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3 **When invasive plants disappear: transformative restoration possibilities in the western**
4 **United States resulting from climate change**

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6 Bethany A. Bradley^{1*} and David S. Wilcove^{1,2}

7 ¹Woodrow Wilson School of Public and International Affairs, Princeton University, Princeton,
8 NJ 08544

9 ²Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544

10

11 *Corresponding Author

12 Phone: 609 258 2392; Fax: 609 258 0390

13 Email: bethanyb@princeton.edu

14

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20 **Abstract**

21 Most ecologists believe that climate change poses a significant threat to the persistence of
22 native species. However, in some areas climate change may reduce or eliminate non-native
23 invasive species, creating opportunities for restoration. If invasive species are no longer suited to
24 novel climate conditions, the native communities that they replaced may not be viable either. If
25 neither invasive nor native species are climatically viable, a type of ‘transformative’ restoration
26 will be required, involving the translocation of novel species that can survive and reproduce
27 under new climate conditions. Here, we illustrate one approach for restoration planning by using
28 bioclimatic envelope modeling to identify restoration opportunities in the western United States
29 where the invasive plant cheatgrass (*Bromus tectorum*) is no longer climatically viable under
30 2100 conditions projected by the GFDL2.1 coupled atmosphere-ocean general circulation model.
31 We then select one example of a restoration target area and identify novel plant species that
32 could become viable at the site in the wake of climate change. We do so by identifying the
33 closest sites that currently have climate conditions similar to those projected at the restoration
34 target area in 2100. This approach is a first step toward identifying appropriate species for
35 transformative restoration.

36 **Introduction**

37 Climate change has the potential to alter significantly the distributions of species and change
38 the composition of plant and animal communities (Peterson et al., 2002; Pearson & Dawson,
39 2003; Root et al., 2003; Thuiller et al., 2005a; Araujo & Rahbek, 2006; Hijmans & Graham,
40 2006; Araujo & New, 2007). Large-scale shifts in species distribution present substantial
41 management questions: How do we protect native ecosystems from climate change threats
42 (Hannah et al., 2002; Midgley et al., 2002; Hannah et al., 2007; Pressey et al., 2007)? And, how
43 do we select appropriate species for restoration to account for climate change (Harris et al.,
44 2006)?

45 In addition to native communities, climate change also is expected to affect the distribution
46 of non-native invasive species (Thuiller et al., 2007). Invasive plants respond positively to
47 disturbance, and some species show enhanced competitiveness due to rising CO₂ levels (Sasek &
48 Strain, 1988; Smith et al., 2000; Ziska et al., 2005), which may lead to an overall increase in risk
49 of invasion with climate change (Dukes & Mooney, 1999; Moore, 2004). However, in other
50 cases invasive species may become less competitive in certain areas due to climate change
51 (Bradley et al., 2008). Reduced competitiveness of invasive species would create unprecedented
52 restoration opportunities.

53 Any restoration opportunities associated with climate change present a major challenge to
54 ecologists and land managers. If climate conditions become unsuitable for invasive species,
55 those same conditions may render the site unsuitable for native species. Moreover, it is possible
56 that *other* non-native, invasive species, previously excluded from a given site due to climatic
57 conditions, will be able to occupy that site as a result of climate change. Therefore, the
58 necessary action may not always be traditional restoration (returning native species to a site

59 where they once occurred), but rather something different—a type of ‘transformative’ restoration
60 in which novel plant species are introduced. Ideally, these novel species will be (1) indigenous
61 to the broader biome or ecoregion, (2) non-invasive, (3) capable of sustaining native fauna, and
62 (4) well suited to the new climate conditions of the restoration site. Here we focus on a method
63 for identifying those plant species best suited to establish under projected climate-change
64 conditions.

65 One approach for assessing potential distribution changes of native and invasive plants
66 involves bioclimatic envelope modeling (see reviews by Franklin, 1995; Guisan & Zimmermann,
67 2000; Pearson & Dawson, 2003; Guisan & Thuiller, 2005). Bioclimatic envelope models have
68 been widely used to assess risk from invasive species (Welk et al., 2002; Rouget et al., 2004;
69 Thuiller et al., 2005b; Mau-Crimmins et al., 2006), identify suitable locations for species
70 restoration (Pearce & Lindenmayer, 1998), and project the effects of climate change on species
71 distributions (Root et al., 2003; Thomas et al., 2004; Thuiller, 2004; Araujo et al., 2005;
72 Kueppers et al., 2005; Hijmans & Graham, 2006). Bioclimatic envelope modeling uses a
73 species’ geographic distribution to empirically define a climatic ‘niche’, or the climate
74 conditions in which a species can persist. At the regional scale a bioclimatic envelope can
75 provide a useful first-order approximation of the potential changes in species distribution
76 associated with climate change (Pearson & Dawson, 2003). These spatially explicit projections
77 provide a framework for assessing risk, planning monitoring efforts, and conducting climate
78 manipulation experiments.

79 Realized ecological niche is limited by a number of variables in addition to climate,
80 including topography, soils, land use, and species interactions (Davis et al., 1998; Dormann,
81 2007). As a result, it has been argued that a better approach would be to use local experimental

82 and observational knowledge of plant physiology and competition to build up to regional
83 projections (Woodward & Beerling, 1997). This type of bottom-up approach has been used, for
84 example, by Bradford and Lauenroth (2006), who defined limits to invasive cheatgrass (*Bromus*
85 *tectorum*) establishment based on physiological limitations observed in eastern Washington by
86 Hulbert (1955) and Harris (1967). However, just as it is uncertain whether regional relationships
87 hold at a local level, it is also uncertain whether local climate constraints hold at a regional scale.
88 Without any means for validation, it is unclear under what circumstances a top-down
89 (bioclimatic envelope) or bottom-up (physiological) model is more appropriate. Integration of
90 both approaches will be needed for more robust projections of the ecological implications of
91 climate change.

92 Here, we use bioclimatic envelope modeling to identify invaded locations with the potential
93 for restoration due to climate change (Bradley et al., 2008), and we suggest an approach for
94 identifying those plant species that are likely to be climatically suitable for establishment on the
95 site in the wake of climate change. We illustrate this approach using the GFDL2.1 coupled
96 atmosphere-ocean general circulation model (AOGCM) and the invasive plant cheatgrass (*B.*
97 *tectorum*) in the western United States.

98 First, we apply *B. tectorum*'s modeled bioclimatic envelope to conditions in the year 2100 as
99 projected by GFDL2.1. We identify lands where *B. tectorum* currently is established that are
100 likely to become climatically unsuitable for the species, creating restoration potential. Second,
101 we select one target location with restoration potential, create a bioclimatic envelope using future
102 climate, and match that bioclimatic envelope to current climate conditions to identify novel plant
103 species in nearby regions that could become viable at the restoration target area. Planning for

104 transformative restoration may become increasingly important as both native and invasive
105 species ranges shift due to global climate change.

106

107 **Background**

108 *B. tectorum* is an invasive annual grass common to mid to low elevation basins in the western
109 United States, many of which have been grazed heavily by domestic livestock since the mid to
110 late 1800s. *B. tectorum* dominates tens of thousands of km² throughout Nevada, Utah, southern
111 Idaho, eastern Oregon, and eastern Washington (Mack, 1981). *B. tectorum* primarily invades
112 sagebrush (*Artemisia tridentata*) shrubland, but it also is expanding in hotter, drier salt desert
113 (*Atriplex spp.*) shrubland and cooler, more mesic pinyon-juniper (*Pinus monophylla*, *Juniperus*
114 *spp.*) woodland (Billings, 1990; Knapp, 1996; Chambers et al., 2007). *B. tectorum* invasions
115 reduce biodiversity and ecosystem carbon storage (Bradley et al., 2006), decrease the ability of
116 ecosystems to support grazing by domestic livestock, and increase the probability of major fire
117 events in native and managed ecosystems (Whisenant, 1990; D'Antonio & Vitousek, 1992;
118 Chambers et al., 2007).

119 **Methods**

120 Datasets

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

130 Current climate conditions were derived from the PRISM dataset (Daly et al., 2002), a
131 0.04166 DD interpolation of weather gages in the United States that accounts for climatic
132 variation associated with topography. The climatic variables interpolated by PRISM are mean
133 monthly and annual precipitation, minimum temperature, and maximum temperature over the
134 1971-2000 time period.

135 Year 2100 climate conditions were created by adding climate change estimated by the
136 GFDL2.1 model (Delworth et al., 2006), using the SRESA1B scenario (Nakicenovic & Swart,
137 2000), to current climate conditions based on the PRISM dataset. The GFDL2.1 model
138 (Delworth et al., 2006) was selected because the modeling group is U.S.-based, and because the
139 model performed well when compared to historical stream flow measurements, suggesting that
140 its projections of changing precipitation may be more reliable than some other AOGCMs (Milly
141 et al., 2005). The SRESA1B scenario represents a ‘middle of the road’ future trajectory resulting

142 in a doubling of CO₂ to 720 ppm by 2100 (Nakicenovic & Swart, 2000). We use a single
143 AOGCM and scenario to illustrate a bioclimatic envelope modeling approach for selecting
144 suitable plant species for transformative restoration.

145 We calculated mean monthly and annual precipitation, minimum temperature, and maximum
146 temperature modeled for 1971-2000 (comparable to current conditions) and for 2090-2100
147 (estimated future conditions) based on the GFDL2.1 projection. We then subtracted mean late
148 20th century climate conditions from mean late 21st century climate conditions to derive
149 estimated change in annual and monthly precipitation and temperature. Due to the coarse spatial
150 resolution of the climate projection (2° Lat x 2.5° Lon), GFDL2.1 projected climate change was
151 added to the PRISM current climate interpolation to better account for local climatic and
152 topographic heterogeneity.

153 Modeling

154 The bioclimatic envelope was created using the four climate variables that most constrain *B.*
155 *tectorum* distribution today. Climate variables that most constrain a species distribution are
156 those where the climate space that the species encompasses is small relative to the total climate
157 space available regionally. Constraint (termed specialization by Hirzel et al., 2002) was
158 determined based on the ratio of the median distance from the mean climate value for pixels with
159 *B. tectorum* presence to the median distance from the mean climate value for all pixels (Bradley,
160 2008). Lower values indicate better constraint and thus better climatic predictors of *B. tectorum*
161 presence. In cases where adjacent monthly climatic variables were highly correlated (e.g., April-
162 May precipitation), we used a seasonal average to minimize redundancy.

163 The bioclimatic envelope was based on Mahalanobis distance (Farber & Kadmon, 2003;
164 Tsoar et al., 2007). Mahalanobis distance is a multivariate technique that defines perpendicular

165 major and minor axes and calculates distance from a centroid relative to covariance of axes
166 lengths. Unlike the commonly used BIOCLIM (Busby, 1991), which uses a box model to define
167 climate suitability, Mahalanobis distances can be represented by an ellipse. Hence, if the species
168 is present within a narrow range of precipitation, but a wide range of temperature, equal
169 Mahalanobis distances would cover a small range of precipitation, but a large range of
170 temperature. The smaller the Mahalanobis distance, the more likely climate conditions are
171 suitable for the species. Suitable climatic conditions for *B. tectorum* invasion were defined as all
172 land area with a Mahalanobis distance equal to or less than the value that encompassed 95% of
173 the species distribution.

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

179 From the areas that have restoration potential, we arbitrarily selected one Great Basin
180 location (restoration target area) in southern Nevada and assessed how climate conditions are
181 projected to change in that location. The example restoration target area for this study is located
182 in Lincoln County in southeast Nevada, and encompasses Dry Lake Valley west of the town of
183 Pioche. Land cover in this area is primarily sagebrush (*A. tridentata*) shrubland and mixed salt
184 desert scrub dominated by *Atriplex* spp. (USGS, 2004). We then created a bioclimatic envelope
185 based on the spatial distribution of the restoration target area and the 2100 projected climatic
186 conditions. We used the same input climatic variables used to construct the initial model for *B.*
187 *tectorum*. The bioclimatic envelope of the restoration target area was applied to current climate

188 conditions to identify lands that, based on Mahalanobis distance, are currently most climatically
189 similar to the GFDL2.1 projection for the restoration target area in 2100. Land cover in areas
190 that are currently most similar to the GFDL2.1 projected climate for the restoration target area
191 was identified based on the southwest ReGAP (USGS, 2004) land cover classification.

192 **Results**

193 We created the bioclimatic envelope model based on the climatic variables that most
194 constrained *B. tectorum* distribution. In order of importance, these climatic variables were
195 summer (Jun-Sep) precipitation, average annual precipitation, spring (Apr-May) precipitation,
196 and winter (Dec-Feb) maximum temperature (Bradley, 2008). The Mahalanobis distance that
197 encompassed 95% of the current distribution was 3.5 (Figure 1A).

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

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

208 Based on the projected 2100 climate of the restoration target area, the region that currently
209 exhibits the most similar conditions is located in the Mojave Desert in southern California
210 (Figure 2). The majority of land cover in the most climatically similar locations is dominated by
211 creosote (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) according to the southwest
212 ReGAP land cover classification (USGS, 2004) (Table 2). However, *L. tridentata* and *A.*
213 *dumosa* shrublands have Mahalanobis distances of up to 9.5, whereas the Mahalanobis distance
214 that encompasses 95% of the restoration target area's distribution is only 3.2. Hence, the best

215 candidate for transformative restoration actually falls outside of the restoration target area's
216 bioclimatic envelope.

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

223

224 **Discussion**

225 This paper illustrates one approach for identifying species that could survive under future
226 climate change conditions. This type of modeling work is a useful first step for restoration
227 planning on lands currently dominated by invasive species that may retreat in response to global
228 climate change. It is likely that climate change will lead to range shifts of both native and
229 invasive species (Hughes, 2000; Peterson et al., 2002; Pearson & Dawson, 2003; Root et al.,
230 2003; Thomas et al., 2004; Thuiller et al., 2005a; Hijmans & Graham, 2006). Planning for this
231 change through modeling, monitoring, and experimental work will lead to more successful
232 ecological restoration.

233 The concept of transformative restoration will become increasingly relevant with climate
234 change. Harris et al. (2006) present this as a challenge between valuing the past and valuing
235 future resiliency. They argue that 'ecological integrity', the sustainable functioning of a site, will
236 become a critical target for restoration in the context of climate change (Harris et al., 2006).
237 Ecological integrity will be difficult to define, but effective land management must be both

238 flexible and adaptive, shifting management strategies as climate changes (Chambers & Pellant,
239 2008).

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

255 The methodology presented here uses a single AOGCM (GFDL2.1) to identify areas where
256 *B. tectorum* will become less viable and to estimate the most climatically suitable plant species
257 for one restoration target. A single AOGCM is useful for illustrative purposes. However, for
258 planning purposes, we recommend using an ensemble of AOGCMs to forecast changes in
259 species distribution and to identify plant species that may be appropriate for a given restoration
260 project. An ensemble approach uses projections from multiple AOGCMs or multiple IPCC

261 scenarios (Nakicenovic & Swart, 2000) to identify potential change (Araujo & New, 2007). This
262 approach decreases uncertainty in the projected change to species distributions. In the western
263 United States, this is particularly important due to highly variable precipitation projections
264 resulting from the region's complex topography and the challenges of modeling El Nino events
265 (Randall et al., 2007).

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

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

281 That said, the appropriate timeline for restoration is unclear because the AOGCM climate
282 projection used here is for the year 2100. The timescale at which *B. tectorum* becomes less
283 competitive is uncertain. It may become gradually less competitive with rising temperatures and

284 decreased precipitation, or it may cross a threshold beyond which it is no longer viable.
285 Similarly, it is uncertain whether novel species targeted for restoration can survive under current
286 climate conditions. Only experimental manipulations can address these questions.

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

294

295 **Conclusions**

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

304

305 **Implications for Practice**

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

318

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321 groups for providing their data for analysis, the Program for Climate Model Diagnosis and
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324 The IPCC Data Archive is supported by the Office of Science, U.S. Department of Energy. We
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326 comments on a draft of this manuscript.

327 Table 1: Climatic conditions most important for *B. tectorum* distribution for the target restoration
 328 site in southern Nevada. The climate in 2100 as projected by the GFDL2.1 model using scenario
 329 A1B is slightly warmer and considerably drier.

Target Restoration Site: Southern Nevada				
	Current Climate Conditions		2100 Climate Conditions	
	Min	Max	Min	Max
Jun-Sep monthly ppt (cm)	1.6	3.1	1.2	2.7
Annual ppt (cm)	20.8	46.0	12.2	35.8
Apr-May monthly ppt (cm)	1.5	3.2	0	0.6
Dec-Feb tmax (°C)	6.7	11.2	7.8	12.5

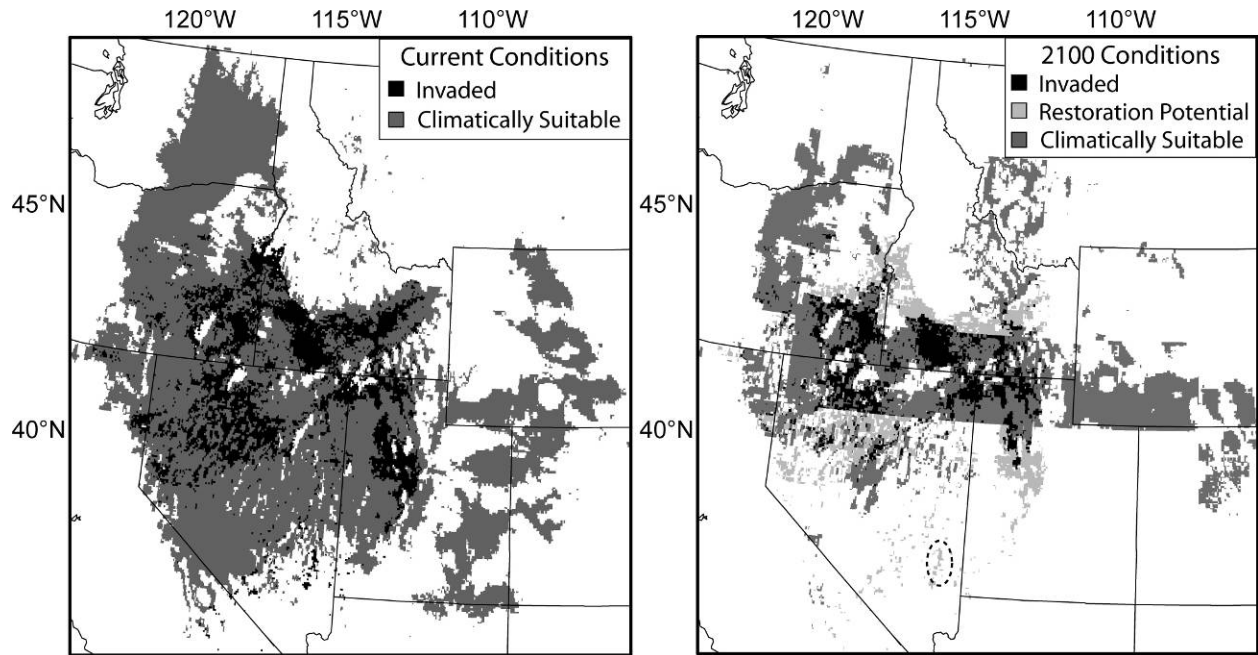
330

331

332 Table 2: Land cover, based on ReGAP (USGS, 2004), in areas that are currently most
 333 climatically similar to the target restoration site’s likely climatic conditions in 2100 (based on the
 334 GFDL2.1 model). The distribution of climatically similar lands is shown in Figure 2.

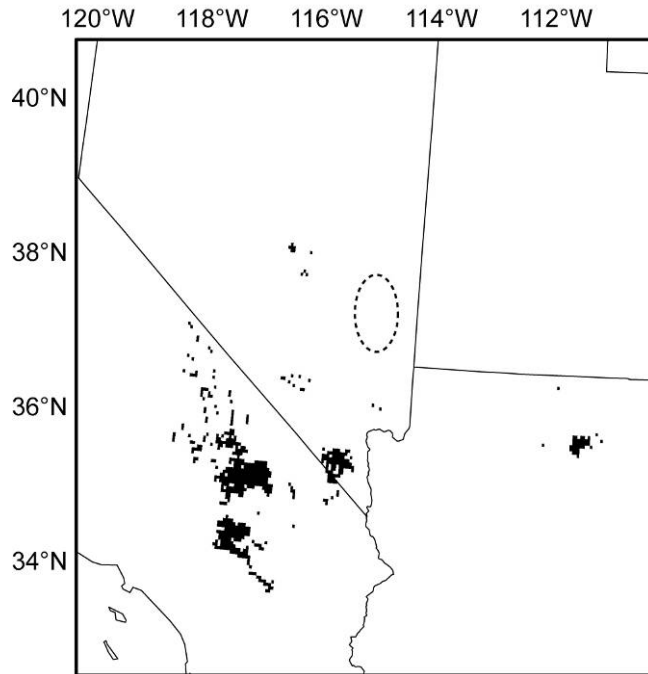
Land Cover	Percent
Mojave Creosotebush	69
Mojave Mixed Scrub	10
Barren	4
Salt Desert Shrub	4
Blackbrush	4
Great Basin Mormon Tea	3
Great Basin Grassland	2
Shadscale mixed grass	2
Rabbitbrush	1
Pinyon-Juniper	<1
Agriculture	<1
Sagebrush	<1

335



336

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



345

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

- 350 Araujo, M. B., and M. New 2007. Ensemble forecasting of species distributions. *Trends in*
 351 *Ecology & Evolution* **22**:42-47.
- 352 Araujo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard 2005. Validation of species-climate
 353 impact models under climate change. *Global Change Biology* **11**:1504-1513.
- 354 Araujo, M. B., and C. Rahbek 2006. How does climate change affect biodiversity? *Science*
 355 **313**:1396-1397.
- 356 Billings, W. D. 1990. *Bromus tectorum*, a Biotic Cause of Ecosystem Impoverishment in the
 357 Great Basin. Pages 301-322 in G. M. Woodwell, editor. *Patterns and processes of biotic*
 358 *impoverishment*. Cambridge University Press, New York.
- 359 Bradford, J. B., and W. K. Lauenroth 2006. Controls over invasion of *Bromus tectorum*: The
 360 importance of climate, soil, disturbance and seed availability. *Journal of Vegetation*
 361 *Science* **17**:693-704.
- 362 Bradley, B. A. 2008. Regional Analysis of Impacts of Climate Change on Cheatgrass Invasion
 363 Shows Potential Risk and Opportunity. In Press, *Global Change Biology*.
- 364 Bradley, B. A., R. A. Houghton, J. F. Mustard, and S. P. Hamburg 2006. Invasive grass reduces
 365 aboveground carbon stocks in shrublands of the Western US. *Global Change Biology*
 366 **12**:1815-1822.
- 367 Bradley, B. A., and J. F. Mustard 2005. Identifying land cover variability distinct from land
 368 cover change: Cheatgrass in the Great Basin. *Remote Sensing of Environment* **94**:204-
 369 213.
- 370 Bradley, B. A., D. S. Wilcove, and M. Oppenheimer 2008. Climate Change and Plant Invasion:
 371 Restoration Opportunities Ahead? Submitted to *Global Change Biology*.
- 372 Busby, J. R. 1991. BIOCLIM - a bioclimate analysis and prediction system. *Plant Protection*
 373 *Quarterly* **6**:8-9.
- 374 Chambers, J. C., and M. Pellant 2008. Climate Change Impacts on Northwestern and
 375 Intermountain U.S. Rangelands. *Rangelands*.
- 376 Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker 2007. What makes
 377 Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological*
 378 *Monographs* **77**:117-145.
- 379 D'Antonio, C. M., and P. M. Vitousek 1992. Biological Invasions By Exotic Grasses, The Grass
 380 Fire Cycle, And Global Change. *Annual Review of Ecology and Systematics* **23**:63-87.
- 381 Daly, C., W. P. Gibson, G. H. Taylor, G. L. Johnson, and P. Pasteris 2002. A knowledge-based
 382 approach to the statistical mapping of climate. *Climate Research* **22**:99-113.
- 383 Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood 1998. Making mistakes
 384 when predicting shifts in species range in response to global warming. *Nature* **391**:783-
 385 786.
- 386 Delworth, T. L., A. J. Broccoli, A. Rosati, R. J. Stouffer, V. Balaji, J. A. Beesley, W. F. Cooke,
 387 K. W. Dixon, J. Dunne, K. A. Dunne, J. W. Durachta, K. L. Findell, P. Ginoux, A.
 388 Gnanadesikan, C. T. Gordon, S. M. Griffies, R. Gudgel, M. J. Harrison, I. M. Held, R. S.
 389 Hemler, L. W. Horowitz, S. A. Klein, T. R. Knutson, P. J. Kushner, A. R. Langenhorst,
 390 H. C. Lee, S. J. Lin, J. Lu, S. L. Malyshev, P. C. D. Milly, V. Ramaswamy, J. Russell, M.
 391 D. Schwarzkopf, E. Shevliakova, J. J. Sirutis, M. J. Spelman, W. F. Stern, M. Winton, A.
 392 T. Wittenberg, B. Wyman, F. Zeng, and R. Zhang 2006. GFDL's CM2 global coupled

393 climate models. Part I: Formulation and simulation characteristics. *Journal of Climate*
394 **19**:643-674.

395 Dormann, C. F. 2007. Promising the future? Global change projections of species distributions.
396 *Basic and Applied Ecology* doi:10.1016/j.baae.2006.11.001.

397 Dukes, J. S., and H. A. Mooney 1999. Does global change increase the success of biological
398 invaders? *Trends in Ecology & Evolution* **14**:135-139.

399 Farber, O., and R. Kadmon 2003. Assessment of alternative approaches for bioclimatic modeling
400 with special emphasis on the Mahalanobis distance. *Ecological Modelling* **160**:115-130.

401 Franklin, J. 1995. Predictive vegetation mapping: Geographic modelling of biospatial patterns in
402 relation to environmental gradients. *Progress in Physical Geography* **19**:474-499.

403 Grayson, D. K. 1993. *The desert's past: a natural prehistory of the Great Basin*. Smithsonian
404 Institution Press, Washington.

405 Guisan, A., and W. Thuiller 2005. Predicting species distribution: offering more than simple
406 habitat models. *Ecology Letters* **8**:993-1009.

407 Guisan, A., and N. E. Zimmermann 2000. Predictive habitat distribution models in ecology.
408 *Ecological Modelling* **135**:147-186.

409 Hannah, L., G. Midgley, S. Anelman, M. Araujo, G. Hughes, E. Martinez-Meyer, R. Pearson,
410 and P. Williams 2007. Protected area needs in a changing climate. *Frontiers in Ecology*
411 *and the Environment* **5**:131-138.

412 Hannah, L., G. F. Midgley, T. Lovejoy, W. J. Bond, M. Bush, J. C. Lovett, D. Scott, and F. I.
413 Woodward 2002. Conservation of biodiversity in a changing climate. *Conservation*
414 *Biology* **16**:264-268.

415 Harris, G. A. 1967. Some Competitive Relationships between *Agropyron Spicatum* and *Bromus*
416 *Tectorum*. *Ecological Monographs* **37**:89-&.

417 Harris, J. A., R. J. Hobbs, E. Higgs, and J. Aronson 2006. Ecological restoration and global
418 climate change. *Restoration Ecology* **14**:170-176.

419 Hijmans, R. J., and C. H. Graham 2006. The ability of climate envelope models to predict the
420 effect of climate change on species distributions. *Global Change Biology* **12**:2272-2281.

421 Hirzel, A. H., J. Hausser, D. Chessel, and N. Perrin 2002. Ecological-niche factor analysis: How
422 to compute habitat-suitability maps without absence data? *Ecology* **83**:2027-2036.

423 Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent?
424 *Trends in Ecology & Evolution* **15**:56-61.

425 Hulbert, L. C. 1955. *Ecological Studies of Bromus-Tectorum and Other Annual Bromegrasses*.
426 *Ecological Monographs* **25**:181-213.

427 Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert -
428 History, persistence, and influences to human activities. *Global Environmental Change-*
429 *Human and Policy Dimensions* **6**:37-52.

430 Kueppers, L. M., M. A. Snyder, L. C. Sloan, E. S. Zavaleta, and B. Fulfrost 2005. Modeled
431 regional climate change and California endemic oak ranges. *Proceedings of the National*
432 *Academy of Sciences of the United States of America* **102**:16281-16286.

433 Mack, R. N. 1981. Invasions of *Bromus tectorum* L. into Western North America: An Ecological
434 Chronicle. *Agro-Ecosystems* **7**:145-165.

435 Mau-Crimmins, T. M., H. R. Schussman, and E. L. Geiger 2006. Can the invaded range of a
436 species be predicted sufficiently using only native-range data? *Lehmann lovegrass*
437 (*Eragrostis lehmanniana*) in the southwestern United States. *Ecological Modelling*
438 **193**:736-746.

439 Midgley, G. F., L. Hannah, D. Millar, M. C. Rutherford, and L. W. Powrie 2002. Assessing the
440 vulnerability of species richness to anthropogenic climate change in a biodiversity
441 hotspot. *Global Ecology and Biogeography* **11**:445-451.

442 Milly, P. C. D., K. A. Dunne, and A. V. Vecchia 2005. Global pattern of trends in streamflow
443 and water availability in a changing climate. *Nature* **438**:347-350.

444 Moore, P. D. 2004. Plant ecology - Favoured aliens for the future. *Nature* **427**:594-594.

445 Nakicenovic, N., and R. Swart. 2000. *Special Report on Emissions Scenarios*. Cambridge
446 University Press, Cambridge, England.

447 Pearce, J., and D. Lindenmayer 1998. Bioclimatic analysis to enhance reintroduction biology of
448 the endangered helmeted honeyeater (*Lichenostomus melanops cassidix*) in southeastern
449 Australia. *Restoration Ecology* **6**:238-243.

450 Pearson, R. G., and T. P. Dawson 2003. Predicting the impacts of climate change on the
451 distribution of species: are bioclimate envelope models useful? *Global Ecology and*
452 *Biogeography* **12**:361-371.

453 Peterson, A. T., M. A. Ortega-Huerta, J. Bartley, V. Sanchez-Cordero, J. Soberon, R. H.
454 Buddemeier, and D. R. B. Stockwell 2002. Future projections for Mexican faunas under
455 global climate change scenarios. *Nature* **416**:626-629.

456 Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling, and K. A. Wilson 2007. Conservation
457 planning in a changing world. *Trends in Ecology & Evolution* **22**:583-592.

458 Randall, D. A., R. A. Wood, S. Bony, R. Colman, T. Fichefet, J. Fyfe, V. Kattsov, A. Pitman, J.
459 Shukla, J. Srinivasan, R. J. Stouffer, A. Sumi, and K. E. Taylor 2007. *Climate Models*
460 *and Their Evaluation*. Pages 74 in S. Solomon, D. Qin, M. Manning, Z. Q. Chen, M.
461 Marquis, K. B. Averyt, M. Tignor and H. L. Miller, editors. *Climate Change 2007: The*
462 *Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment
463 Report of the Intergovernmental Panel on Climate Change. Cambridge University Press,
464 Cambridge, UK and New York, NY.

465 Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds 2003.
466 Fingerprints of global warming on wild animals and plants. *Nature* **421**:57-60.

467 Rouget, M., D. M. Richardson, J. L. Nel, D. C. Le Maitre, B. Egoh, and T. Mgidi 2004. Mapping
468 the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland
469 using climatic suitability. *Diversity and Distributions* **10**:475-484.

470 Sasek, T. W., and B. R. Strain 1988. Effects of Carbon-Dioxide Enrichment on the Growth and
471 Morphology of Kudzu (*Pueraria-Lobata*). *Weed Science* **36**:28-36.

472 Smith, S. D., T. E. Huxman, S. F. Zitzer, T. N. Charlet, D. C. Housman, J. S. Coleman, L. K.
473 Fenstermaker, J. R. Seemann, and R. S. Nowak 2000. Elevated CO₂ increases
474 productivity and invasive species success in an arid ecosystem. *Nature* **408**:79-82.

475 Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F.
476 N. Erasmus, M. F. De Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S.
477 Van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L.
478 Phillips, and S. E. Williams 2004. Extinction risk from climate change. *Nature* **427**:145-
479 148.

480 Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change.
481 *Global Change Biology* **10**:2020-2027.

482 Thuiller, W., S. Lavorel, M. B. Araujo, M. T. Sykes, and I. C. Prentice 2005a. Climate change
483 threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of*
484 *the United States of America* **102**:8245-8250.

485 Thuiller, W., D. M. Richardson, and G. F. Midgley 2007. Will Climate Change Promote Alien
486 Plant Invasions? Pages 197-211 in W. Nentwig, editor. Ecological Studies. Springer-
487 Verlag, Berlin Heidelberg.

488 Thuiller, W., D. M. Richardson, P. Pysek, G. F. Midgley, G. O. Hughes, and M. Rouget 2005b.
489 Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global
490 scale. *Global Change Biology* **11**:2234-2250.

491 Tsoar, A., O. Allouche, O. Steinitz, D. Rotem, and R. Kadmon 2007. A comparative evaluation
492 of presence-only methods for modelling species distribution. *Diversity and Distributions*
493 **13**:397-405.

494 Usgs 2004. National Gap Analysis Program. Provisional Digital Land Cover Map for the
495 Southwestern United States. Version 1.0. RS/GIS Laboratory, College of Natural
496 Resources, Utah State University, Logan, UT.

497 Welk, E., K. Schubert, and M. H. Hoffmann 2002. Present and potential distribution of invasive
498 garlic mustard (*Alliaria petiolata*) in North America. *Diversity and Distributions* **8**:219-
499 233.

500 Wessman, C. A., S. Archer, L. C. Johnson, and G. P. Asner 2004. Woodland Expansion in US
501 Grasslands in G. Gutman, editor. *Land Change Science*. Kluwer Academic Publishers,
502 The Netherlands.

503 Whisenant, S. G. 1990. Changing Fire Frequencies on Idaho's Snake River Plains: Ecological
504 and Management Implications. Pages 4-10. Symposium on Cheatgrass Invasion, Shrub
505 Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV.

506 Williams, J. W., and S. T. Jackson 2007. Novel climates, no-analog communities, and ecological
507 surprises. *Frontiers in Ecology and the Environment* **5**:475-482.

508 Woodward, F. I., and D. J. Beerling 1997. The dynamics of vegetation change: health warnings
509 for equilibrium 'dodo' models. *Global Ecology and Biogeography Letters* **6**:413-418.

510 Ziska, L. H., J. B. Reeves, and B. Blank 2005. The impact of recent increases in atmospheric
511 CO₂ on biomass production and vegetative retention of Cheatgrass (*Bromus tectorum*):
512 implications for fire disturbance. *Global Change Biology* **11**:1325-1332.

513
514