g. Brown & Rice 2000; Stromberg et al. 2007; Seabloom 2011; Mordecai et al. 2015).

Land Manager Survey

To evaluate whether our informal observations of preferentially planting perennial species were more widely supported by practitioners' choices, we surveyed 33 land managers, restoration practitioners, and private landowners involved in California prairie restoration (Appendix S1, Supporting Information). Respondents work in prairies throughout the state, including interior and coastal sites, though the majority are located coastally between San Luis Obispo and Mendocino, CA. We asked about the number of species used in restoration plans, how many are typically native annual forbs, and why these species are or are not included in their planting palette (see Appendix S2 for full survey responses).

The average number of projects completed by those surveyed was 5.2 ± 0.8, but respondents indicated that they included native annual forbs in less than half the projects (2.4 ± 0.5). For respondents who indicated that they had included native annual forbs in their projects, their planting palettes contained 27% native annual forb species, a proportion at the low end of the ecological range of what is typically found in high-quality remnant prairies (25–60% of recorded species, e.g. Ford & Hayes 2007; Hayes & Holl 2003; Lulow & Young 2009; Stromberg et al. 2002) (Table 1). This relative under-representation of annual forbs occurred despite respondents recognizing that native annual forbs were a historical component of the ecosystem, provide significant pollinator services, and have aesthetic value (Appendix S2). Practitioners who did include annual forbs were more often those who indicated that the species were the focal target of a project, or that they apply seeds but are not hopeful about their return: in other words, broadcast seeding native annuals is a "spray and pray" technique.

When prompted to list their reason(s) for preferring perennials and avoiding annual forbs, restorationists painted a clear picture about the differential costs and payoffs associated with planting annual and perennial species. Respondents typically did not include annual forbs in their planting palettes because these species are cost-prohibitive (seven respondents); they are incompatible with desired management practices, such as herbicide use (six); their low returns are discouraging (five); and seed typically is not available (four). These responses accurately reflect the ecology of these species. Costs associated with annual forbs can be high because collecting seed is difficult: plants do not appear annually in the same locations, appear patchily or in

Table 1. Number of species of each guild included in restoration projects as reported by survey participants. Values are mean number of species ±1 SE. Proportion of number of species of each guild as a function of the total number of species planted in parentheses. $n = 21$ respondents who do and $n = 12$ who do not include native annual forbs.

Practitioner Category	*Perennial Grasses*	*Perennial Forbs*	*Annual Forbs*
Do not include native annual forbs	3.8 ± 1.0 (64%)	2.1 ± 0.9 (36%)	0 (0%)
Include native annual forbs	4.7 ± 0.3 (31%)	6.5 ± 1.5 (42%)	4.2 ± 1.1 (27%)

small numbers, and the timing of flowering and seed set varies from year to year (Eviner 2014). Furthermore, it is well understood that annual forbs do not return consistently each year when they are planted, giving the appearance of low success.

Respondents indicated that perennial species are preferentially planted because they want fast, visible results, and perennial species typically establish more readily, occupy large footprints, and live longer, reducing the risk of reinvasion by non-native annual grasses (Seabloom et al. 2003; Corbin & D'Antonio 2004). Perennial species are also more likely to ensure that projects meet native cover targets, but this comes at the cost of overlooking a highly diverse and threatened plant guild. Both our survey and the land management literature suggest that land managers are risk averse (Wätzold et al. 2006; Dorrough et al. 2008) and, in short, planting perennials reduces perceived risk.

Moving Toward Restoring the Full Suite of Plant Species

We recognize the challenges of restoring annual species in California prairies and elsewhere. Hence, we offer recommendations to enhance the inclusion of annual plants in restoration efforts. Because so few restoration projects currently incorporate native annual species, even minor increases would be beneficial.

First, restoration plans should require planting or seeding the full suite of vegetative guilds as the reference or desired system, while at the same time recognizing valid concerns regarding the high cost, management challenges, and seed availability of less commonly used species and guilds. For example, California prairie restoration plans could incorporate seeding annual forbs in a small portion of the restoration site, followed by intensive management to favor these species, such as the removal of non-native annual grasses through grass-specific herbicides or well-timed mowing. By planting in only a small subsection of a restoration site, this approach would reduce the labor, cost, and risks, while reflecting the naturally patchy distribution of native annual forbs.

Second, restorationists can reduce risks by planting or seeding annual species in years when they expect particularly high success, such as in the first wet year following drought (Levine & Rees 2004). Several authors have recommended that establishment success could be increased by introducing a smaller number of prairie species over multiple years, rather than using all the propagules in a single year (Seabloom 2011; Stuble et al. 2017; Wilson 2015; Bakker et al. 2003). Additionally, research in restoration settings suggests that some native perennial forbs benefit from priority effects, and seeding annual forbs earlier than perennial grasses might also enhance outcomes (Young et al. 2017).

Third, project objectives and associated monitoring plans should be designed to reflect the varying life history patterns of different plant guilds. For example, given that annual species often do not appear consistently year after year (Eviner 2014), it is more reasonable to expect some individuals to appear every 3–5 years rather than anticipating a high abundance every year. A California prairie monitoring plan species richness target might include two components: a minimum number of native species to appear annually, and a minimum number of species to appear over a 5-year period.

Finally, we call for additional research on specific seed collection and germination methods, propagation techniques, and beneficial management activities of rare, patchily distributed annual species and their seed banks. For example, in Mediterranean regions of Europe, techniques like soil transfers with intact seed banks or haying are sometimes used to introduce a diverse flora rather than seeding individual species (Coiffait-Gombault et al. 2011; Bulot et al. 2014), and these methods could also be useful in California's prairies. Moreover, these species often have specialized habitat requirements or mutualisms that are rarely well documented, but essential for successful reintroduction. Lastly, little is known about the sometimes extensive and long-lasting seed banks of native annual forbs, though restoring these seed banks may be a critical component in the long-term success of some native annual species (Bakker et al. 1996; Satterthwaite et al. 2007).

In conclusion, we have called attention to a case of restoration potentially homogenizing and perennializing a historically diverse habitat that is home to many native annual species, and we have offered suggestions to reverse this trend and promote the large-scale conservation of rare annual species. We hasten to note that this pattern of preferentially including easier-to-propagate and better-studied species and guilds in restoration is not unique to California prairies. For example, in tropical forests many tree species only fruit in certain years and seeds often do not have dormancy, so they cannot be stored for future restoration use (Holl 2012), making them challenging to use for restoration. Similarly, recent analyses of restoration projects in Brazil's mega-diverse tropical forest systems have shown that not all biogeographical regions are adequately represented in nursery-grown stock (Moreira da Silva et al. 2017), and that in the Brazilian Atlantic Forest, tree species with large animal-dispersed seeds are often more costly to obtain than other species and are under-represented in restoration plantings (Brancalion et al. 2018).

We acknowledge that it will not be possible to include all guilds of species in all restoration projects, given the range of restoration goals and the constraints that projects must work within. If a guild or species is to be excluded from restoration efforts and disappear from an ecosystem, let it be an active choice, rather than a disappearance by unintentional omission as we strive for other goals. We contend that for biodiversity-focused restoration projects, restoration practitioners and scientists must collaborate to develop and implement methods and set restoration objectives that restore the full suite of species, including those that are more difficult or risky to incorporate.

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LITERATURE CITED

Bakker JP, Poschlod P, Strykstra RJ, Bekker RM, Thompson K (1996) Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45:461–490

Bakker JD, Wilson SD, Christian JM, Li X, Ambrose LG, Waddington J (2003) Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications 13:137–153

Bartolome JW, Barry WJ, Griggs T, Hopkinson P (2007) Valley grassland. Pages 367–393. In: Terrestrial vegetation of California. University of California Press, Berkeley, CA

Bartolome JW, Allen-Diaz BH, Barry S, Ford LD, Hammond M, Hopkinson P, Ratcliff F, Spiegal S, White MD (2014) Grazing for biodiversity in Californian Mediterranean grasslands. Rangelands 36:36–43

Brancalion PHS, Bello C, Chazdon RL, Galetti M, Jordano P, Lima RAF, Medina A, Pizo MA, Reid JL (2018) Maximizing biodiversity conservation and carbon stocking in restored tropical forests. Conservation Letters 11:1–9

Brandt AJ, Seabloom EW (2012) Seed and establishment limitation contribute to long-term native forb declines in California grasslands. Ecology 93:1451–1462

Brown CS, Rice KJ (2000) The mark of Zorro: effects of the exotic annual grass *Vulpia myuros* on California native perennial grasses. Restoration Ecology 8:10–17

Buisson E, Anderson S, Holl KD, Corcket E, Hayes GF, Peeters A, Dutoit T (2008) Reintroduction of *Nassella pulchra* to California coastal grasslands: effects of topsoil removal, plant neighbour removal and grazing. Applied Vegetation Science 11:195–204

Bulot A, Provost E, Dutoit T (2014) Transférer le sol pour restaurer des communautés végétales: quelles leçons pour mesurer la résilience des pelouses sèches ? (Plaine de La Crau, Sud-Est de la France). Acta Botanica Gallica 161:287–300

Calsbeek R, Thompson JN, Richardson JE (2003) Patterns of molecular evolution and diversification in a biodiversity hotspot: the California Floristic Province. Molecular Ecology 12:1021–1029

Carlsen TM, Menke JW, Pavlik BM (2000) Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. Restoration Ecology 8:18–29

Clary JJ (2008) Rainfall seasonality determines annual/perennial grass balance in vegetation of Mediterranean Iberian. Plant Ecology 195:13–20

Clary JJ (2012) Determinants of perennial and annual grass distribution in Mediterranean-climate California. Plant Ecology 213:1203–1208

Coiffait-Gombault C, Buisson E, Dutoit T (2011) Hay transfer promotes establishment of Mediterranean steppe vegetation on soil disturbed by pipeline construction. Restoration Ecology 19:214–222

Corbin JD, D'Antonio CM (2004) Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85:1273–1283

Cowling RM, Ojeda F, Lamont BB, Rundel PW, Lechmere-Oertel R (2005) Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone Mediterranean-climate ecosystems. Global Ecology and Biogeography 14:509–519

Dorrough J, Vesk PA, Moll J (2008) Integrating ecological uncertainty and farm-scale economics when planning restoration. Journal of Applied Ecology 45:288–295

Elliott S, Navakitbumrung P, Kuarak C, Zangkum S, Anusarnsunthorn V, Blakesley D (2003) Selecting framework tree species for restoring seasonally dry tropical forests in northern Thailand based on field performance. Forest Ecology and Management 184:177–191

Eviner V (2014) Effects of weather variations on species composition and production in California's grasslands. Grasslands 24:2–7

Fick SE, Evett RR (2018) Distribution modelling of pre-Columbian California grasslands with soil phytoliths: new insights for prehistoric grassland ecology and restoration. PLoS One 13:1–16

Ford LD, Hayes GF (2007) Northern coastal scrub and coastal prairie. Pages 180–207. In: Terrestrial vegetation of California. University of California Press, Berkeley, CA

Hamilton JG (1997) Changing perceptions of pre-European grasslands in California. Madrono 44:311–333

Hamilton JG, Holzapfel C, Mahall BE (1999) Coexistence and interference between a native perennial grass and non-native annual grasses in California. Oecologia 121:518–526

Harrison SP, Gornish ES, Copeland S (2015) Climate-driven diversity loss in a grassland community. Proceedings of the National Academy of Sciences 112:8672–8677

Hayes GF, Holl KD (2003) Cattle grazing impacts on annual forbs and vegetation composition of Mesic Grasslands in California. Conservation Biology 17:1694–1702

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2004) Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8:23–29

Holl KD (2002) Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. Journal of Ecology 90:179–187

Holl KD (2012) Restoration of tropical forests. Pages 103–114. In: Restoration ecology: the new frontier. Wiley-Blackwell, Hoboken, NJ

Hughes AR, Grabowski JH, Leslie HM, Scyphers S, Williams SL (2017) Inclusion of biodiversity in habitat restoration policy to facilitate ecosystem recovery. Conservation Letters 00:1–8

Levine JM, Rees M (2004) Effects of temporal variability on rare plant persistence in annual systems. The American Naturalist 164:350–363

Lulow ME, Young TP (2009) High native forb richness in Central Valley "grassland" sites in the western Sacramento Valley and adjacent foothills. Grasslands 14:7–11

Lulow ME, Young TP (2011) Is there still native diversity in California grasslands? Fremontia 39:6–11

McDonald T, Jonson J, Dixon KW (2016) National standards for the practice of ecological restoration in Australia. Restoration Ecology 24: S4–S32

Meli P, Martinez-ramos M, Rey Benayas JM (2014) Combining ecological, social and technical criteria to select species for forest restoration select species for forest restoration. Applied Vegetation Science 17: 744–753

Menke JW (1992) Grazing and fire management for native perennial grass restoration in California grasslands. Fremontia 20:22–25

Minnich RA (2008) California's fading wildflowers: lost legacy and biological invasions. University of California Press, Berkeley, CA

Mordecai EA, Molinari NA, Stahlheber KA, Gross K, D'Antonio C (2015) Controls over native perennial grass exclusion and persistence in California grasslands invaded by annuals. Ecology 96:2643–2652

Moreira da Silva AP, Schweizer D, Rodrigues Marques H, Cordeiro Teixeira AM, Nascente dos Santos TVM, Sambuichi RHR, Badari CG, Gaudare U, Brancalion PHS (2017) Can current native tree seedling production and infrastructure meet an increasing forest restoration demand in Brazil? Restoration Ecology 25:509–515

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858

Polley HW, Derner JD, Wilsey BJ (2005) Patterns of plant species diversity in remnant and restored tallgrass prairies patterns of plant species diversity in remnant and restored tallgrass prairies. Restoration Ecology 13: 480–487

Satterthwaite WH, Holl KD, Hayes GF, Barber AL (2007) Seed banks in plant conservation: case study of Santa Cruz tarplant restoration. Biological Conservation 135:57–66

Seabloom EW (2011) Spatial and temporal variability in propagule limitation of California native grasses. Oikos 120:291–301

Seabloom EW, Harpole WS, Reichman OJ, Tilman D (2003) Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences of the United States of America 100:13384–13389

Stromberg MR, Kephart P, Yadon V (2002) Composition, invasibility, and diversity in coastal California grasslands. Madroño 48:1–47

Stromberg MR, D'Antonio CM, Young TP, Wirka JL, Kephart PR (2007) California grassland restoration. Pages 254–280. In: California grasslands: ecology and management. University of California Press, Berkeley, CA

Stuble KL, Fick SE, Young TP (2017) Every restoration is unique: testing year effects and site effects as drivers of initial restoration trajectories. Journal of Applied Ecology 54:1051–1057

Wätzold F, Drechsler M, Armstrong CW, Baumgärtner S, Grimm V, Huth A, et al. (2006) Ecological-economic modeling for biodiversity management: potential, pitfalls, and prospects. Conservation Biology 20: 1034–1041

Wilson SD (2015) Managing contingency in semiarid grassland restoration through repeated planting. Restoration Ecology 23:385–392

Coordinating Editor: David Norton

Young TP, Stuble KL, Balachowski JA, Werner CM (2017) Using priority effects to manipulate competitive relationships in restoration. Restoration Ecology 25:S114–S123

Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Copy of the land manager survey.
Appendix S2. Results of the land manager survey.
Table 1. The average number of species included in projects by their life history categories, and the total number of common species listed in survey responses.
Table 2. The seven most common perennial grass genera planted in California grassland restoration projects according to survey responses.
Table 3. The six most common native annual forb genera planted in California grassland restoration projects, according to survey responses.
Table 4. Reasons practitioners include or would like to include native annual forb (NAF) species in their restoration projects.
Table 5. Reasons practitioners do not include or are discouraged from including native annual forb (NAF) species in their restoration projects.

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