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Thirty Years of Changes in How We Understand and Steward California's Grasslands

by Valerie Eviner[1] and Michelle Halbur[2]

The California Native Grassland Association's (CNGA's) leadership in the restoration of California grasslands has extended far beyond incorporating the latest science into restoration techniques, it's also pushed the frontiers of research—forging new directions and recruiting and collaborating with researchers to explore novel ways of understanding these grasslands, addressing critical knowledge gaps in our stewardship. This is a short review of some of the major changes in our understanding of California's grasslands in the last 30 years.

1. It's not just the grasses

Over the decades, we've progressed beyond a focus only on native grasses, and have expanded our efforts and attention to forbs—the non-grass herbaceous species, such as our wildflowers. There are four times more forb species than grass species in California's grasslands, and thus these wildflowers comprise the majority of our plant diversity. This diversity provides critical functions, with many of these forbs having traits that are tolerant of drought, fire, gopher activity, and other disturbances (Hallett et al. 2017). As a group, these forbs are the emergency first-responders to many types of grassland disturbances. For example, plots with more grasses and fewer forbs in the seedbank showed a large decrease in plant cover and biomass in response to drought. In contrast, those plots with a seedbank dominated by forbs sustained plant cover and biomass during drought, because the forbs had a higher diversity of stress-tolerant traits, and were able to fill in for the grasses that failed to establish during drought (Hallett et al. 2017). These wildflowers have a long-term seedbank that can remain dormant in the soil, often for decades, and emerge when there is "empty space", usually because grasses fail to establish. This may occur when fire kills much of the grass seed in the thatch layer (Cox and Allen 2008) (Photo 1), or when early-fall rains are followed by drought, leading to germination but then death of annual grasses. Rainfall timing also affects the balance between grasses and forbs. For example, when grasses are

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Photo 1. Creamcups (*Platystemon californicus*) and California poppies (*Eschscholzia californica*) dominate a meadow the spring following the October 2017 Tubbs Fire. *Photo by Gary Morgret at Pepperwood Preserve.*

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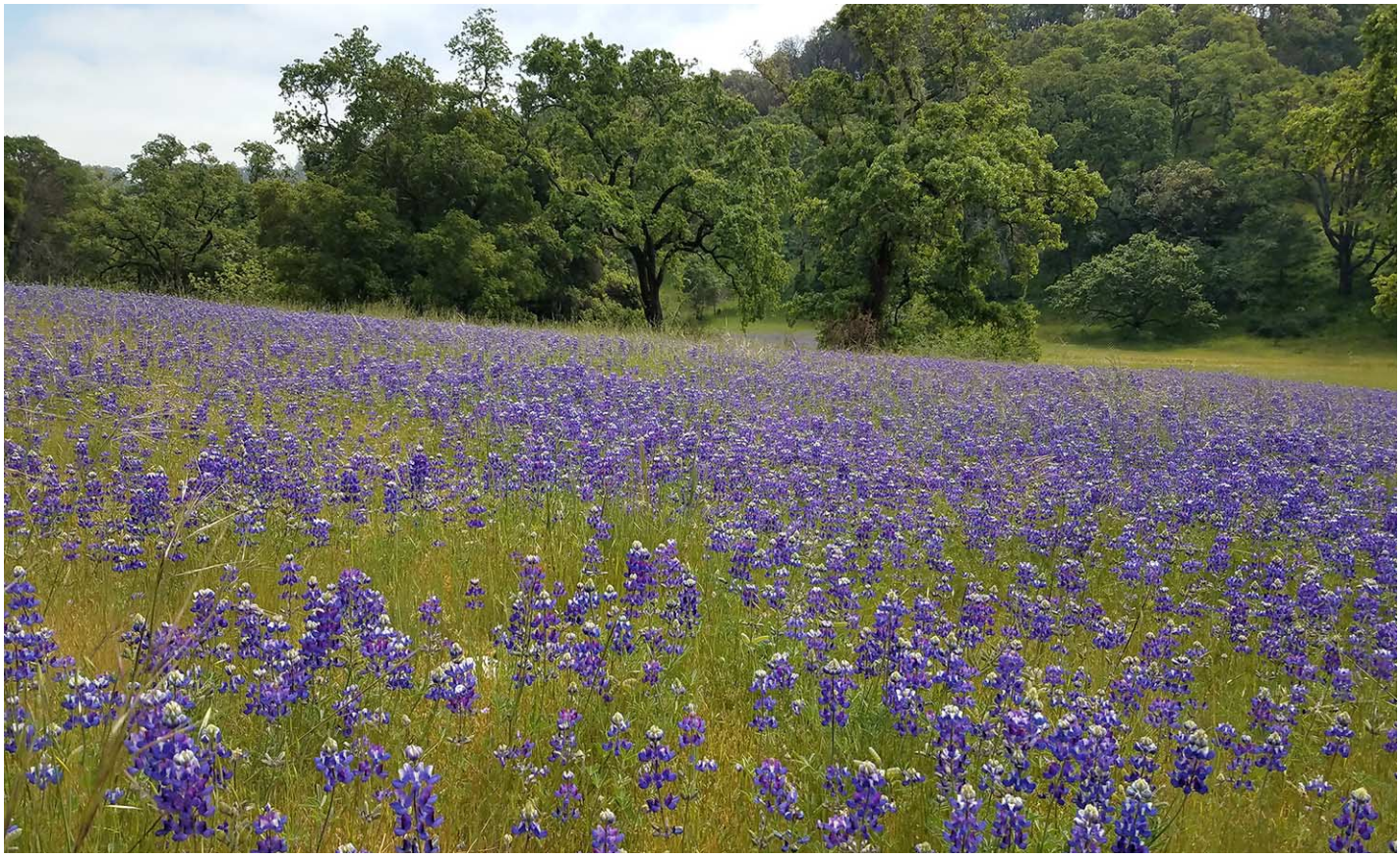

Photo 2. The dry 2020–2021 resulted in widespread domination of lupine across northern California. Pictured here, lupine in Spring 2021, following a 2019 wildfire. *Photo by Valerie Eviner, Pepperwood Preserve.*

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sparse due to early-season drought, filaree (*Erodium* spp.) tends to dominate (Hallett et al. 2019), and when there is an extended drought in the winter or spring, clover and other legume species tend to be prevalent, filling in for the grasses (Pitt and Heady 1978) (Photo 2).

Forbs aren't consistently present in the standing vegetation—their presence blinks on and off, depending on environmental conditions and management. The California super blooms are a great example of this—they occur occasionally, and one shouldn't expect that non-bloom years indicate a decrease in diversity or function of the grasslands. This can be frustrating in restoration, when considerable time, funds, and energy can be invested in establishing forbs, without seeing immediate results. The success of forb restoration comes through establishing a seedbank, from which forbs can emerge episodically under the right conditions. Unfortunately, the resilience of our grasslands may be decreasing due to a decline in the diversity of forbs, specifically native annual forbs, most likely associated with lower mid-winter precipitation (Harrison et al. 2015).

There is evidence that maintaining a robust forb seedbank requires active management of grasses, especially as their thatch builds up. High thatch levels inhibit forbs, and their prevalence increases with thatch removal (Bartolome et al. 2007, LaForgia 2021). Removing thatch through prescribed or cultural burns, grazing, or mowing can be critical to allow forbs to emerge in the standing vegetation, thus replenishing their seedbank (D'Antonio et al. 2000, Hayes and Holl 2003). For example, moderate grazing (compared to low grazing) was shown to be a critical tool for enhancing forbs in the seedbank and increasing their prevalence during drought (Hallett et al. 2017). Grazing for maintenance of forbs can be particularly important in areas with high atmospheric nitrogen deposition, where this pollution fertilizes the soil and increases grass and grass thatch, leading to extensive forb decline (Hernandez et al. 2021). Wildfires (Hernandez et al. 2021) and drought (LaForgia et al. 2018) can also be important natural disturbances that increase forb prevalence and increase the seedbank.

2. It's not just the plants

An important justification for California grassland restoration and conservation is that these grasslands are a hotspot of diversity, providing critical habitat for nearly 90% of the state's rare and endangered plant and animal species (Skinner and Pavlick 1994). This

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Photo 3. Soap plant (*Chlorogalum pomeridianum*) is abundant in the small mammal exclosure (left), and much rarer in the plot with small mammal activity (right). *Photo by Valerie Eviner, at Hopland Research & Extension Center.*

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broad diversity of organisms shapes California's grassland vegetation, and can even influence the balance between native and invasive plants. As indicated in the previous section, grazing can be a critical tool in the management of grassland vegetation, generally increasing the richness of forbs and cover of native grasses, although effects of course depend on site conditions, weather, and the intensity and duration of grazing (Stahlheber and D'Antonio 2013).

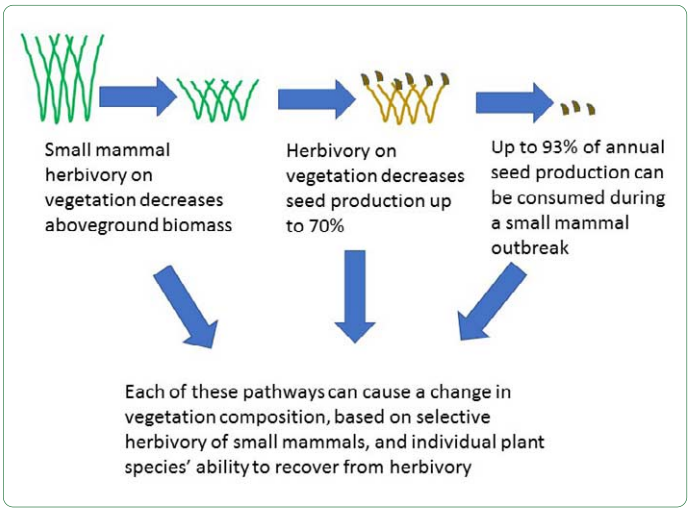

Figure 1. Small mammals impact grassland composition, productivity, seed production, and seed survival.

Small mammals, such as mice, ground squirrels, voles, moles, rabbits, and gophers, are abundant in California's grasslands and serve critical roles as herbivores, granivores, and seed dispersers (reviewed in Eviner 2016). Experimental removal of small mammals demonstrates the many impacts they have (Figure 1). Without small mammal herbivory on live vegetation, aboveground biomass increases by 40–87% (Peters 2007). This herbivory of live plants can decrease seed production by up to 70%. Small mammals also act as granivores, and during population peaks, can consume up to 93% of the annual seed production (Pearson 1964, Batzli and Pitelka 1970). These small mammals can have strong effects on plant community composition—decreasing the density of preferred seed species by 30–62% (Borchert and Jain 1978). For example, small mammals decrease cover of exotic plants, especially exotic forbs (Maron et al. 2014). Purple needlegrass (*Stipa pulchra*) density can decrease by 52% due to voles, mice, squirrels, and rabbits (Orrock et al. 2008). Small mammals particularly decrease plants with bulbs or tap roots (Maron et al. 2014) (Photo 3). Gophers, through their herbivory and disturbance, also can decrease perennial grasses, while increasing annual grasses and forbs (Bartolome et al. 2007, Tyler et al. 2007).

Insects and gastropods also have strong effects on native perennial grasses. Grasshoppers tend to mature in late spring and summer, so have little effect on annual grasses which have largely senesced by that time, but consume perennial grasses and late-season forbs (Porter and

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Photo 4. Post-fire, vegetation biomass is substantially higher on ant mounds (area surrounded by flags) than the surrounding landscape. *Photo by Valerie Eviner, at Hopland Research & Extension Center.*

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Redak 1997). Slugs and snails (especially slugs) can consume high amounts of vegetation biomass, with their exclusion increasing aboveground biomass 28-71%. In a comparison of the effects of exclosures of small mammals vs. gastropods, snails and slugs decreased grassland seedling survival more than small mammals did—particularly decreasing seedling survival of forbs and legumes (Korell et al. 2016). The preferred food of gastropods may also change seasonally, with higher consumption of grasses in the fall, but higher forb consumption in the winter (Peters 2007). Ants also play an important role as seed consumers and dispersers and tend to increase legumes and non-native annual grasses, while decreasing forbs (Hobbs 1985, Peters et al. 2006). Their mounds are hotspots of soil organic matter and nutrient availability as well as soil microbial biomass (Beattie 1989, Boulton et al. 2003), and higher plant biomass on ant mounds is very noticeable post-fire (Photo 4).

Some of the greatest advances in enhancing our understanding of California's grasslands are related to the soil microbial community, with new technologies allowing us to measure their composition and activity. Microbial communities can strongly impact plant growth and the relative amount of growth in roots vs. shoots (Brandt et al. 2009). Different plant species can culture different microbes in the soil, which, in turn, can affect plant growth and competitive ability. For example, when soils are cultured by growing exotic annual grasses for five weeks, those exotic-cultured soils (even when exotic plants are then removed) decrease native grass biomass by 74% (Grman and Suding 2010) (the mechanism is unknown in this experiment). Similarly, exotic grasses change the composition of the soil arbuscular mycorrhizal community. Arbuscular mycorrhizae (AM) are fungi that are symbiotic with plants, exchanging plant carbon for soil resources, including nitrogen, phosphorus, and/or water. Most California grassland plants are reliant on these AM fungi, with growth, seed production, nutrient uptake, and drought stress tolerance being enhanced by this symbiosis (Harrison and Viers 2007). Native and exotic grasses culture different AM communities, and each plant group produces higher biomass and seeds when associated with their own AM community (Nelson and Allen 1993, Hausmann and Hawkes 2009, Vogelsang and Bever 2009, Haussman and Hawkes 2010). Exotic grasses have been shown to decrease AM in soil, decreasing native performance (Vogelsang and Bever 2009). This is particularly of concern because when plant communities consist of both native and exotic grasses, the effects of exotic grasses on AM are dominant (Vogelsang and Bever 2009, Haussmann and Hawkes 2009). These experiments largely have focused on the establishment phase of restoration—highlighting the importance of the soil microbial community to successful native restoration. Fortunately, there is one study that indicates that once native species establish, the AM community reverts to AM associated with native grasses (Nelson and Allen 1996), suggesting that soil microbial communities can be restored through plant restoration, over the long term.

Restoration efforts that use soil inoculation of AM from native soils can enhance native performance, but inoculation with commercial AM does not appear effective at enhancing natives (Emam 2015,

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Koziol et al 2018). In some cases, AM can help exotic plants become more competitive. AM form networks, plumbing into many individual plants simultaneously, moving nutrients such as phosphorus between plants (Chiariello et al. 1982). This network appears to help the non-native Napa starthistle (*Centaurea melitensis*) dominate over purple needlegrass presumably by parasitizing purple needlegrass through the AM (Callaway et al. 2003). Our best current understanding is that AM can play a critical role in native restoration, but we still have a lot to learn about how to manage the preferred types of AM, particularly in the presence of exotic annual grasses.

Another type of soil microbe also influences interactions between native and exotic grassland plants. Nitrifying bacteria convert plant-available nitrogen in soil from the ammonium to the nitrate form. As nitrate, this nitrogen can move more extensively through the soil, and is at greater risk for leaching losses. A series of studies at Hopland Research & Extension Center indicated that annual exotic grasses increase the population size of nitrifying bacteria and alter their community composition, doubling the rate of nitrification (Hawkes et al. 2005). In a greenhouse trial, nitrification inhibitors, commonly used in agriculture, were applied to soils cultured by exotic grasses, and resulted in nearly double native grass growth (Waitman 2019, Eviner et al. in prep.). This suggests that native restoration may benefit from reversing the soil changes that occur due to exotic grass invasion. A key challenge in understanding and managing soil nutrient cycling effects on plants, is that its effects vary from experiment to experiment. Native grasses have been shown to both increase and decrease nitrogen cycling, compared to exotic grasses, and more work needs to understand the site- and time-specific nature of these effects (Eviner and Firestone 2007, Eviner 2016, Carey et al. 2017).

Native grass establishment can also be limited by the pathogens they culture in their own soil, with their growth more than doubling with soil sterilization (Waitman 2019). Viruses are important pathogens that can limit native grass establishment. Barley yellow dwarf virus and cereal dwarf virus, spread by aphids, can decrease survivorship of native grasses by 50–80% (Malmstrom et al. 2006, Borer et al 2007), with effects increasing in the presence of annual grasses. These viruses have much more muted effects on annual grasses, since these grasses die each year and are not stressed long-term by the viruses.

3. Ecosystem services

Native grasslands are not just important for species conservation, but also provide many ecosystem services that benefit humans. As discussed previously, perennial grasses and native forbs are important for persistence of plant cover during drought, and rapid establishment following fires. Wildflowers in our grasslands are critical for supporting pollinators for California's agriculture (Kremen et al. 2004, Chaplin-Kramer et al. 2011). Carbon storage is important for mitigating climate change, and soil carbon can provide drought resilience by enhancing water infiltration and storage. The impacts of native grass restoration on soil carbon are mixed. A comparison of remnant stands of native grasses vs. invaded annual stands indicates that remnant perennial grasslands have higher soil carbon (Koteen et al. 2011). In studies of restored grassland sites, some show that planting perennial grasses does not change soil carbon (Potthof et al. 2005), while others show changes in the distribution of carbon, with deeper carbon that increases water holding capacity, providing deep-soil late-season water that extends the growing season for both native and exotic grasses (Eviner et al. in prep). Decisions of where to prioritize native restoration can be aided by a better understanding of which ecosystem services will be most enhanced by restoration, and how that varies by location across the landscape.

4. Future challenges and priorities

Conservation of remnant grasslands

Over the last few decades, there has been remarkable progress in techniques and resources to improve the restoration of California's native grasslands, as highlighted in every CNGA event and publication. While planting natives is critical for the restoration of our native grasslands (Seabloom et al. 2003), there is still high variability in the success of restoration projects, and high uncertainty in the best restoration approaches at a given site, and under a given set of weather conditions (Nolan et al. 2021). Given the importance of our grasslands in supporting diverse species and ecosystem services that Californians depend on, restoration efforts are critical. However, our top priority should be conserving remnant native grasslands. It is unrealistic to assume that we have the ability to replace grasslands that are being destroyed through land-use change—relying on mitigation is risky and expensive.

Landscape-scale approaches to conservation and restoration

Where grasslands occur and how they are managed across the landscape will strongly affect their regulation of ecosystem services, such as support of pollinators, water infiltration and storage, water purification, erosion control, fire control, and invasive species control. Regional planning across multiple partners and landowners is critical for managing these ecosystem services, and a landscape framework must be used to prioritize which grasslands will be conserved, where grasslands will be restored, and how grasslands will be managed and for what suite of goals. This landscape approach becomes more important under changing environmental conditions, where conservation of our grasslands will not just entail protecting them from development. Grassland distribution is projected to change with shifts in wildfire and climate, and changes in management such as grazing and prescribed fire (Eviner 2016). Coastal grasslands are likely

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to shift with sea-level rise, and riparian grasslands and wet meadows are changing due to hydrological shifts (from stream incision to changes in the timing and duration of flooding or inundation). Managing our grasslands under these complex changes requires extensive mapping of grasslands and their potential habitat and ecosystem service values, a better understanding of grassland community dynamics under a changing climate, and identifying how vulnerable each patch may be to current and future changes. Coordinated efforts between public land agencies, land trusts, conservation groups, and private landowners will be critical for achieving landscape-level conservation and restoration of grassland species and ecosystem services.

Changing resilience of grasslands

Numerous studies highlight the challenges of grassland stewardship and resilience in the future. News headlines describe unprecedented conditions in terms of warmer temperatures, droughts, changes in the timing of rainfall, and shifts in the frequency, intensity, and size of wildfires.

Restoration goals and approaches need to consider these changing conditions. Which species are most suited to the management and environmental conditions available? Which locations are most critical to restore? With fewer, and potentially larger, rainstorms with more dry periods between them, how do we successfully establish restoration sites (especially if we don't have access to irrigation)? Research in the last 30 years has highlighted the importance of selecting species based on their functions—which conditions they can tolerate (e.g. drought), and which conditions they can ameliorate (e.g. increasing soil water storage, increasing soil fertility). Plant traits can guide which species may be most tolerant or vulnerable to various challenges. Trait-based approaches have identified drought-adapted species, which include species that are highly plastic in their physiology and morphology (Luong et al. 2021, Funk et al. 2021). Relying on drought-adapted species can have tradeoffs, however, since these species tend to grow more slowly, and decrease plant production (Wolf et al. 2021).

There is increasing interest in restoration that proactively addresses climate change by sourcing species and genotypes from warmer, drier regions (e.g. Southern California), but this is highly contentious. Planting genotypes from other areas can provide plants adapted to novel environmental conditions, but can also cause unintended harm in numerous ways, including becoming invasive, disrupting existing local adaptations, disrupting the ability of the local community to respond to climate change, introducing pathogens, driving local species loss, altering community response to disturbance regimes, and disrupting the provisioning of ecosystem services (Hewitt et al. 2011, Alexander et al. 2015, Bucharova et al. 2018). Restoration has often focused on the importance of selecting local populations for restoration—those that are adapted to site-specific environmental conditions and community interactions, and that don't disrupt the evolutionary adaptations that local genotypes have developed (Knapp and Rice 1994). However, there is substantial debate about whether reliance on local genotypes is adequate for rapidly changing conditions. So far there is consensus that at least over the short term, reliance on local genotypes may be effective if it focuses on diverse local seed collections—including from diverse sites, especially including the poorest sites, and during the poorest years (Havens et al. 2015, Ramalho et al. 2017, Bucharova et al. 2018). For example, there can be substantial variability in plant traits (particularly phenology) across topographic positions within a landscape (Olliff-Yang and Ackerly 2020). It is also important to ensure that these restoration approaches extend beyond seed sourcing, with restoration plantings occurring across diverse sites within a region, creating refuges under variable conditions.

It is particularly critical to plant diverse species into restoration projects. When looking at native restored communities over time, the cover of natives as a group can be stable across disturbances and a variable environment, but different types of environmental changes lead to different individual species becoming more or less dominant (Seabloom 2007). For example, over 15 years post-restoration, native wildrye (*Elymus glaucus, Leymus triticoides*) dominated during the initial wetter years, while purple needlegrass became dominant during and after drought, and blue grass (*Poa secunda*) only had substantial cover during drought years (Eviner et al. in prep.). Diverse plant communities can have more reliable productivity year to year (Hallett et al. 2017) and can be critical in supporting pollinators by cumulatively providing flower resources over time, particularly under changing conditions (Olliff-Yang et al. 2020). Diverse native plantings are also critical for one of California restoration's greatest challenges-weed control. The most effective long-term weed control is achieved by suppressing exotic weeds with native plants with similar traits (e.g. similar seasonality, rooting depth, etc.) (Young et al. 2009), and a diversity of native perennial grasses can effectively suppress noxious weeds like goatgrass (*Aegilops* spp.) and medusahead (*Elymus caput-medusae*), even during their peak years (Eviner and Malmstrom 2018).

While warming, drought, and wildfires provide challenges to stewarding our grasslands, California's grasslands have experienced these conditions in the past and have evolved under these perturbations. We need to be vigilant against other environmental changes that may disrupt the evolved resilience of these grasslands. One example is nitrogen deposition—pollution from excess nitrogen in the atmosphere as a result of fossil fuel combustion, volatilization from agricultural systems, and fires. Nitrogen deposition changes plant

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species composition and favors plants that are weedier and more vulnerable to droughts (reviewed in Eviner et al. 2016). Similarly, as grasslands become more fragmented and managed by smaller landholders, there is less management (e.g. grazing, mowing, prescribed fires), which can lead to increased weeds, loss of resilience (e.g. loss of a robust wildflower seedbank), reductions in connectivity, and loss of many ecosystem services (Ferranto et al. 2011). While mitigation of climate change is difficult because it occurs at a global scale, changes in nitrogen deposition and land use are determined by regional-scale activities and policies, and California can take concrete steps to ensure these environmental changes don't limit our grasslands' resilience to climate change.

Meeting the challenges of restoring and conserving our grasslands under future conditions will require close collaboration between conservationists, managers, and researchers—and thus a continuation of the important leadership role that CNGA provides.

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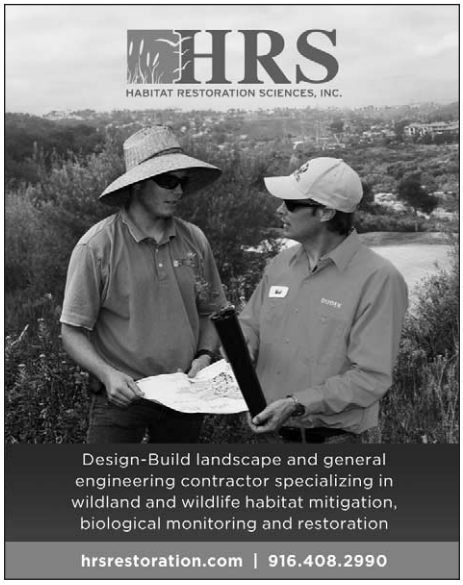
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