2-6-2020

Restoration in the face of changing climate: importance of persistence, priority effects and species diversity

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Abstract

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Keywords

Prairie, Global Change, Priority Effects, Stability, Alternate Stable States, Persistence

Disciplines

Biodiversity | Ecology and Evolutionary Biology | Environmental Sciences

Comments

This is the peer reviewed version of the following article: Wilsey, Brian. "Restoration in the face of changing climate: importance of persistence, priority effects and species diversity." *Restoration Ecology* (2020), which has been published in final form at doi: 10.1111/rec.13132. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions.

Restoration in the face of changing climate: importance of persistence, priority effects and species diversity

Running head: Emerging issues in grassland restoration

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Author contributions: BW conceived the research and wrote the paper.

Abstract

Grasslands are extensive, surprisingly biodiverse, highly altered by humans, and not as well protected as other biomes. Restoration provides an opportunity to reverse degradation and increase local biodiversity. Here, I review emerging issues that will become increasingly important to the science and practice of restoration ecology. First, the global change dilemma. Restorations typically target species that were dominant before the Industrial Revolution, in effect, looking back in time. However, increasing atmospheric CO_2 and methane, temperature, and nutrients, which are already having significant effects, will result in novel conditions that are unlike the past. Biotic introductions have occurred concurrently with climate change, altering the seed bank and propagule pressure from surroundings. Designing seed mixes with high diversity will increase the likelihood that species will be present that respond favorably to changes. Second, more research is needed on persistence as a long-term measure of stability. What is perhaps most important to restoration is how persistent restorations are on decade to century scales, and restorations are now of sufficient quantity and age to test questions about persistence. Third, the importance of stochastic processes due to priority effects have been supported by recent studies and have challenged the deterministic assembly model. Target species establishment could be improved by changing the order of introduction of species. Finally, grasslands provide many ecosystem services to society, including nutrient capture, food production, carbon storage, tourism and recreation, and nectar and pollen production. Grasslands are important culturally as outdoor science laboratories. For these reasons, I suggest that grasslands provide an excellent model system for restoration ecology.

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/rec.13132

Conceptual implications:

- Global change presents a dilemma to restoration ecology because future climates will not match the climate of pre-settlement vegetation. Designing seed mixes with high genetic and species diversity will increase the likelihood that species that will respond favorably to change will be present.
- Alternate states and the importance of priority effects found in recent studies challenge the deterministic assembly model.
- Grasslands provide many services to society, and are important culturally as outdoor science laboratories. For these reasons, I suggest that grasslands provide an excellent model system for restoration ecology.

INTRODUCTION

Grasslands are important to society due to their wide extent and high biodiversity. Approximately 20-25% of the earth's surface is grassland, and this value is close to 40% when tundra and shrublands are included with grasslands (reviewed by Wilsey 2018). Native unplowed grassland can be surprisingly diverse, with 15-20 plant species coexisting in an area < 0.5 m^2 (Pärtel & Zobel 1999, Martin et al. 2005, Polley et al. 2005). Temperate and tropical grasslands and savannahs are among the most altered and least protected biome types (Hoekstra et al. 2004), leading Hoekstra et al. to conclude that we have a 'biome crisis' in addition to an extinction crisis.

Restoration of grasslands may provide an opportunity. Restoration projects are expected to increase in number, as the United Nations has designated the 2020s as the "Decade on Ecosystem Restoration", demonstrating the excitement and broad awareness of restoration by society. Here I review four topics that I suggest are going to be increasingly relevant in the near future in grassland restoration ecology research and practice: 1) the fact that the climate of the future will not match the climate of the pre-Industrial Revolution era (usually the target reference point for restorations), 2) persistence of restorations as an understudied aspect of stability, 3) increased recognition that priority effects are important, and 4) cultural aspects of ecosystem services. This list is far from complete, and there are many other important topics that are not covered here, including the importance of linking sites with corridors (Damshen et al. 2019).

THE GLOBAL CHANGE DILEMMA

The earliest restorations were based on the goal of establishing late successional native species that matched pre-Industrial Revolution vegetation (Clements 1916, Egler 1954, reviewed by Young et al. 2001). One of the first restoration experiments in North America (Fermi lab in the 1970s) introduced species in order based on their successional status (Campbell & Hooymans 2016). In areas that are near high quality remnants, passive restoration (removal of the reason for degradation without adding propagules) can lead to diverse restorations that are similar in composition to the remnants (Prach et al. 2019). However, more commonly, the landscape around our restorations is highly modified, and propagules have to be actively introduced (Harris et al. 2006; Hobbs 2007). In cases where the seedbank and surrounding matrix are highly modified and exotic dominated, this approach can fail to establish some important native species and restorations can become highly invaded by non-planted species (Martin & Wilsey 2012, 2014).

The dilemma facing this traditional restoration approach is that the climates and regional species pools of the present and future do not match pre-industrial revolution conditions (Figure 1). For example, earlier communities grew under an atmospheric CO_2 concentration of approximately 270 p.p.m., whereas CO_2 today is 400 p.p.m. and rising (Blunder & Arndt 2018). Carbon dioxide is having large effects on grassland primary productivity currently, which we know by comparing productivity at present day CO_2 levels and pre-industrial revolution levels, and this is expected to continue into the future (which we know by comparing present-day CO_2 to future levels, Polley et al. 2019). Average temperatures are rising, and precipitation has become more variable (Knapp et al 2002, 2008; Fay et al. 2008; Smith et al. 2016). These altered climatic conditions might lead to unanticipated results in restorations, including more tree encroachment in sub-humid grasslands that are now receiving higher rainfall totals (Briggs et al. 2005), and more desertification in arid grassland restorations that are getting drier (Peters et al. 2012). Nutrient additions of N and P due to human activities have also vastly increased (Harpole et al. 2016), and there are many non-native species that are now in the regional species pool and seed bank that were not present during pre-settlement times (Figure 1, reviewed by Wilsey 2018). Grassland restorations are now conducted in the presence of a large set of non-native grass and forb species (Hobbs 2007), at least outside of Europe where eutrophication plays a much more limiting role in restoration than non-native species. These new conditions are not under the control of restorationists, but have to be considered in designing seed mixes and management plans.

This global change dilemma is a major challenge to restoration ecology, and we should change our rationales and plans accordingly. Seed mixes of the future should be designed in a way to maximize community persistence and resistance to climate extremes, and they should be resistant to invasion by non-native species from the region. I suggest that this could be achieved by designing seed mixes with high functional, genetic and species diversity, and by including species that possess traits (Funk et al. 2008) that are resistant to these environmental changes. For example, Isbell et al. (2015) found in a meta-analysis of 39 biodiversity-ecosystem functioning experiments that species-rich plots resisted extreme weather events better than species poor plots (Figure 2). This result could be used to inform restoration projects in a way so that they maximize species and functional diversity in mixes. A greater number of species (and genotypes) should maximize the likelihood that we will include species that are important in responding to changes in the climate. The sampling effect, which is one mechanism that explains the increases in primary productivity and other ecosystem measures with increased species richness, may be especially important in restorations. The sampling effect is often viewed as a problem with experimental designs, but it can be important in a restoration context (Flombaum et al. 2017). If it is not known which species will respond to novel climatic conditions *a priori*, then it would advantageous to include as many species in the seed mix as possible to increase the likelihood that you will include key species. The key species in restorations of the future may not be as well- known as the key species in agricultural monocultures.

All of the vast literature on ecosystem stability is relevant to restoration ecology, and new findings in that discipline should be considered by restorationists (Loreau 2012, Isbell et al. 2015, Craven et al. 2018). Ecosystem stability in grasslands, usually measured as the consistency of production across time periods, has been found to increase with both species growth asynchrony and composition (Craven et al. 2018). Across the 39 biodiversity-ecosystem functioning experiments mentioned above, communities with species that had asynchronous growth had higher stability than communities with synchronous growth (Craven et al. 2018). Composition had effects above and beyond richness; species rich plots were more likely to be stable when they included the species that have trait values that confer stability (Polley et al. 2013). Specifically, stability was highest when species with conservative traits were dominant (Polley et al. 2007, 2013), such as the grass little bluestem (*Schizachyrium scoparium*). Other measures of stability such as preventing invasion by weedy species were also higher when plantings are species diverse than when they are species poor (Kennedy et al. 2002; Wilsey & Polley 2002; Losure et al. 2007). Seed mixes that have a stable set of species, in diverse combinations, should be more resistant to climate changes, and this should be expanded on in future experimental studies. More work is especially needed on the traits that confer stability across species in the face of global change, and whether stability in the face of one global change factor confers stability to other factors.

Climatically extreme years, which are predicted to be more common in the future, are likely to bring surprises in species composition of our restorations. More research is needed on this, but preliminary work suggests that extreme years will result in very different outcomes. Manning & Baer (2018) conducted a study with common seed mixes seeded in three years that differed in precipitation. They found that the dominant seeded species differed between a dry year and average years. A volunteer annual native (*Conyza canadensis*) varied in cover from 16 – 73% across planting years. Groves & Brudvig (2019) conducted an experiment with common seed mixes with and without rainout shelters to determine how wet and dry years might differ in composition. They found that prairie seedling composition varied across planting years and precipitation treatments. Establishment also differed across years under a common precipitation amount, which suggests other year-to-year effects that were unrelated to precipitation. Stuble et al. (2017) found similar differences among California grassland seedings, and hypothesized that every year might be unique for restoration. Years may not give completely unique outcomes, but different climatic conditions during establishment could lead to significant spatial variability among restorations that are planted at different times, leading to patchiness (Wilsey 2010, Martin and Wilsey 2012, Howe and Martinez-Garza 2014). This stochastic aspect of restorations is ripe for further study.

TEMPORAL STABILITY OF RESTORATIONS: NEED FOR LONG TERM STUDIES USING PERSISTENCE AS A MEASURE

Stability in the face of outside pressures is a key measure of success in restoration ecology (SER Primer). Restorations have now been around long enough to test whether plantings are successful long-term, and hundreds of different sites done by government and university organizations are available for further study. Community stability has several important components (Pimm 1984; Rahel 1990; Donohue et al. 2016), including variability (CV) in ecosystem processes over time, resistance or resilience to environmental extremes or disturbance, and persistence. Most studies have focused on variability over time (Loreau 2012). I would argue that persistence is the most relevant measure for restorations (Buzemer & van der Putten 2007; Roscher et al. 2009; Doherty et al. 2011; Huang et al. 2013). As defined by Donohue et al. (2016), persistence is 'the length of time a system maintains the same state before it changes in some defined way. It is often used as a measure of the susceptibility of systems to invasion by new species or the loss of native species.' If the restoration changes too much, it is more likely to shift to an alternate state (Holling 1973). After a restoration is planted and monitoring programs have started, I would argue that managers are less interested in whether biomass production varies from year to year (CV), and more interested in how well the original grassland has persisted. Are the species seeded still present at the site many years after planting (i.e., is it persistent)? Are the relative abundances of target species still similar to what they were during early years (i.e., is it persistent)? Or, have invasive species replaced the original species that were planted (i.e., it is not persistent)? Normal changes that occur among planted species are to be expected and encouraged (for example late successional species from the seed mix showing up later in the restoration process), but the collapse of the original composition into a simplified non-native composition would have low persistence. In the tallgrass prairie region of North America, sampling of older restorations by Norland et al. (2015) found that 31% of 123 sites sampled were now perennial exotic grass dominated, and roughly half of 93 sites sampled by Kaul and Wilsey (in review) had >50% cover by exotic species.

Developing predictions for when target species composition persists and when it does not remains an understudied topic.

Studies on persistence will be able to address the ninth attribute of restored ecosystems in the SER Primer: “9. The restored ecosystem is self-sustaining to the same degree as its reference ecosystem, and has the potential to persist indefinitely under existing environmental conditions. Nevertheless, aspects of its biodiversity, structure and functioning may change as part of normal ecosystem development, and may fluctuate in response to normal periodic stress and occasional disturbance events of greater consequence. As in any intact ecosystem, the species composition and other attributes of a restored ecosystem may evolve as environmental conditions change.” The many thousands of grassland restorations that have been planted, all of various ages, paired with nearby remnants as controls, would be excellent for addressing these questions. Testing could then be done on what environmental factors predict high persistence. Persistence, or the lack thereof, may be more sensitive than the CV of biomass production to the climatic changes mentioned above.

Measurements of persistence could be quantified with dissimilarity measures between seed mixes and restorations at different ages, using presence-absence dissimilarity measures such as Jacaard’s presence-absence index or with Bray-Curtis dissimilarity (BC):

$$BC = \sum | p_{ij} \text{ before} - p_{ij} \text{ after} | / \sum (p_{ij} \text{ before} + p_{ij} \text{ after})$$

p_{ij}, p_{ij} is the relative abundance of species i before (seed mix, or planting in early years) in site j and after (planting many years later) restoration has occurred. In some cases, a target species composition could be used instead of seed mixes for the ‘before’ state. The persistence measure would be 1 – BC, or the similarity between before and after time has passed.

Questions that could be addressed with these measures are as follows, are the significant predictors for persistence similar to the significant predictors for more commonly assessed stability measures such as the CV of biomass production, and resistance and resilience to weather extremes (Figure 2)? If they are different, why? Are early predictors from the first few years of establishment success the same predictors of persistence after many years? Is persistence predicted by dominant or rare species, and what traits are correlated with persistence? Do non-random extinctions of species during restoration reduce persistence in the long run? Is persistence higher in species diverse plantings than in species poor plantings (Huang et al. 2013)? Finally, do arrival order and priority effects predict long-term persistence? These questions can be tested by sampling the hundreds of now decades old restoration seedings done by government and non-government agencies and universities over the years (e.g. Grman et al. 2013, Norland 2015, Larson et al. 2018, Kaul and Wilsey in review). These older plantings contain a vast amount of useful information, and could be sampled in addition to the new experiments that are produced each year.

THE NEW APPRECIATION FOR PRIORITY EFFECTS

Although restorations most commonly add species at the same time in a single seed mix, in intact systems, species become active at different times of the year (Howe 1994) and can vary in their order of arrival at a site (Fukami 2015). Harper (1961) was the first to study priority effects with grassland species. He found that the dominance of *Bromus rigidus* could be reduced from 75 to 10% when another species (*Bromus madritensis*) was seeded three weeks before *B. rigidus*. These results were underappreciated until the study of priority effects re-emerged in the mid-2000s (Chase 2003; Ejracœs et al. 2006; Körner et al. 2008; Brudvig 2011).

Priority effects predict that arrival order will be important to the outcome in restorations. They can be negative when earlier arriving species suppress establishment of later arriving species, or positive if they increase establishment (DeLory et al. 2019a). The information from priority effect studies can be used to establish target species (often late successional native species) before non-target species (often exotic species) arrive and get established. Early arriving species can suppress later establishing species in competitive environments, or they can facilitate later arriving species in situations where N-fixing legumes are present (Temperton et al. 2007). Early arriving species can also affect soil feedback mechanisms, leading to soil legacies (Grman & Suding 2010). Priority effects form the basis of some management actions, where target native species are established early in the restoration process or exotics are targeted with herbicides before native seed is added, or beneficial groups (e.g. legumes) are seeded before target species (e.g. Firn et al. 2010; Wainwright et al. 2011; Bennet et al. 2019).

The primary ecological theories (r* and Modern Coexistence Theory) that have influenced restoration until recent years downplay the idea that arrival order will be important. The r* theory (Tilman 1982) predicts that competitive outcomes can be predicted by the amount of a limiting resource that can be captured by a species. If a species can capture the resource and drive it to a low level, and then continue to have positive growth rates under this low resource level, then it will outcompete its neighbors. Thus, the species with the lowest r* will win at competition. This theory has been helpful to restoration ecology, as it has led to many studies that look at trade-offs in the capture of multiple limiting resources, and trade-offs have been found to be important to diversity maintenance (Harpole et al. 2016). However, two assumptions that underlie r* theory are not always true: competition is not always symmetrical (Demalich 2016), and recent research has shown that it does matter when the most competitive species arrives. If a competitive species arrives after a less competitive species has established, it is much less likely to competitively exclude the first (Harper 1961). Modern coexistence theory predicts that species will coexist when negative intraspecific interactions are stronger than negative interspecific interactions, and when fitness differences among species are small. Modern coexistence theory allows for priority effects to occur in special situations where interspecific interactions are greater than intraspecific interactions (Chesson 2018), which allows for a destabilizing effect (Fukami et al. 2016). A destabilizing effect can occur in restorations when an early arriving species arrives and achieves higher biomass than other species. The difference in sizes can result in asymmetrical competition and reduced intraspecific-interspecific interaction ratios (Figure 3), which can lead to competitive exclusion even in cases that normally allow coexistence (i.e., when alphas of Lotka Volterra equations are < 1.0). Competitive exclusion will occur in cases where interspecific interactions are strong, and many species may fail to appear in a restoration as a result. In grasslands, which I would argue are strongly non-equilibrium systems, local competitive exclusions due to priority effects can persist for long time periods, long enough to consider a restoration a failure. This effect can be overcome by establishing target species early in a restoration (Martin & Wilsey 2012). Adding seeds of rare species before common species should lead to higher species diversity than seeding them at the same time (Werner et al. 2015).

Establishing target species early can lead to greater success that adding them later, after more competitive species arrive (Dickson & Busby 2009; Eddy & Van Auken 2019). Grman & Suding (2010) found that exotics reduced native species establishment when they arrived first due to asymmetrical competition and soil legacy effects in a controlled greenhouse experiment. Recent long-term field studies have found strong priority effects (Weidlich et al. 2017, DeLory et al. 2019a), and in some cases the effects persisted for 8-10 years (Martin & Wilsey 2012, 2014; Werner et al. 2015). Martin & Wilsey (2012, 2014) seeded field plots with a prairie mix either before or after early arriving species established, and found that establishment from the mix was reduced, and the proportion of exotic species was increased, compared to when species were seeded at the same time. Differences persisted for eight years (until the end of the experiment) and were resistant to a second seed addition of the native seed mix (Martin & Wilsey 2014). Werner et al. (2015) found that grass-forb ratios varied between cases where grasses arrived earlier than forbs (and vice versa), with grass priority over forbs being strong and persistent for at least 8 years after establishment.

These results suggest that we can plant restorations in a way to maximize the likelihood of target species establishment. Much of previous research has focused on the arrival order of functional groups rather than species in order to increase generality (e.g. DeLory et al. 2019a) due to the high amount of variation in species composition from place to place among grasslands. Dominant grasses as a group greatly suppress forb establishment and species diversity in many restorations (e.g. McCain et al. 2010, DeLory et al. 2019a). Dickson and Busby (2009) used forb and grass functional groups to address arrival order effects. Seeding forbs before grasses led to more diverse restorations than seeding them together (Dickson & Busby 2009). Grasses as a group typically have negative priority effects, whereas legumes have positive priority effects compared to treatments where all functional groups are seeded at the same time (DeLory et al. 2019a). However, in many areas with high invasion pressure, and in areas where invasion has the strongest effect on target species establishment (Kaul and Wilsey in review), grasses may also be important in preventing invasion (Figure 4). If grasses are important in preventing invasion (Fargione et al. 2003), then having some grass in the mix may be better than having no grasses (Figure 4). Thus, the ideal grass : forb ratio might be dependent on the amount of invaders and resource availability in the environment. The basic design of Dickson and Busby could be applied in sites that vary in their invasive species propagule pressure, and could compare a variety of ratios of grasses and forbs to address questions about the best timing and ratios to use. For example, is a grass : forb ratio of 0.05 : 0.95 better for invasion resistance than 0 : 100 grasses : forbs? What ratio is best? How long should we wait until we add the grasses in later? Tests of this hypothesis can utilize the strength of structural equation modeling to test the direct effects of grasses on diversity (McCain et al. 2010) and the indirect effects of grasses reducing the abundance of invaders (Figure 4). Grasses can suppress diversity directly, but their negative effect on invaders could lead to a positive effect on forb establishment when they are rare (negative times a negative path equals a positive, Figure 4). In situations where few or no invaders are present, the pathway through invaders drops out, and the model simplifies to one in which grasses limit diversity directly when they are abundant. Future research can test this model and address these questions.

Priority effects have been found to be especially important in predicting exotic species dominance, which is a key factor explaining poor target species establishment in some restorations (Kaul and Wilsey in review). Establishing native species before exotics arrive can lead to better establishment in restorations where exotics are problematic (Grman & Suding 2010; Wainwright et al. 2011). Kaul and Wilsey (in review) found that restoration success was highest in areas where exotic species were low in abundance, suggesting that restorationists should focus their attentions to less invaded sites. Exotic species that were most problematic were perennial grasses that did not drop out after the first few years. Dickson et al. (2012) found that when one of three common exotic species arrives before other species, it can reduce the establishment of other species to a greater extent than when all are seeded together. Wilsey et al. (2015) found that 14 exotic species suppressed the establishment and diversity of prairie species to a much greater extent than 14 native species. Suppression was strongly related to regeneration traits that were related to fast and early growth in exotics (i.e., high germination rate, short time before first germinant emerged, seedling growth rates). Delory et al. (2019b) found that an exotic species (*Senecio inaequidens*) in Europe benefited more from arriving early than the native species that it was invading. When the natives were seeded before this species, they successfully established. The authors suggested that the native species stands should resist invasion as long as they are not disturbed. In general, results of these studies indicate that exotic priority effects over natives are stronger than the inverse. Target native species should be established early in the process in restorations with high invasive species pressure.

The increased appreciation for priority effects raises questions for future research projects. New questions to test include, are priority effects contingent on resource availability? Nutrient availability is a key variable in restoration, and many European projects remove topsoil to reduced N concentrations before sites are seeded (Rasran et al. 2007). Reduced nutrient availability may alter priority effects, and more studies with a topsoil removal x priority effect treatments would be helpful. Kardol et al. (2013)

found that priority effects are stronger when nutrient availability is high, and weaker when it is low. In contrast, Goodale & Wilsey (2018) found that drier and more variable rainfall actually led to stronger priority effects than constant rainfall amounts. It is unknown how other environmental changes and variability influence priority effects. Priority effects may lead to alternate states only in especially productive environments (Chase 2003; Hobbs and Norton 2004, Kardol et al. 2013, Weidlich et al. 2017). Arrival order and priority effects have been found to greatly reduce species diversity in North American grasslands (e.g. Martin and Wilsey 2012, Dickson et al. 2012, Wilsey et al. 2015, Goodale and Wilsey 2018), and these factors may be a major understudied determinant of biodiversity maintenance. We need more studies on how the strength of priority effects varies across environmental conditions and soil types (Weidlich et al. 2017), and grassland restorations are excellent systems to test these ideas.

CULTURAL ASPECTS OF ECOSYSTEM SERVICES IN GRASSLANDS

Finally, the importance of grasslands to ecosystem services is underappreciated compared to forested systems (Bengtsson et al. 2019). In some heavily agricultural regions, restoration seedings are numerous and the total size of the restoration areas can greatly exceed the size of remnant (unplowed) areas. For example, in the USA state of Iowa, the hundreds of roadside and conservation plantings, not including many private and county-level sites equaled 60,906 ha, whereas remnants in the state have 12,400 ha (Kaul & Wilsey 2019). Grassland restorations are large and numerous enough in some areas to be considered a significant land-use category in modern-day landscapes. Grassland restorations could provide many services to society, such as increased water quality when perennial grasslands replace annual crop fields, meat and dairy production, medicinal and wild food plants, soil C storage, tourism and recreation (Bengtsson et al. 2019). The integration of restoration into agricultural fields will provide ecosystem services in the places that need them the most (Schulte et al. 2017). The role of grasslands in producing nectar and pollen to support pollinators, which in turn will help to pollinate crop plants, requires more study. There may be tradeoffs between ecosystem services in some cases where the most productive species are not the best species for pollinators. The multifunctionality of grasslands remains an important topic of study, and we need more information on when and if ecosystem service trade-offs exist (Martin et al. 2014; Zirbel et al. 2019).

The underappreciation of grasslands has led to an unfortunate call to plant trees in relic grassland sites to sequester atmospheric C (Bastin et al. 2019, Temperton et al. 2019, Veldman et al. 2019). Most carbon in grasslands is stored belowground and is poorly assessed, and grassland rooting depth is typically deeper than it is in forest soils. Carbon storage in deeper soils is especially understudied (Upton et al. 2020). Ward et al. (2016) found that 60% of soil C was below 30 cm in European grasslands, yet most studies of soil carbon are conducted in shallow soils. For example, the median depth of soil C studies in grasslands was 15 cm as of the year 2001; this increased to only 20 cm by 2017

(Conant et al. 2001, 2017). Our recent results suggest that soil C under restored native grassland plots is greater than exotic plots, but that this was only found in deeper soil depths (50-100 cm) (Wilsey et al. 2020). There may be more soil carbon than we are aware of in the deeper soil layers of grasslands.

In their overview of ecosystem services in grasslands, Bengtsson et al. (2019) points out that grasslands are important culturally as outdoor science laboratories, and this is viewed as being highly valuable by grassland experts. Grasslands are widely used to test restoration questions, and theory is increasingly being used to frame questions (Wainwright et al. 2018). Approximately 1/3 of the studies reviewed by Wainwright were done in grasslands, and grasslands were the most common system studied in theory-based restoration studies. Grasslands provide many advantages to other ecosystem types, including low stature and small size of plants, ability to conduct manipulative community assembly experiments, and greater linkages between theory-based researchers and field practitioners. The relevant time scale for restoration studies in grasslands is shorter than in deserts and forests, which are dominated by very long-lived woody plants. I expect that grasslands can provide an excellent model system for future studies on restoration ecology, providing “acid-tests” for ecological theories (Bradshaw 1987) and producing information on how to restore this underappreciated biome type (Hoekstra et al. 2004).

In conclusion, results of recent studies suggest that creating seed mixes with high species and functional diversity, which will create patchiness in the environment, may be the best strategy for dealing with anticipated climate change. Temperature and rainfall predictions for the future are for conditions not seen in the past. For example, in many grasslands are expected to be warmer, wetter, with more variable rainfall conditions (Suttle et al. 2007, Knapp et al. 2008). Grasslands typically vary along a hot-dry to cold-wet continuum, and warm-wet will be a new condition for grasslands. The sampling effect, in that a greater number of species in the seed mix will ensure that the species that will have positive responses to these changes may be the best strategy in grassland restorations, which tend to be somewhat unpredictable. Recent research indicates that arrival order is a major predictor of target species establishment, and this suggest that target species should be established early in the restoration process. High diversity restorations should be able to persist into the future to achieve the ecosystem services that we are expecting from them.

Acknowledgements. I would like to thank Andrew Kaul, Lars Brudvig, Vicky Temperton, and an anonymous reviewer for comments on an earlier version of this manuscript.

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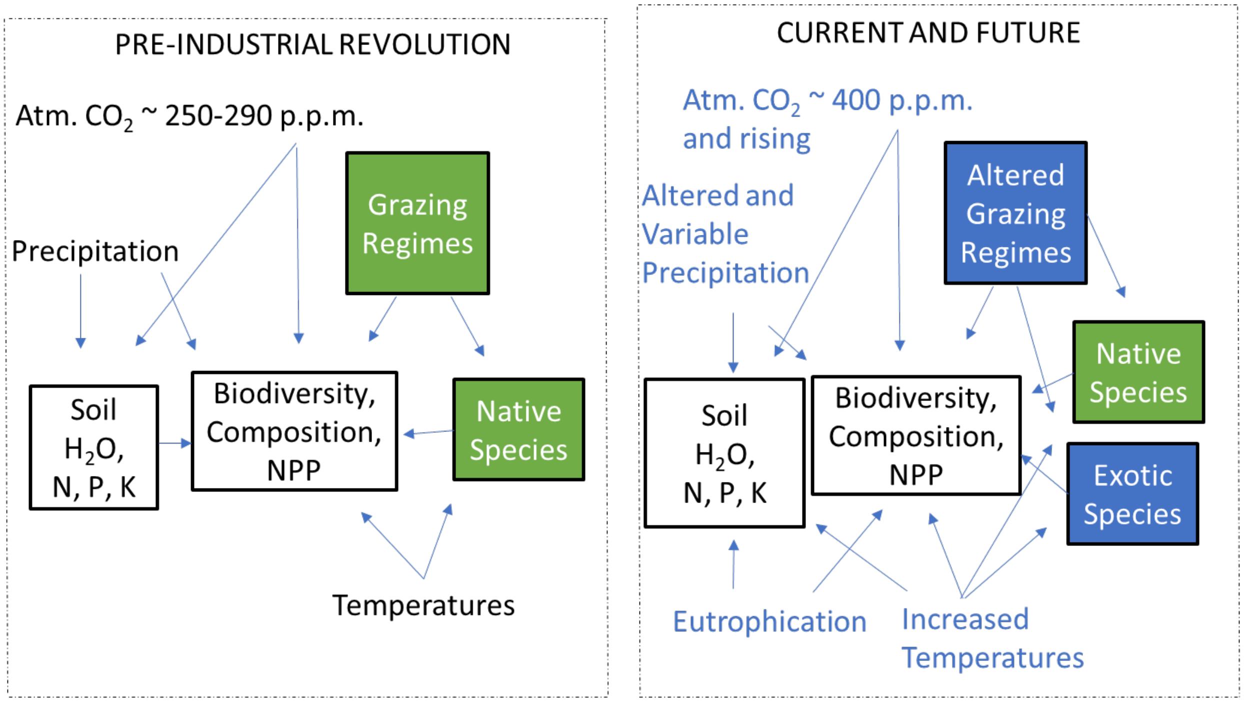


Figure 1. The Climate Change Dilemma for grassland restoration ecology. Conditions during pre-industrial revolution, which are commonly used as the reference point for restoration projects (left) were much different from present and future conditions (right). Future restoration plans should take into accounting these changing conditions.

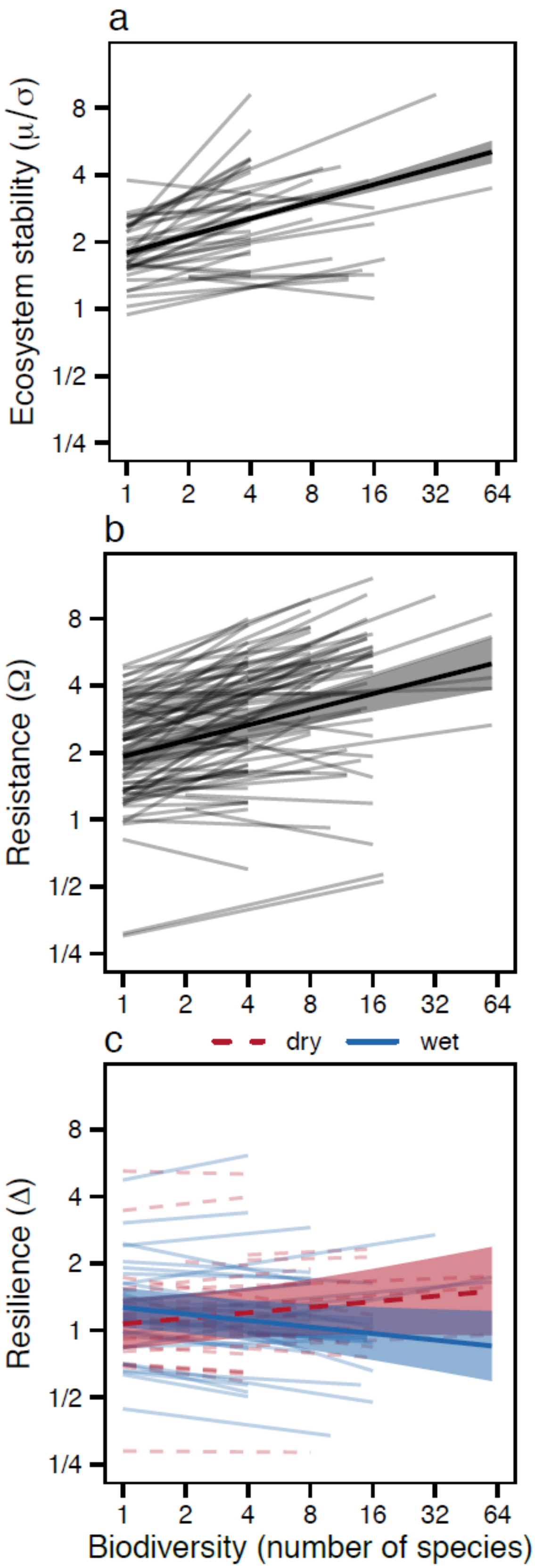
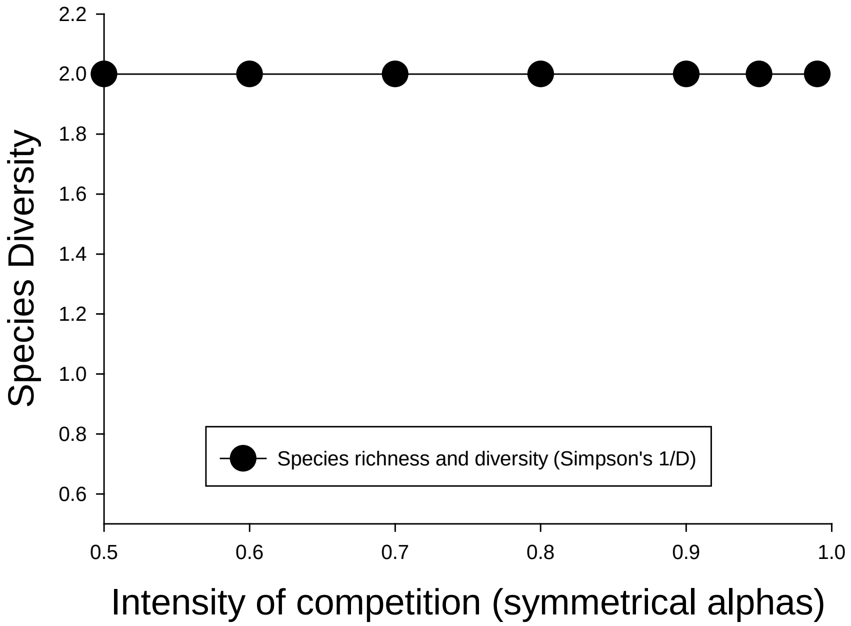

a
Ecosystem stability (μ/σ)
8
4
2
1
1/2
1/4
1
2
4
8
16
32
64
b
Resistance (Ω)
8
4
2
1
1/2
1/4
1
2
4
8
16
32
64
c
dry
wet
Resilience (Δ)
8
4
2
1
1/2
1/4
1
2
4
8
16
32
64
Biodiversity (number of species)

Figure 2. Isbell et al. (2015) found that the number of species planted per plot was positively correlated with ecosystem stability (consistent biomass production across time, a) and resistance to climate extremes (b) across 46 experiments. Resilience depended more on extreme dry vs. extreme wet events than number of species planted (c). Figure used with permission (Nature Springer).


2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
Species Diversity
0.5
0.6
0.7
0.8
0.9
1.0
Intensity of competition (symmetrical alphas)
Species richness and diversity (Simpson's 1/D)

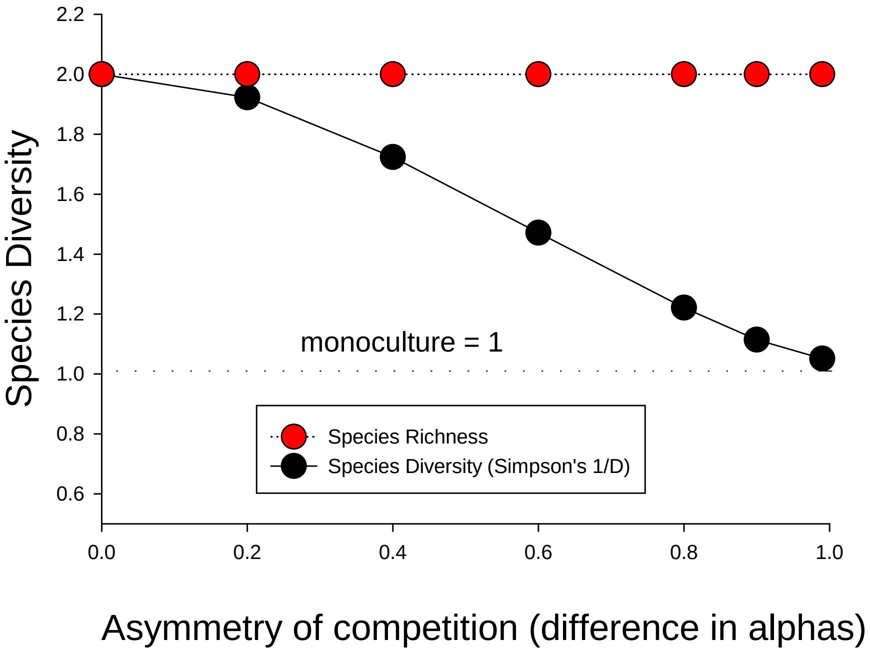

2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
Species Diversity
monoculture = 1
Species Richness
Species Diversity (Simpson's 1/D)
0.0
0.2
0.4
0.6
0.8
1.0
Asymmetry of competition (difference in alphas)

Figure 3. Asymmetry of competition provides a mechanism behind species diversity declines with priority effects from early arriving species. Asymmetry of competition reduces diversity more than intensity of competition in situations where coexistence is possible (Lotka-Volterra equations with alpha < 1.0). In the top panel, the strength of competition intensity was varied from 0.5 – 0.99 using symmetrical measures of alpha (i.e., competition effects both species equally, but intensity varies). The number of individuals of each species goes down with increasing intensity, but their relative abundances remain equal (2 species equally abundant at all levels of alpha). In the bottom panel, alpha averaged 0.5 between the two species, but the level of asymmetry was varied from 0.5-0.5, to 0.6-0.4, 0.7-0.3, 0.8-0.2, 0.9-0.1, 0.95-0.05, and 0.99-0.01. Species diversity declined as asymmetry increased but not when intensity increased. This analysis used an analytical model with Lotka-Volterra equations with two species mixtures (N_1 and N_2):

$$N_1(\mathrm{t}+1) = N_1(t)(1 + r_1(1 - \frac{N_1(t) + \alpha_{12}N_2(t)}{K_1}))$$

$$N_2(\mathrm{t}+1) = N_2(t)(1 + r_2(1 - \frac{N_2(t) + \alpha_{21}N_1(t)}{K_2}))$$

Where K is carrying capacity and α_{12} and α_{21} are competition coefficients (effect of species 2 on 1 and effect of species 1 on 2, respectively). K and r for both species used values of 1000 and 0.5 over 50 time steps. Positive priority effects could also be modelled this way with positive alpha values.

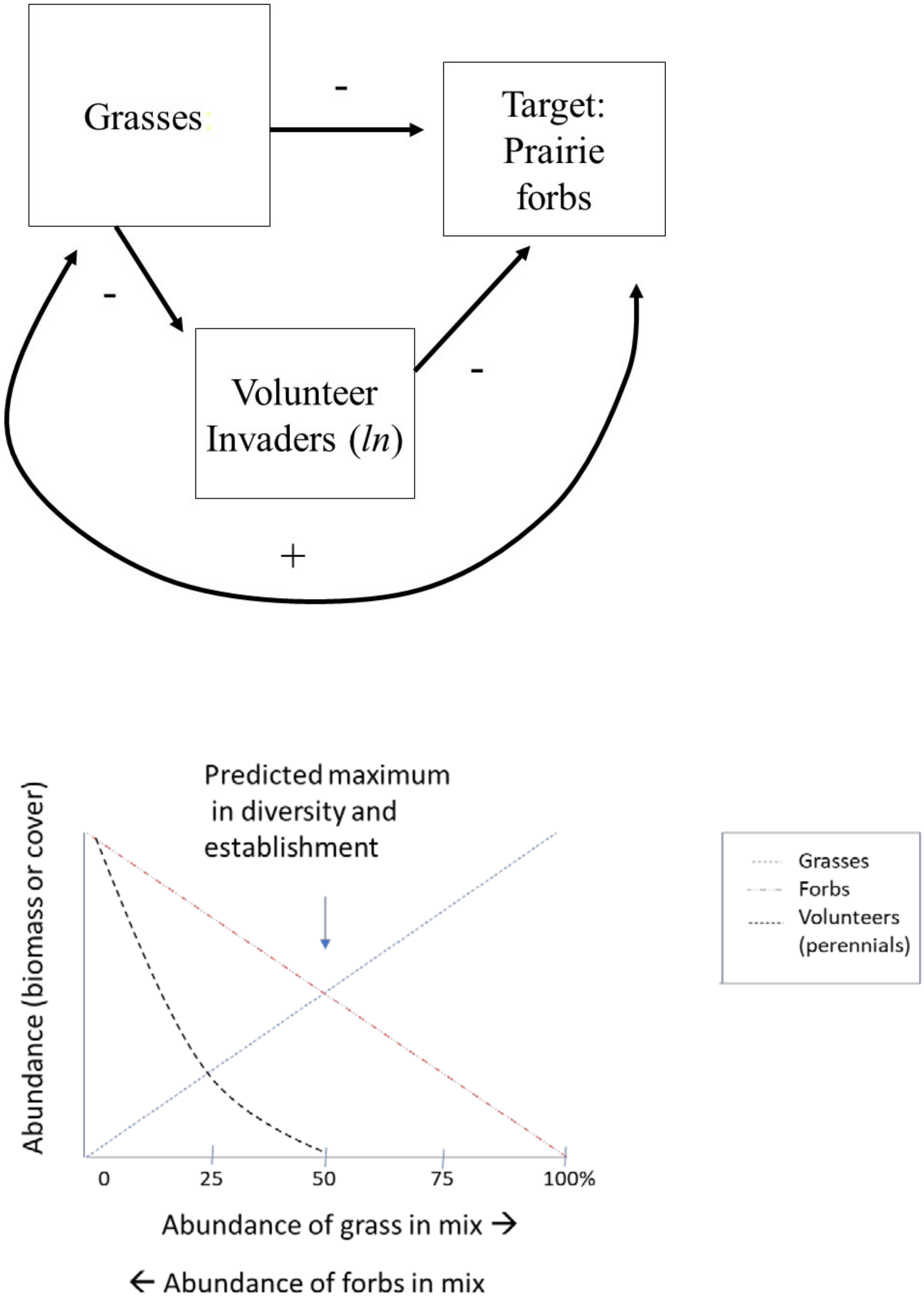


Figure 4. Predictions for testing the importance of grass : forb ratios to prairie grassland establishment and diversity (Structural Equation Modeling top panel, predicted relationships bottom panel) in tallgrass

prairie systems of North America. A structural equation model with direct effects of grasses on forb establishment, and indirect effects of grasses on forb establishment through grasses role in reducing unplanted weeds (mostly exotic grass species in North America) can be used to test the effects of grass ratios in seed mixes in restoration.