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When Invasive Plants Disappear: Transformative Restoration Possibilities in the Western United States Resulting from Climate Change

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Abstract

Most ecologists believe that climate change poses a significant threat to the persistence of native species. However, in some areas climate change may reduce or eliminate non-native invasive species, creating opportunities for restoration. If invasive species are no longer suited to novel climate conditions, the native communities that they replaced may not be viable either. If neither invasive nor native species are climatically viable, a type of "transformative" restoration will be required, involving the translocation of novel species that can survive and reproduce under new climate conditions. Here, we illustrate one approach for restoration planning by using bioclimatic envelope modeling to identify restoration opportunities in the western United States, where the invasive plant cheatgrass (*Bromus tectorum*) is no longer climatically viable under 2100 conditions projected by the Geophysical Fluid Dynamics Laboratory (GFDL2.1) coupled atmosphere-ocean general circulation model. We then select one example of a restoration target area and identify novel plant species that could become viable at the site in the wake of climate change. We do so by identifying the closest sites that currently have climate conditions similar to those projected at the restoration target area in 2100. This approach is a first step toward identifying appropriate species for transformative restoration.

Key words: bioclimatic envelope modeling, *Bromus tectorum*, climate change, ecological niche, invasive species, restoration, species distribution.

Introduction

Climate change has the potential to significantly alter the distributions of species and change the composition of plant and animal communities (Peterson et al. 2002; Pearson & Dawson 2003; Root et al. 2003; Thuiller et al. 2005*a*; Araujo & Rahbek 2006; Hijmans & Graham 2006; Araujo & New 2007). Large-scale shifts in species distribution present substantial management questions: How do we protect native ecosystems from climate change threats (Hannah et al. 2002; Midgley et al. 2002; Hannah et al. 2007; Pressey et al. 2007)? And, how do we select appropriate species for restoration to account for climate change (Harris et al. 2006)?

In addition to native communities, climate change also is expected to affect the distribution of non-native invasive species (Thuiller et al. 2007). Invasive plants respond positively to disturbance, and some species show enhanced competitiveness due to rising CO_2 levels (Sasek & Strain 1988; Smith et al. 2000; Ziska et al. 2005), which may lead to an overall increase in risk of invasion with climate change (Dukes & Mooney 1999; Moore 2004). However, in other cases invasive species may become less competitive in certain areas due to climate change (Bradley et al. 2009). Reduced competitiveness of invasive species would create unprecedented restoration opportunities.

Any restoration opportunities associated with climate change present a major challenge to ecologists and land managers. If climate conditions become unsuitable for invasive species, those same conditions may render the site unsuitable for native species. Moreover, it is possible that *other* non-native invasive species, previously excluded from a given site due to climatic conditions, will be able to occupy that site as a result of climate change. Therefore, the necessary action may not always be traditional restoration (returning native species to a site where they once occurred), but rather something different—a type of "transformative" restoration in which novel plant species are introduced. Ideally, these novel species will be (1) indigenous to the broader biome or ecoregion, (2) non-invasive, (3) capable of sustaining native fauna, and (4) well suited to the new climate conditions of the

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restoration site. Here we focus on a method for identifying those plant species best suited to establish under projected climate change conditions.

One approach for assessing potential distribution changes of native and invasive plants involves bioclimatic envelope modeling (see reviews by Franklin 1995; Guisan & Zimmermann 2000; Pearson & Dawson 2003; Guisan & Thuiller 2005). Bioclimatic envelope models have been widely used to assess risk from invasive species (Welk et al. 2002; Rouget et al. 2004; Thuiller et al. 2005*b*; Mau-Crimmins et al. 2006), identify suitable locations for species restoration (Pearce & Lindenmayer 1998), and project the effects of climate change on species distributions (Root et al. 2003; Thomas et al. 2004; Thuiller 2004; Araujo et al. 2005; Kueppers et al. 2005; Hijmans & Graham 2006). Bioclimatic envelope modeling uses a species' geographic distribution to empirically define a climatic "niche" or the climate conditions in which a species can persist. At the regional scale, a bioclimatic envelope can provide a useful first-order approximation of the potential changes in species distribution associated with climate change (Pearson & Dawson 2003). These spatially explicit projections provide a framework for assessing risk, planning monitoring efforts, and conducting climate manipulation experiments.

Realized ecological niche is limited by a number of variables in addition to climate, including topography, soils, land use, and species interactions (Davis et al. 1998; Dormann 2007). As a result, it has been argued that a better approach would be to use local experimental and observational knowledge of plant physiology and competition to build up to regional projections (Woodward & Beerling 1997). This type of bottom-up approach has been used, for example, by Bradford and Lauenroth (2006), who defined limits to invasive cheatgrass (*Bromus tectorum*) establishment based on physiological limitations observed in eastern Washington by Hulbert (1955) and Harris (1967). However, just as it is uncertain whether regional relationships hold at a local level, it is also uncertain whether local climate constraints hold at a regional scale. Without any means for validation, it is unclear under what circumstances a top-down (bioclimatic envelope) or bottom-up (physiological) model is more appropriate. Integration of both approaches will be needed for more robust projections of the ecological implications of climate change.

Here, we use bioclimatic envelope modeling to identify invaded locations with the potential for restoration due to climate change (Bradley et al. 2009), and we suggest an approach for identifying those plant species that are likely to be climatically suitable for establishment on the site in the wake of climate change. We illustrate this approach using the GFDL2.1 coupled atmosphere-ocean general circulation model (AOGCM) and the invasive plant cheatgrass (*B. tectorum*) in the western United States.

First, we apply *B. tectorum's* modeled bioclimatic envelope to conditions in the year 2100 as projected by GFDL2.1. We identify lands where *B. tectorum* currently is established that are likely to become climatically unsuitable for the species, creating restoration potential. Second, we select one target location with restoration potential, create a bioclimatic envelope using future climate, and match that bioclimatic envelope to current climate conditions to identify novel plant species in nearby regions that could become viable at the restoration target area. Planning for transformative restoration may become increasingly important as both native and invasive species ranges shift due to global climate change.

Background

Bromus tectorum is an invasive annual grass common to mid to low elevation basins in the western United States, many of which have been grazed heavily by domestic livestock since the mid to late 1800s. *Bromus tectorum* dominates tens of thousands of kilometer square throughout Nevada, Utah, southern Idaho, eastern Oregon, and eastern Washington (Mack 1981). *Bromus tectorum* primarily invades sagebrush (*Artemisia tridentata*) shrubland, but it also is expanding in hotter, drier salt desert (*Atriplex* spp.) shrubland and cooler, more mesic pinyon-juniper (*Pinus monophylla, Juniperus* spp.) woodland (Billings 1990; Knapp 1996; Chambers et al. 2007). *Bromus tectorum* invasions reduce biodiversity and ecosystem carbon storage (Bradley et al. 2006), decrease the ability of ecosystems to support grazing by domestic livestock, and increase the probability of major fire events in native and managed ecosystems (Whisenant 1990; D'Antonio & Vitousek 1992; Chambers et al. 2007).

Methods

Datasets

Regional species distribution is based on a 1-km resolution map of *B. tectorum*-dominated lands in the Great Basin derived from remote sensing (Bradley & Mustard 2005). This map was based on inter-annual measurements of community greenness; *B. tectorum*-dominated lands have higher inter-annual variability due to their amplified growth response during wet years compared to uninvaded shrublands (Bradley & Mustard 2005). The map of *B. tectorum* presence was converted to 0.04166 decimal degree (DD) resolution (approximately 4.5 km) using a majority filter to create a spatial resolution comparable to PRISM interpolated climatic data (Daly et al. 2002). The use of the majority filter means that "presence" within a 0.04166 DD pixel signifies that *B. tectorum*-dominated lands exist within a portion, but not necessarily all, of the pixel.

Current climate conditions were derived from the PRISM dataset (Daly et al. 2002), a 0.04166 DD interpolation of weather gages in the United States that accounts for climatic variation associated with topography. The climatic variables interpolated by PRISM are mean monthly and annual precipitation, minimum temperature, and maximum temperature over the 1971–2000 time period.

Year 2100 climate conditions were created by adding climate change estimated by the GFDL2.1 model (Delworth et al. 2006), using the SRESA1B scenario (Nakicenovic & Swart 2000), to current climate conditions based on the PRISM dataset. The GFDL2.1 model (Delworth et al. 2006) was selected because the modeling group is U.S. based, and because the model performed well when compared with historical stream flow measurements, suggesting that its projections of changing precipitation may be more reliable than some other AOGCMs (Milly et al. 2005). The SRESA1B scenario represents a "middle of the road" future trajectory resulting in a doubling of CO_2 to 720 ppm by 2100 (Nakicenovic & Swart 2000). We use a single AOGCM and scenario to illustrate a bioclimatic envelope modeling approach for selecting suitable plant species for transformative restoration.

We calculated mean monthly and annual precipitation, minimum temperature, and maximum temperature modeled for 1971–2000 (comparable to current conditions) and for 2090–2100 (estimated future conditions) based on the GFDL2.1 projection. We then subtracted mean late twentieth century climate conditions from mean late twenty-first century climate conditions to derive estimated change in annual and monthly precipitation and temperature. Owing to the coarse spatial resolution of the climate projection (lat $2^\circ \times$ lon 2.5°), GFDL2.1 projected climate change was added to the PRISM current climate interpolation to better account for local climatic and topographic heterogeneity.

Modeling

The bioclimatic envelope was created using the four climate variables that most constrain *B. tectorum* distribution today. Climate variables that most constrain a species distribution are those where the climate space that the species encompasses is small relative to the total climate space available regionally. Constraint (termed specialization by Hirzel et al. 2002) was determined based on the ratio of the median distance from the mean climate value for pixels with *B. tectorum* presence to the median distance from the mean climate value for all pixels (Bradley 2009). Lower values indicate better constraint and thus better climatic predictors of *B. tectorum* presence. In cases where adjacent monthly climatic variables were highly correlated (e.g., April–May precipitation), we used a seasonal average to minimize redundancy.

The bioclimatic envelope was based on Mahalanobis distance (Farber & Kadmon 2003; Tsoar et al. 2007). Mahalanobis distance is a multivariate technique that defines perpendicular major and minor axes and calculates distance from a centroid relative to covariance of axes lengths. Unlike the commonly used BIOCLIM (Busby 1991), which uses a box model to define climate suitability, Mahalanobis distances can be represented by an ellipse. Hence, if the species is present within a narrow range of precipitation, but a wide range of temperature, equal Mahalanobis distances would cover a small range of precipitation, but a large range of temperature. The smaller the Mahalanobis distance, the more likely climate conditions are suitable for the species. Suitable climatic conditions for *B. tectorum* invasion were defined as all land area with a Mahalanobis distance equal to or less than the value that encompassed 95% of the species distribution.

The bioclimatic envelope developed from current climate conditions was then applied to the estimated 2100 climate conditions based on the GFDL2.1 projection. Using the same Mahalanobis distance, we calculated all land areas that remain climatically suitable for *B. tectorum*. We also identified all currently invaded areas that do not remain climatically suitable according to the GFDL2.1 model. These areas were identified as having restoration potential.

From the areas that have restoration potential, we arbitrarily selected one Great Basin location (restoration target area) in southern Nevada and assessed how climate conditions are projected to change in that location. The example restoration target area for this study is located in Lincoln County in southeast Nevada, and encompasses Dry Lake Valley west of the town of Pioche. Land cover in this area is primarily sagebrush (*A. tridentata*) shrubland and mixed salt desert scrub dominated by *Atriplex* spp. (USGS 2004). We then created a bioclimatic envelope based on the spatial distribution of the restoration target area and the 2100 projected climatic conditions. We used the same input climatic variables used to construct the initial model for *B. tectorum*. The bioclimatic envelope of the restoration target area was applied to current climate conditions to identify lands that, based on Mahalanobis distance, are currently most climatically similar to the GFDL2.1 projection for the restoration target area in 2100. Land cover in areas that are currently most similar to the GFDL2.1 projected climate for the restoration target area was identified based on the southwest ReGAP (USGS 2004) land cover classification.

Results

We created the bioclimatic envelope model based on the climatic variables that most constrained *Bromus tectorum* distribution. In order of importance, these climatic variables were summer (June–September) precipitation, average annual precipitation, spring (April–May) precipitation, and winter (December–February) maximum temperature (Bradley 2009). The Mahalanobis distance that encompassed 95% of the current distribution was 3.5 (Fig. 1A).

Based on the GFDL2.1 model projection, invasion risk in the western United States by 2100 will contract in southern Nevada and Utah, and expand slightly in parts of Wyoming and Montana (Fig. 1B). However, on currently invaded lands, there is a substantial reduction of risk on more than 50% of total pixels. *B. tectorum* is likely to become less climatically viable, and hence less competitive, on lands in southern Utah, southern Nevada, and Idaho under this scenario. Each of these potential restoration targets may have separate and distinct projected future climate conditions making different species of plants most appropriate for restoration.

Climate conditions at the restoration target location (Fig. 1B) are projected by GFDL2.1 to become slightly warmer and drier (Table 1). The most dramatic change is projected for average spring precipitation, which decreases from a range of 1.5–3.2 cm to a range of 0–0.6 cm.

Based on the projected 2100 climate of the restoration target area, the region that currently exhibits the most similar conditions is located in the Mojave Desert in southern California

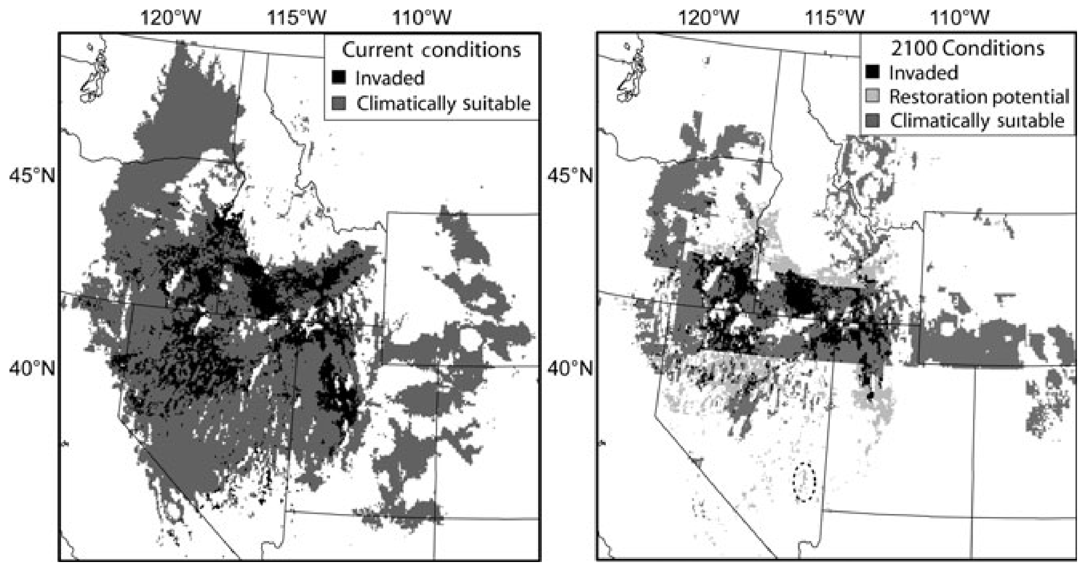

Figure 1. Current invasion risk and future restoration potential of *Bromus tectorum* invasion in the western United States. (A) Current *B. tectorum* invasion in the Great Basin as defined by remote sensing (Bradley & Mustard 2005) and lands with similar climate conditions that are climatically suitable for invasion. (B) Future climatic suitability to *B. tectorum* under the GFDL2.1 AOGCM scenario A1B for 2100. Black areas are currently invaded lands that remain climatically suitable and light gray areas are currently invaded lands that become climatically unsuitable and have restoration potential. The dashed circle shows the target location used to select appropriate species for restoration based on the GFDL2.1 projected climate conditions.

Table 1. Climatic conditions most important for *Bromus tectorum* distribution for the target restoration site in southern Nevada.

	Target Restoration Site: Southern Nevada			
	Current Climate Conditions		*2100 Climate Conditions*	
	Minimum	*Maximum*	*Minimum*	*Maximum*
June–September monthly ppt (cm)	1.6	3.1	1.2	2.7
Annual ppt (cm)	20.8	46.0	12.2	35.8
April–May monthly ppt (cm)	1.5	3.2	0	0.6
December–February tmax (°C)	6.7	11.2	7.8	12.5

The climate in 2100 as projected by the GFDL2.1 model using scenario A1B is slightly warmer and considerably drier.

(Fig. 2). The majority of land cover in the most climatically similar locations is dominated by creosote (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) according to the southwest ReGAP land cover classification (USGS 2004) (Table 2). However, *L. tridentata* and *A. dumosa* shrublands have Mahalanobis distances of up to 9.5, whereas the Mahalanobis distance that encompasses 95% of the restoration target area's distribution is only 3.2. Hence, the best candidate for transformative restoration actually falls outside of the restoration target area's bioclimatic envelope.

GFDL2.1 climate projections for the restoration target represent "no-analog" novel conditions for the western United States (Williams & Jackson 2007). That is, projected future climate conditions are unlike any current climate conditions in the region. Bioclimatic envelope modeling provides a framework for identifying restoration potential and targeting appropriate communities to establish, but experiments clearly would be needed to evaluate the viability of suggested novel plant species.

Discussion

This paper illustrates one approach for identifying species that could survive under future climate change conditions. This type of modeling work is a useful first step for restoration planning on lands currently dominated by invasive species that may retreat in response to global climate change. It is likely that climate change will lead to range shifts of both native and invasive species (Hughes 2000; Peterson et al. 2002; Pearson & Dawson 2003; Root et al. 2003; Thomas et al. 2004; Thuiller et al. 2005*a*; Hijmans & Graham 2006). Planning for this change through modeling, monitoring, and experimental work will lead to more successful ecological restoration.

The concept of transformative restoration will become increasingly relevant with climate change. Harris et al. (2006) present this as a challenge between valuing the past and valuing future resiliency. They argue that "ecological integrity," the sustainable functioning of a site, will become a critical target for restoration in the context of climate change (Harris

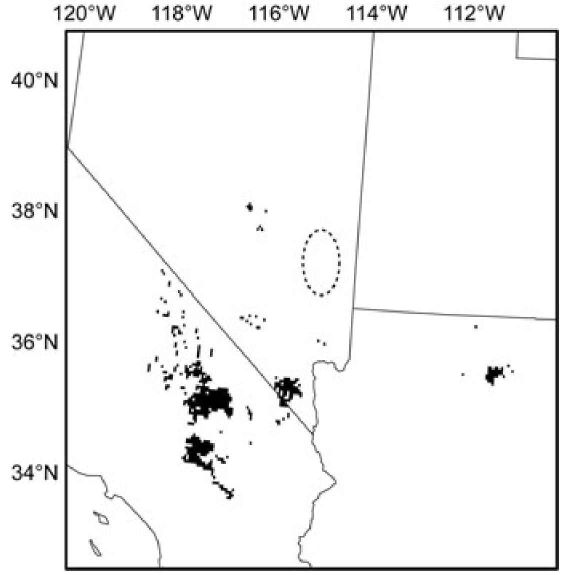

Figure 2. Vegetation in climatically similar landscapes (black pixels) is most likely to be suitable for the target restoration site (dashed circle) under future conditions projected by the GFDL2.1 2100 scenario.

Table 2. Land cover, based on ReGAP (USGS 2004), in areas that are currently most climatically similar to the target restoration site's likely climatic conditions in 2100 (based on the GFDL2.1 model).

Land Cover	*Percent*
Mojave Creosotebush	69
Mojave Mixed Scrub	10
Barren	4
Salt Desert Shrub	4
Blackbrush	4
Great Basin Mormon Tea	3
Great Basin Grassland	2
Shadscale mixed grass	2
Rabbitbrush	1
Pinyon-Juniper	<1
Agriculture	<1
Sagebrush	<1

The distribution of climatically similar lands is shown in Figure 2.

et al. 2006). Ecological integrity will be difficult to define, but effective land management must be both flexible and adaptive, shifting management strategies as climate changes (Chambers & Pellant 2008).

The target species for "transformative" restoration, *L. tridentata* and *A. dumosa*, need to be assessed further to determine how well they meet the criteria outlined for an acceptable novel species. *L. tridentata* and *A. dumosa* are indigenous to the semiarid biome of the southwestern United States, but fall outside of the Great Basin ecoregion. It is unclear whether *L. tridentata* and *A. dumosa* meet the criterion of being non-invasive. These species migrated northwards into the Mojave Desert during the Holocene, and their distributions have been relatively stable since (Grayson 1993). However, woody expansion of *L. tridentata* into grasslands of the southwest is an ongoing concern (Wessman et al. 2004). Any introduction of novel species, even with an aim of assisting natural migration pathways, must be approached with extreme caution. *Larrea tridentata* and *A. dumosa* have promise for fulfilling the criterion of sustaining native fauna. As shrubs, they are more likely than other structural forms of vegetation to support fauna native to sagebrush shrubland, although this would require extensive field work to confirm. Finally, although the GFDL2.1 model projects no-analog climate conditions at the restoration target, *L. tridentata* and *A. dumosa* exist under conditions similar to the novel climate and are viable candidates for transformative restoration.

The methodology presented here uses a single AOGCM (GFDL2.1) to identify areas where *Bromus tectorum* will become less viable and to estimate the most climatically suitable plant species for one restoration target. A single AOGCM is useful for illustrative purposes. However, for planning purposes, we recommend using an ensemble of AOGCMs to forecast changes in species distribution and to identify plant species that may be appropriate for a given restoration project. An ensemble approach uses projections from multiple AOGCMs or multiple Intergovernmental Panel on Climate Change (IPCC) scenarios (Nakicenovic & Swart 2000) to identify potential change (Araujo & New 2007). This approach decreases uncertainty in the projected change to species distributions. In the western United States, this is particularly important due to highly variable precipitation projections resulting from the region's complex topography and the challenges of modeling El Nino events (Randall et al. 2007).

A list of potential plant species based on ensemble envelope models will be a valuable starting point, but the candidates must be tested experimentally and modeled locally using soil and topographic information. Further, the appearance of "no-analog" communities (Williams & Jackson 2007), or climate conditions projected to occur in the future that do not currently exist regionally, is a concern. Although bioclimatic envelopes encompass some no-analog climate conditions, if the conditions do not currently exist, it is difficult to know if they will be suitable for a given species. In these cases, greenhouse or field experiments are needed to simulate future no-analog conditions and determine the responses of plants.

Viable native species for transformative restoration and effective establishment protocols should be identified soon because restoration opportunities at these sites may be short-lived. Other invasive species better suited to the new climate conditions could quickly invade. For example, red brome (*Bromus madritensis* ssp. *rubens*) is an abundant invader in the Mojave Desert and may move north into the restoration target with climate change. Restoration efforts in response to climate change are much more likely to be successful if desirable species are established before new invaders arrive.

That said, the appropriate timeline for restoration is unclear because the AOGCM climate projection used here is for the year 2100. The timescale at which *B. tectorum* becomes less competitive is uncertain. It may become gradually less competitive with rising temperatures and decreased precipitation or it may cross a threshold beyond which it is no longer viable.

Similarly, it is uncertain whether novel species targeted for restoration can survive under current climate conditions. Only experimental manipulations can address these questions.

Finally, it is possible that some invasive plants will persist even when their invasion risk is markedly reduced by climate change. In these cases, physiological limitations rather than bioclimatic envelopes will be more appropriate for predicting invasive species viability. Clearly, restoration planning with climate change is a complex issue that will require multiple avenues of research. Climate manipulation experiments and regular monitoring of potential restoration targets will be needed to assess the response of invasive species to changing climate and to seize restoration opportunities as they arise.

Conclusions

The possibility that some seemingly ineradicable invasive species will become less competitive on portions of their range due to climate change creates an unusual opportunity for ecological restoration. Many landscapes in the western United States have been profoundly altered by *Bromus tectorum*, and restoring lands currently dominated by this invasive species could reduce fire risk and soil erosion as well as increase biodiversity. However, some sites "abandoned" by *B. tectorum* may well be colonized by new alien species if we do not proactively establish native or novel species. A bioclimatic envelope approach is a useful first step toward restoration planning in the context of climate change.

Implications for Practice

- Climate change may create restoration opportunities on landscapes dominated by invasive plants if climate conditions become unsuitable for the invader.
- However, climate conditions may render these same areas unsuitable for native species that once occurred there, creating new challenges for restoration ecologists and practitioners.
- Bioclimatic envelope modeling can be used to identify locations where the current climate is most similar to the projected future climate of a given restoration target area in order to identify viable species for "transformative" restoration.
- Once potentially viable species are identified, landscape scale modeling and experimental work will be needed to evaluate species viability and establish restoration protocols.
- Integrated modeling, monitoring, and experimental work will be critical for effective restoration planning in the context of climate change.

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