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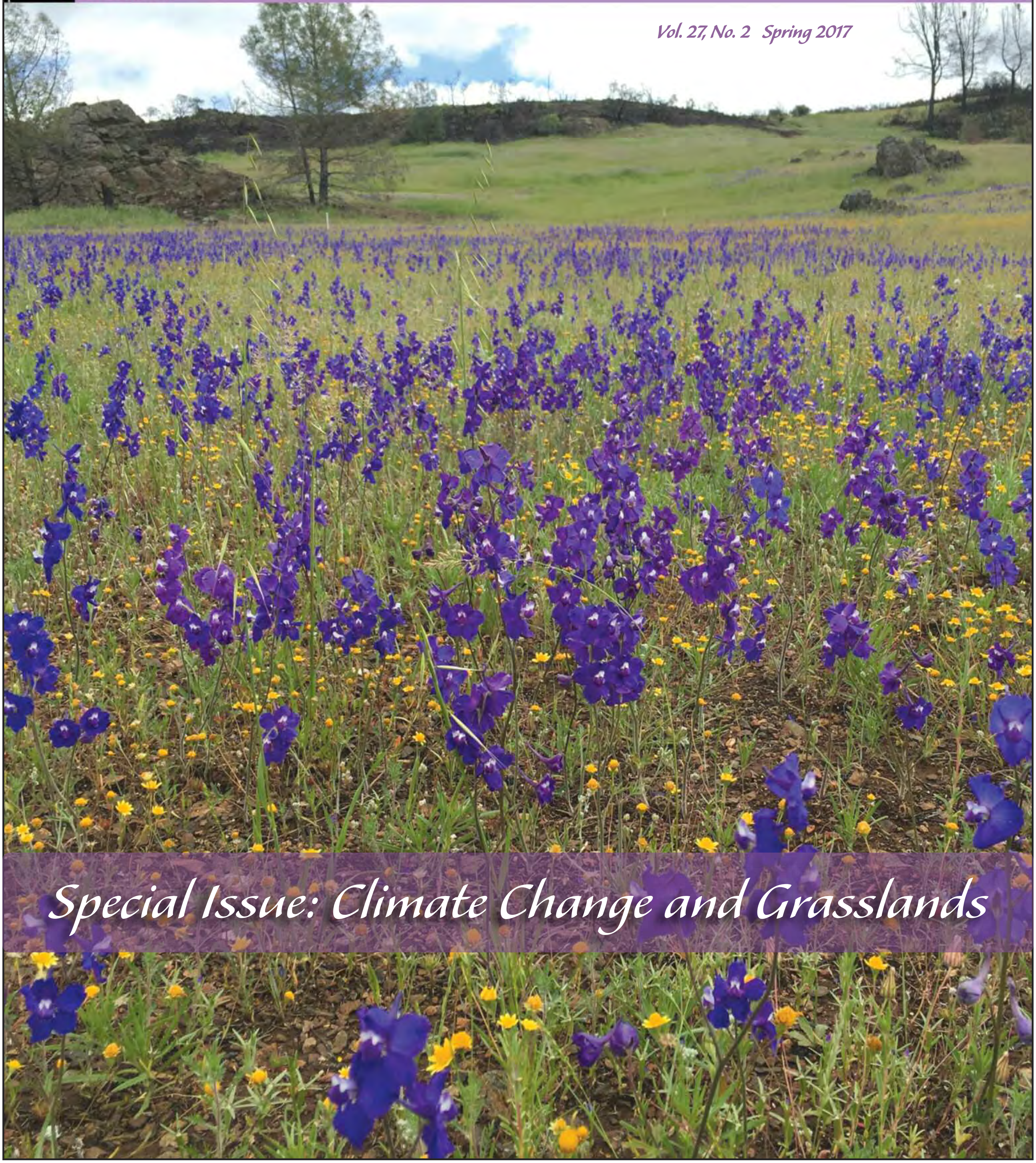

Special Issue: Climate Change and Grasslands

Experimental Approaches to Addressing Climate Change Challenges in Prairie Restoration

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Abstract

Climate change is one of the greatest threats to the future of biodiversity on the planet. As the climate shifts, species that cannot move or adapt quickly enough are at risk of being left behind, or even losing their habitats entirely (Malcolm et al. 2002, Thuiller et al. 2005, Burrows et al. 2014). Conservationists and restoration practitioners are working to incorporate climate change projections into their long-term strategies. Here we explore some challenges that restoration practitioners encounter in the face of climate change and suggest possible research agendas to maximize our chances of success. We illustrate these with examples from our own research.

Climate change offers multiple interrelated challenges for restoration

There is no longer any doubt that the earth is warming at an unprecedented rate (Pachauri et al. 2014). The consequences of this shift include rising sea levels and latitudinal and altitudinal shifts in the distributions of species and the habitats they depend upon. This warming is also increasing evaporation from the ocean, resulting in overall increases in global precipitation (Trenberth 2011). Patterns of rainfall at the regional level are less certain, and this drives much of the difficulty in predicting the *effects* of climate change (Walther et al. 2002): Some regions are expected to experience increases in rainfall, while others will experience decreases. Rainfall is also likely to become more variable from year to year (Pachauri et al. 2014, Berg and Hall 2015) and an increasing likelihood that rainfall events will occur as fewer, more intense episodes, the latter of which is already being documented (and Soden 2008). Even in regions that will experience increases or no change in total rainfall, drought stress also might be increased due to the warming temperatures (AghaKouchak et al. 2014).

The combined effects of climate change are also contributing to climate patterns that have no recent historical equivalents (i.e., "analogs"), but instead incorporate previously unseen combinations of mean precipitation, rainfall patterns, and temperatures (Williams and Jackson 2007). Such "non-analog" climatic conditions complicate restoration efforts, as practitioners have no reliable reference communities upon which to make restoration decisions. In light of these novel combinations of climate variables, the relatively straightforward prediction of species' and communities' movement pole-ward and up in elevation may prove overly simplistic.

How can restoration respond to both predictable and novel changes?

One option is to continue creating restoration plans that seek to recreate local historical reference communities. This may appear short-sighted, but we are still not sure precisely how most organisms (especially plants) will respond to uncertain climate change projections, and their historic distributions may not be entirely defined by climate; for example, interactions with other species may be important (Suttle et al. 2007, Gilman et al. 2010, HilleRisLambers et al. 2013). Given this uncertainty, many feel that a default "do no harm" approach is one that continues to approximate historical reference communities. However, even current climates have already shifted from their historical means, and so local reference communities may already be 'behind the curve' (Bradley et al. 2009).

Another approach is to try to get ahead of the curve, and plant species or communities that we anticipate will be better suited to projected future climates (McLachlan et al. 2007, Thomas 2011). This strategy raises at least two possible concerns. First, it assumes that climate projections are accurate (which is more likely for temperature than for rainfall at this stage) at the scale for which the planting is being conducted, and that we understand which climate variables drive

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Figure 1. Dr. Kurt Vaughn and Dr. Stephen Fick seeding prairie restoration experimental plots at the Hopland Research and Extension Center.

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Experimental Approaches *continued*

species and community responses (see Funk et al. 2008). Second, the practitioner must decide how far into the future to make their projection. Too far out, and the current plantings may fail, but not far enough, and they will become too quickly out of date (Broadhurst et al. 2008). This approach also doesn't provide any better understanding of the potential for local ecotypes (i.e., populations of plants that are adapted to local environments) to tolerate possible changes or whether existing populations have the capacity to adapt (Aitken and Whitlock 2013). Planning tools are available in some regions to help practitioners wishing to choose species or ecotypes based on future climate projections (e.g., **www.seedlotselectiontool.org**), but they are not currently in widespread use and more research is needed.

An additional strategy is to plant a wider mixture of species and ecotypes, matching a range of current conditions and future projections (Lesica and Allendorf 1999, Broadhurst et al. 2008). This can be thought of as "planting them all, and let nature sort them out". If approached thoughtfully, this could be designed to inform restoration strategies for an accelerated version of natural migration patterns (Sgrò et al. 2011). One question that arises is how different ecotypes will respond when planted in competition with each other or under variable environmental conditions. A recent experiment in California grasslands demonstrated that planting a variety of ecotypes did not increase the "home-field advantage" of local ecotypes, suggesting that a mixture of ecotypes may provide some room to sort themselves out over a number of years (Balachowski 2015). Another study found that ecotypes from southern California, which historically have experienced greater between-year variation in precipitation, were better able to respond to different watering regimes relative to ecotypes from central and northern California (Pratt and Mooney 2013). Sorting out the importance of traits that confer an advantage competitively under one set of environmental conditions from those that confer tolerance and survival under another will be important for understanding the persistence of different ecotypes over years with variable weather.

Research Approaches

Research can help pave the way to deciding which of these approaches are likely to be successful, and how best to carry them out. Traditional approaches to climate change research, as it relates to plant communities, include a) temperature and/or precipitation manipulations (e.g., Walker et al. 2006, Suttle et al. 2007, Young et al. 2015), and b) modeling the climatic tolerances of individual species or vegetation types (e.g., Araújo and Rahbek 2006, Hijmans and Graham 2006, Thorne et al. 2016, Hereford et al. 2017). Although each can be useful, both have limitations that may limit their broader effectiveness in practical use (Araujo and Peterson 2012, Schwartz 2012). Increasing the number of research studies using traditional experimental approaches such as planting common gardens (Miller et al. 2011), reciprocal transplants (Johnson et al. 2015), and competition gradients with seeding rates (Dyer and Rice 1997) would provide much needed information regarding the capacity of restoration as a tool to mitigate the impacts of climate change.

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Figures 2–4. Temporal priority prairie restoration experimental plots.

Experimental Approaches *continued*

Alternative approaches

We have been exploring an additional research strategy using natural variation in climate over locations and time to examine the longer-term consequences of climate for plant community development. Practitioners have long noted that restoration outcomes vary strongly from site to site and year to year, suggesting that they will indeed be strongly sensitive to climate change. However, linking this observation to experimental work on climate change and restoration has lagged.

Successional theory suggests that plant communities will converge on a particular stable state determined by long-term climate means (and soil conditions). More recently, assembly theory has suggested that variation in conditions at the time of establishment can produce different communities that are essentially stable (Young et al. 2001, MacDougall et al. 2008, Baeten et al. 2010). Differences in initial conditions driving long-term differences in community composition may include different arrival times of species, giving an advantage to species that arrive first (a "temporal priority"), and weather in the year of establishment. Variability in these conditions geographically, and over time, may alter relative success among species during establishment in ways that can structure longer-term communities.

We have been studying the power of temporal priority to drive differences in community structure in a series of experiments in California's Central Valley grasslands (Figures 1–4). This factor can provide broad insights into how various initial conditions may affect community assembly and trajectories. The emerging themes from this research suggest that:

- Temporal priority can have profound effects on short-term community development (Porensky et al. 2012, Vaughn and Young 2015, Stuble et al. 2017a);
- Initial differences can extend to longer-term shifts in community trajectories (Werner et al. 2016);
- Temporal priority advantage may not be consistent across species and guilds (Lulow 2004, Werner et al. 2016, Young et al. 2017); and
- Small differences across sites and planting years can strongly influence the strength of temporal priority and community structure (Young et al. 2015, 2017, Stuble et al. 2017b).

As between-year differences in weather might promote the initial establishment of some species over others, they can also create priority advantages for certain species. We expect therefore that the patterns we see from the manipulated temporal priority of species would also play out as differences in restoration outcomes driven by weather patterns experienced in the year of establishment.

If climatic variation in the years of establishment can have long-term implications for community structure, might it also provide a window into how communities will respond to climate change? If so, then examining species or communities that establish in years more closely resembling projected future climates may tell us how they may respond to climate change. With California's high between-year variation in weather, many species have persisted despite not successfully recruiting each year — but will there be a tipping point when those recruitment years become too few and far between? We now have evidence of just such effects in restorations of California grasslands from temporal priority experiments (Stuble et al. 2017a,b).

We have also shown that between-year differences in rainfall can have predictable effects on community structure, potentially allowing projections beyond current data sets (Stuble et al. 2017b). Thus, while our predictions held up in 3 of 4 years (in nine separate experiments), these projections faltered in an unusual weather year in which rain fell in a few heavy rain events (a weather pattern that, while currently unusual, is precisely the direction of some climate projections; see Cayan et al. 2008). On the one hand, this suggests that non-analog climates will pose a serious obstacle to our ability to project community responses to climate change. On the other hand, historically extreme weather patterns do occur occasionally, and perhaps these rare years can provide useful windows into an uncertain future (Stuble et al. 2017a). In this way, multi-year experiments can be used to predict which species or source populations are likely to thrive under various ranges of conditions. These types of results would allow restoration practitioners to manage not only for a single predicted future, but to select species or ecotypes likely to succeed under a range of potential future conditions.

Lastly, seeding or planting the same plant material across known differences in available soil moisture along topographic and soil gradients at the same time provides an opportunity to learn about the range of tolerance among species and ecotypes. Restoration studies

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conducted in this manner have found significant differences both among species within plant groups and more general patterns across plant guilds (Lulow et al. 2007, Kimball et al. 2017).

Conclusion

The relationship between ecological restoration and climate change it still very much in flux. Both the nature of the climatic challenges and the possible responses to them are far from resolved. It is likely that only as multiple approaches are undertaken, and found to be variously effective within certain regions or climatic contexts, will any sort of consensus occur. Until then, we suspect that ecological restoration will need to continue to be light on its feet, trying new ideas and adjusting on the fly. Luckily, ecological restoration has a long history of doing precisely that.

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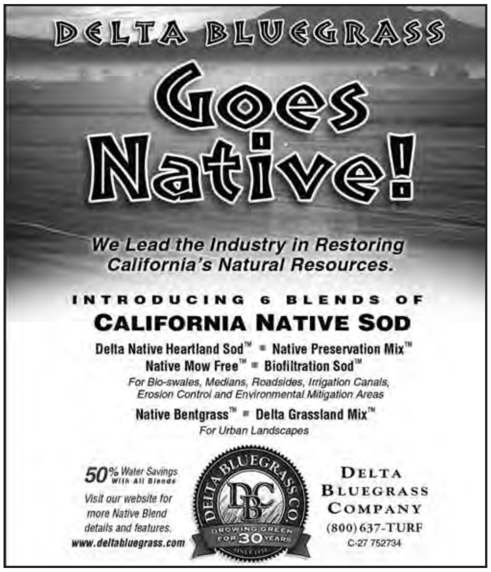

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