

Native and exotic plant cover vary inversely along a climate gradient 11 years following stand-replacing wildfire in a dry coniferous forest, Oregon, USA

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Citation	Dodson, E. K., & Root, H. T. (2015). Native and exotic plant cover vary inversely along a climate gradient 11 years following stand-replacing wildfire in a dry coniferous forest, Oregon, USA. <i>Global Change Biology</i> , 21(2), 666–675. doi: 10.1111/gcb.12775
DOI	10.1111/gcb.12775
Publisher	John Wiley & Sons Ltd.
Version	Accepted Manuscript
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse

Received Date : 13-May-2014

Revised Date : 07-Sep-2014

Accepted Date : 03-Oct-2014

Article type : Primary Research Articles

Title: Native and exotic plant cover vary inversely along a climate gradient 11 years following stand-replacing wildfire in a dry coniferous forest, Oregon, USA.

Running head: Post-fire recovery varies with climate

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Keywords

cheatgrass, climate change type drought, exotic invasion, medusahead, ponderosa pine forest, state change

Type of Paper: Primary Research Article

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/gcb.12775

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Abstract

Community re-assembly following future disturbances will often occur under warmer and more moisture-limited conditions than when current communities assembled. Because the establishment stage is regularly the most sensitive to climate and competition, the trajectory of recovery from disturbance in a changing environment is uncertain, but has important consequences for future ecosystem functioning. To better understand how ongoing warming and rising moisture limitation may affect recovery, we studied native and exotic plant composition 11 years following complete stand-replacing wildfire in a dry coniferous forest spanning a large gradient in climatic moisture deficit (CMD) from warm and dry low elevation sites to relatively cool and moist higher elevations sites. We then projected future precipitation, temperature and CMD at our study locations for four scenarios selected to encompass a broad range of possible future conditions for the region. Native perennials dominated relatively cool and moist sites 11 years after wildfire, but were very sparse at the warmest and driest (high CMD) sites, particularly when combined with high topographic sun exposure. In contrast, exotic species (primarily annual grasses) were dominant or co-dominant at the warmest and driest sites, especially with high topographic sun exposure. All future scenarios projected increasing temperature and CMD in coming decades (e.g., from 4.5% to 29.5% higher CMD by the 2080's compared to the 1971-2000 average), even in scenarios where growing season (May-September) precipitation increased. These results suggest increasing temperatures and moisture limitation could facilitate longer-term (over a decade) transitions toward exotic-dominated communities after severe wildfire when a suitable exotic seed source is present.

Introduction

Future ecosystems will face increasing aridity and drought (Schwalm et al. 2012, Cook et al. 2013), combined with rising temperatures that exacerbate moisture limitations (Breshears et al. 2005; Williams et al. 2013; Zhao et al. 2013). Climate changes may be particularly influential for ecosystem reorganization following disturbance (Dale et al. 2001; Turner et al. 2010; Anderson-Teixera et al. 2013); especially because climate changes are likely to increase the probability of some severe disturbances. For example, earlier snowmelt and longer dry seasons could increase forest fire size (Westerling et al. 2006), fire severity (Miller et al. 2009; Rogers et al. 2011), and days with extreme wildfire weather (Luo et al. 2013). However, the potential effects of warmer and drier conditions on vegetation recovery after severe wildfire are poorly understood, due in part to the difficulty of examining large stochastic severe disturbance events such as wildfire. Variation in responses along elevation gradients can provide insights into potential ecosystem responses to a changing climate at larger spatial scales than are typically possible in experimental manipulations (Sundqvist et al. 2013). To better understand the potential effects of increasing temperatures and moisture stress after disturbance we sampled vegetation 11 years after complete stand-replacing fire (all overstory trees killed) in a dry coniferous forests across an elevation gradient (> 700m) that spanned a considerable range in temperature and precipitation.

Current plant communities may reflect favorable past establishment conditions; communities reassembling after disturbance will face new environmental conditions (Anderson-Teixera et al. 2013). The seedling stage is often more sensitive to climate (Grubb 1977; Jackson et al. 2009; Johnstone et al. 2010) and competition from exotic species (Young and Allen 1997; McGlone et al. 2012; Larios et al. 2013) than established individuals of the

same species. Moisture availability has been shown to be a dominant driver of plant communities even in low energy systems (le Roux et al. 2013). In many semi-arid climates perennial species establish from seed only infrequently, during favorable moist years (Donovan et al. 1993; Young et al. 1999; Humphrey and Schupp 2004). Similarly, severe moisture limitation can result in high mortality of re-sprouting shrubs following wildfire (Pratt et al. 2014). In contrast, it has long been known that drought can shift dominance from perennial species to annual species (e.g., Pechanec et al. 1937; Robertson 1939). Thus, forecast increases in aridity from drought (Schwalm et al. 2012) could limit recovery of perennial species and possibly increase dominance of annual species following disturbances such as wildfire.

Climate change may also facilitate invasion by exotic species (Smith et al. 2000; Meador et al. 2012; Sandel and Dangremond 2012), especially when combined with increasing disturbances, which often favor exotic invasion (Hobbs and Huenneke 1992; Alpert et al. 2000). Exotic annual grasses may be of particular concern in dry coniferous forests, as they have already invaded millions of ha in adjacent shrub steppe ecosystems in western North America (Meador et al. 2012) with considerable economic and ecological ramifications (e.g., Davies and Svejcar 2008; Meador et al. 2012; Balch et al. 2013). Exotic annual grasses are often strongly inhibited by an intact forest canopy (e.g., Pierson et al. 1990; Lovtang and Reigel 2012) and cold temperatures (Chambers et al. 2007; Lovtang and Reigel 2012). However, after fire (either wildfire or prescribed) annual grasses can invade forested (or formerly forested) sites (Young and Evans 1970; Kerns et al. 2006; Keeley and McGinnis 2007; McGone et al. 2009; Meador et al. 2012). Furthermore, continued warming (Sandel and Dangremond 2012) and rising CO₂ atmospheric concentrations (Smith et al.

2000) are likely to further benefit exotic annual species, suggesting these species could be primed to invade formerly forested ecosystems following stand-replacing wildfire.

We examined community reassembly 11 years following stand-replacing wildfire across an elevation gradient (> 700 m) that varied considerably in temperature and moisture availability (Climatic Moisture Deficit (CMD); Wang et al. 2012). We addressed three research questions:

- (i) Does the cover of native plants vary across the gradient and do responses differ for short-lived and perennial species?
- (ii) Does exotic cover or relative exotic cover vary across the gradient?
- (iii) How do these results relate to projected climate changes at these sites under a range of future scenarios?

Materials and Methods

Study Site and Data Collection

The Eyerly fire was started by lightning on July 9, 2002 and burned a total of 9362 ha with a total of 5188 ha burning at stand-replacing severity (Dodson and Root 2013).

Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests dominated lower elevations with occasional western juniper (*Juniperus occidentalis* Hook.) whereas higher elevations are comprised of mixed conifer forests including ponderosa pine, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), incense cedar (*Calocedrus decurrens* (Torr.) Florin), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) and western larch (*Larix occidentalis* Nutt.). The most abundant understory species (by cover) 11 years after stand-replacing wildfire in our

sample included several native shrubs (*Ceanothus sanguineus* Pursh, *Ceanothus velutinus* Douglas ex Hook., *Ceanothus prostratus* Benth., *Arctostaphylos patula* Greene, *Salix scouleriana* Barratt ex Hook.) and two exotic annual grasses (*Bromus tectorum* L. and *Taeniatherum caput-medusae* (L.) Nevski). The majority of precipitation in the region falls during the cool season while summers are warm and dry (Meigs et al. 2009). Soils are well-drained volcanic sandy loams and loamy sands (Meigs et al. 2009). Fires were historically frequent in this region, with many burning at low severity (Weaver 1959), although some mixed severity fire also occurred (Meigs et al. 2009). Much of this region has recently (since 2002) burned in several high and mixed severity wildfires (Meigs et al 2009).

The eastern slope of the Cascade Range has one of the strongest precipitation gradients in North America, with precipitation rapidly decreasing from west to east and as elevation decreases (PRISM Group, Oregon St. Univ., <http://prism.oregonstate.edu/>; Meigs et al., 2009). The burned area (part of the eastern slope of Green Ridge) is also geologically simple and the soils are quite uniform (Swedberg 1973), making it ideally suited for isolating the effects of climate. Climate values for the 1970-2000 period were calculated using ClimateWNA (Wang et al. 2012). Mean annual precipitation for plots in this study ranged from 302 to 836 mm/yr, increasing with elevation (Table S1). Mean annual temperature ranged from 6.7 to 9.8°C decreasing with elevation. This formed a strong gradient in climatic moisture deficit (CMD; Wang et al. 2012), which ranged from 483 to 813 mm annually (Table S1). This range (330 mm) is much larger than the 26 mm standard deviation found by Wang et al. (2012) for calculations of CMD using 56 weather stations distributed across western North America. Spring CMD (Wang et al. 2012) was strongly correlated with annual CMD ($r^2 = 0.99$ for linear correlation), thus sites that are the driest throughout the year are also driest in the spring when plants are establishing. The Eyerly fire took place during a

multiyear drought in much of the western United State (Schwalm et al. 2012). The nearest weather station to the study sites (Pelton Dam; about 17 km northeast of the fire; <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?or6532>) recorded 45% of the normal May-July (primary growing season) in 2003 (first recovery year) and 93% in 2004. Similarly, estimated annual CMD (Wang et al. 2012) was 57 mm above the 19701-2000 normal in 2003 (first fire recovery year) and 35 mm above normal in 2004.

We established 31 plots in areas with complete overstory mortality (no live trees remaining) at the time of sampling 11 years post-fire (Fig. 1a). Each plot consisted of a transect with ten 1-m² quadrats spaced five meters apart in two rows oriented along the contour. Cover of each individual species was estimated to the nearest percent in each quadrat. Suitable burn patches were selected to span the gradient from warm dry sites to relatively cool and moist sites and were selected subjectively from site visits based on the following criteria: at least 200 m from a previous plot, complete stand replacing wildfire with a sufficient buffer to establish a plot with at least 40 m to roads and live trees, located on public land not closed due to nesting sites of sensitive raptors, at least 50 trees per ha >25 cm diameter at breast height prior to wildfire, and no evidence of post-fire management (e.g., salvage logging or tree planting). Plot starting points were then selected randomly within the patch. Using small quadrats as in this study allows detection of dominant community trends, but may not capture uncommon species or less conspicuous trends (e.g., Abella et al. 2004). This biases us against detecting subtle differences in the community, which are often the dominant response after silvicultural manipulations in similar dry forests (Abella et al. 2004; Metlen and Fiedler 2006).

We extracted soil moisture holding capacity in the top 100 cm for each plot from the Web Soil Survey (Soil Survey Staff 2013). We calculated heat load index (HLI) following McCune (2007) for each plot from the slope, aspect and latitude. Steep SW facing slopes have high HLI, whereas steep NE facing slopes have the lowest HLI (McCune 2007). Plant attributes (i.e., provenance, lifespan) follow the USDA PLANTS database (2013). Finally, we calculated relative cover of exotic species by dividing the total plant cover by the cover from exotics then multiplying by 100.

Analyses

We used generalized linear models (proc GLM in SAS version 9.3, SAS institute, Cary, NC) to evaluate the effects of CMD and HLI on native perennial cover, native short-lived species cover (annuals and biennials), total exotic cover, and relative exotic cover. Temperature, growing season (May-September) precipitation and elevation were all strongly collinear with CMD (Fig. S1), thus we include only CMD as a predictor in the models, but acknowledge that changes along the gradient could be due to any of these factors in our interpretation (e.g., Dormann et al. 2013). Similarly, soil moisture holding capacity was strongly correlated with CMD ($r^2 = 0.86$ with a quadratic term included), thus likely exacerbating moisture limitations at high CMD sites, though differences in soil moisture holding capacity (a range of 29 mm among sites) were much smaller than the range in CMD (330 mm). Similarly, Swedberg (1973) noted that changes in vegetation along the climate gradient in this region are much larger than explained by differences in soils. CMD and HLI were considered as candidate predictor variables for each response variable and eliminated from the model in a step-wise backward elimination if not significant. Backward elimination often results in similar models and model performance as model selection

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techniques such as Akaike's information criterion (AIC; Murtaugh 2009). Residuals were plotted against fitted values and predictor variables to ensure assumptions of independence, normality and equal variance were not violated. Native short-lived species cover, exotic cover, and relative exotic cover required a natural log (+ 0.1) transformation to meet parametric assumptions.

We used ClimateWNA (Wang et al. 2012) to estimate climatic moisture deficit (CMD) at exact sample locations (based on latitude, longitude and elevation) in this study and to project future climate under four scenarios. CMD is a useful measure for vegetation that describes the amount of moisture that must be met from sources other than precipitation for plant growth at a monthly time scale (Wang et al. 2012). We selected two General Circulation Models (GCMs) from the fourth IPCC assessment (AR4): UKMO-HadCM3 (Hadley) and CISRO-MK3 (CIRSO). The Hadley model predicts warm and dry conditions for the Pacific Northwest, while CISRO is cooler and wetter (Rogers et al. 2011); thus this combination spans a wide range of possible future conditions. We followed Mote and Salathé (2010) and used B1 as low emission scenario and A1B as the high emission scenario, even though A1B is often considered a moderate emission scenario (Mote and Salathé 2010). Climate change predictions for each climate change scenario are from the 2080's. We compared projected precipitation and CMD values with the 1971-2000 values for each scenario.

Results

We sampled 102 total species in stand-replacing patches 11 years after the Eyerly fire on the 31 plots. A total of 11 exotic species were sampled, with two exotic annual grasses (*Bromus tectorum* and *Taeniatherum caput-medusae*) comprising 87% of the total exotic cover. Vegetation communities varied strongly across the climate gradient represented by climatic moisture deficit (CMD). Perennial species cover varied significantly with CMD and the topographic heat load index (HLI), which together explained 83% of the variation in native perennial cover (Table 1). Perennial native cover declined strongly with increases in CMD, from an estimated 102% cover with a CMD of 500 mm to an estimated 25% cover with a CMD of 800 mm at the mean HLI (Fig. 2). Similarly, cover of native perennial species was lower where the heat load index was high (Table 1).

Native short-lived species comprised far less total cover than native perennials and showed the opposite response to CMD, with higher cover on plots with high moisture stress (Fig. 1; Table 1). Modeled cover of native short-lived species increased from about 0.5% at a CMD of 500 mm to an estimated 3% cover at 800 mm CMD (Fig. 2) with CMD explaining 28% of the variation in native short-lived species cover (Table 1).

Exotic cover and relative exotic cover also varied significantly with CMD, with higher values at high levels of CMD (Table 1). Similarly, exotic cover was higher on plots with a higher heat load index (Table 1). Total exotic cover increased from an estimated value of < 0.5% cover at 500 mm CMD to 11% at 800 mm CMD at the mean HLI (Fig. 3). Changes in relative exotic cover were even more striking (Fig. 1; Fig. 3): at the mean HLI

and relatively low CMD (500 mm) estimated relative exotic cover was < 0.5%, but increased to an estimated 27% at a CMD of 800 mm and ranged as high as 90% on one plot with high CMD (810 mm; Fig. 3). Of the 15 plots with a CMD above 700 mm, 12 had relative exotic cover $\geq 10\%$ and eight had relative exotic covers > 30% (Fig. 3b). In contrast, none of the 12 plots with CMD < 650 mm had a relative exotic cover above 15% and nine had relative exotic cover < 7% (Fig. 3b). Both exotic cover and relative exotic cover also increased with increasing HLI.

Forecast mean annual temperatures for the 2080's compared to the 1970-2000 reference condition increased for all scenarios (Fig. 4a), while changes in growing season (May-September) precipitation varied depending on the choice of GCM (Fig. 4b). Predicted temperature increases ranged from 1.3 to 4.3 degrees Celsius, with larger increases with the Hadley model and higher emissions (Fig. 4a). The CIRSO model predicted increases in growing season precipitation under both emission scenarios, with an increase of over 18.5 mm with the A1B emission scenario, an increase of over 20% relative to the reference period (Fig. 4a). In contrast, growing season precipitation declined under both emission scenarios in the Hadley model predictions, with decreases exceeding 20 mm under both scenarios (>23% decrease relative to the 1970-2000 baseline; Fig. 4a).

Consistent with changes in temperature, but in contrast to the mixed results for growing season precipitation, all four future scenarios examined suggest increases in CMD by the 2080's relative to the 1970-2000 baseline scenario (Fig. 4b). Future increases in CMD ranged from a low of 31 mm (a 4.5% increase above the 1970-2000 mean from the sites in this study) to an increase of 202 mm (a 29.5% increase above the mean from the sites in this

study; Fig. 4b). Increases in CMD were lower using the CIRSO model for both emissions scenarios, likely due to the increase in growing season precipitation relative to declines with the Hadley model (Fig. 4). These forecast changes in CMD could have large effects on ecosystem recovery, particular under the most extreme scenario (higher emissions in the Hadley model). For example, in the current study a site with a CMD of 600 (at the median heat load index) had a modeled relative exotic cover of only 1.6%. Holding other variables constant (for illustrative purposes), under the most extreme scenario we modeled (an increase in CMD of 202 mm for the Hadley model in the A1B emission scenario) the estimated relative exotic cover would increase to 28.5%.

Discussion

Understanding post-disturbance recovery is critical for predicting ecosystem services and functions in a changing environment (Anderson-Teixera et al. 2013). In this study, native perennial cover and exotic dominance varied inversely across the gradient from warm dry sites to cool moist sites more than a decade following wildfire, suggesting climate as a potential key driver of post-fire community assembly in these dry forest ecosystems. The dominance of perennial native species at more mesic sites (lower CMD) is consistent with strong native recovery noted after fires on relatively mesic sites in previous studies (Donato et al. 2009; Dodson and Peterson 2010; Halofsky et al. 2011) and with patterns of tree regeneration from seed following the Eyerly fire (Dodson and Root 2013). This is also generally consistent with the hypothesis that ecosystem resilience is positively related to productivity or establishment favorability for pre-disturbance communities (Larson et al. 2008; Dynesius et al. 2009). This strong native recovery at more mesic sites may contribute to high biodiversity characteristic of early seral sites in forested ecosystems (e.g., Swanson et

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al. 2010). In contrast, exotics were abundant and native perennials were sparse at the warmest and driest plots, particularly on slopes with high sun exposure. The lack of native recovery at the most moisture-stressed sites is consistent with recent studies demonstrating high mortality for recovering native perennials after wildfire with high moisture stress (Pratt et al. 2014). These results and projected increases in temperature and CMD across all four climate change scenarios suggest increasing susceptibility of dry forests conversion to communities dominated by exotic annual grasses following stand-replacing disturbance.

The potential for drought to shift communities from perennials to annuals has long been recognized (e.g., Pechanec et al. 1937; Robertson 1939). Indeed, both native short-lived species and exotics (dominated by annual grasses) increased with CMD, while native perennials declined in this study. The multi-year drought in the western US at the time of the fire (Schwalm et al. 2012) probably contributed to lower perennial native recovery (e.g., Pratt et al. 2014). Many native perennials in semi-arid regions only recruit new seedlings during favorable moist years (Donovan et al. 1993; Young et al. 1999; Humphrey and Schupp 2004). Even perennial shrubs that resprout following fire may be subject to high mortality rates under dry conditions (Pratt et al. 2014). The soil surface can reach very high temperatures even in undisturbed ponderosa pine forests (Kolb and Robberecht 1996), with even higher temperatures likely after wildfires remove vegetation and litter layers. Such high temperatures strongly exacerbate water limitations (Breshears et al. 2005; Williams et al. 2013; Zhao et al. 2013). The increased moisture availability at mesic sites and on slopes that receive less radiation may have facilitated rapid recovery of native perennial species in this study. Previous studies have documented declines in exotic annual grass dominance 6 to 11 years following disturbances that coincided with native perennial recovery (e.g., Bates et al. 2005). However, high relative exotic cover 11 years following wildfire, combined with the

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scarcity of tree regeneration at dry forest sites on this fire (Dodson and Root 2013; Fig. S2) and in other studies (Roccaforte et al. 2012; Collins and Roller 2013), which can strongly suppress exotic annual grasses (Pierson et al. 1990; Lovetang and Reigel 2012) suggest limited potential for natural recovery of native vegetation. Furthermore, forecast increases in temperature, moisture deficits, and severe droughts (Schwalm et al. 2012) will likely further reduce native community recovery, especially at warm and dry sites.

Both native perennials and exotics (dominated by annuals) were strongly correlated with the climatic gradient in this study, making it difficult to ascertain the potential effects of exotic invasion on natives (or vice versa) in this observational study. For example, strong responses by the native plant community may limit invasion (Chambers et al. 2007) potentially explaining the lack of exotic cover at mesic sites where native perennials dominated. In this case, exotic annual grasses may have been able to invade dry sites following wildfire because of the poor recovery by perennial native vegetation (i.e., passengers of environmental change sensu MacDougall and Turkington 2005). Alternatively, the strong response by exotic annual grasses at the driest sites may have inhibited colonization by native perennials (drivers of environmental changes sensu MacDougall and Turkington 2005). Indeed, previous work suggests that exotic annual grasses can exclude natives, reducing biodiversity (i.e., Humphrey and Schupp 2004; Davies and Svejcar 2008). Further experimental studies will be needed to understand the mechanisms driving the patterns observed in this study.

Invasion requires the combination of a suitable habitat and propagules of an exotic species adapted to the site (Alpert et al. 2000). The warm dry sites in this study likely had a

greater seed source due to their proximity to more heavily invaded shrub steppe ecosystems (Lovtang and Reigel 2012), potentially contributing to heavier invasion at these sites. However, exotic annual grasses, including cheatgrass and medusahead, are widespread in many dry coniferous forests in Oregon and California (e.g., Young and Evans 1970; Lovtang and Reigel 2012; Fischer and Charnley 2012). Even at low levels, cheatgrass can pose a strong threat of invasion after disturbance once introduced to the seedbank (Lovtang and Reigel 2012). The broad distribution of exotic annuals in our study area including some presence in higher elevation forests (Lovtang and Reigel 2012), the consistent effects of CMD and HLI, and the occurrence of exotic annual grasses on more mesic sites (often in discrete patches around native perennials; Fig. 1d; or under dominant native species; Fig. S3) suggest that seed limitation was probably not the only factor limiting invasion at higher elevation mesic sites. Vigorous native responses can limit invasion by exotic annual grasses (Chambers et al. 2007), as may have occurred at mesic sites in this study. Similar declines in exotic abundance with elevation have been well documented (e.g., Keeley et al. 2003; Dodson and Peterson 2010; Alexander et al. 2011). Many exotic species are adapted to lower elevation environments (Alexander et al. 2011), with factors such as colder temperatures at higher elevations in particular, able to limit invasion by exotic grasses (e.g., Chambers et al. 2007; Lovtang and Reigel 2012). If future climate change increases temperatures and raises moisture stress, as predicted, it could remove both biological (e.g., strong native recovery) and physiological (e.g., cold temperature) constraints on exotic invasion.

The ecosystem impacts of exotic invasion are probably more effectively expressed by relative abundance as compared with absolute abundance or species richness (e.g., Seabloom et al. 2013). It is possible that even relatively high exotic cover, when combined with moderate to high native cover, may maintain many of ecosystem functions provided by native

species. For example, a forest with an exotic understory is more likely to maintain ecosystem services such as carbon storage and habitat for arboreal wildlife than a formerly forested site with the same abundance of exotics, but lacking a forest overstory. Furthermore, if native species remain present in the community, they may be able to recruit during years with more favorable weather conditions (Donovan et al. 1993; Young et al. 1999; Humphrey and Schupp 2004), which could coincide with decreased exotic cover over time (Bates et al. 2005). The stronger pattern of relative cover than total exotic cover with CMD in this study suggests that the warmest and driest sites are subject to the greatest ecosystem impacts from exotic species and the least likely to recover naturally, particularly in a warmer and drier future.

Increasing CO₂ concentrations, which are primarily responsible for climate change, could also increase water-use efficiency in plants (e.g., Drake et al. 1997), thus potentially mitigating rising aridity. This increase in water-use efficiency could potentially allow native perennials to re-establish under drier conditions than currently suitable. However, effects on water-use efficiency effects may vary depending on life stage (e.g., Knapp and Soule 2011). Recent studies suggest that increasing CO₂ concentrations may not balance increasing water stress due to rising temperatures for seedling establishment (Perry et al. 2013; Duan et al. 2014), raising questions about the benefits for post-fire re-establishment of perennials. Furthermore, rising CO₂ may favor exotic species over natives (e.g., Smith et al. 2000; Tooth and Leishman 2013), suggesting global changes in both the atmosphere and climate could exacerbate rather than limit exotic invasion in dry forest ecosystems in the future.

The strong pattern in the present observational study suggests that increasing temperatures and decreasing moisture availability may be key drivers of vegetation changes following wildfire in the future, but caution is warranted in extrapolating these results. The simple geology and uniform soils in this area (Swedberg 1973) combined with the very strong climatic gradient (PRISM Group, Oregon St. Univ., <http://prism.oregonstate.edu/>; Meigs et al., 2009) were useful for isolating the effects of climate in this study, but caution is warranted in extending findings to areas with higher variability in soils and weaker climate gradients. The significant effect of heat load index for most responses evaluated in this study demonstrates how fine-scale environmental variations may affect recovery; and indeed may take on primary importance where overall gradients in climatic moisture availability are not as strong. Similarly, recent studies have documented the primary role of fine-scale variations in soil moisture in driving plant community dynamics (e.g., le Roux et al. 2013). Further study is needed to determine how ecosystems will recovery after severe disturbances in an era of climate change across a broad range of conditions, and how different factors (e.g., climate, seed source, etc.) drive observed differences in recovery such as documented in this study. Whether exotic and native plants respond inversely to the same climate gradient or the apparent inverse pattern is caused by their interactions remains an important avenue for future research.

The results of this study suggest that the warmer and drier (i.e., higher CMD) climate predicted for the future may alter recovery dynamics in dry coniferous forest following severe wildfire, with implications for ecosystem functioning and climate feedbacks (Anderson-Tiexera et al. 2013). The first two years of post-fire recovery in this study occurred during a multi-year drought in western North America (Schwalm et al. 2012), which likely limited native perennial recovery similar to results from previous studies (e.g., Pratt et

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al. 2014). Projected increases in CMD under the cooler and wetter CSIRO model (Mote and Salathe 2007; Rogers et al. 2011) are similar to the CMD found the first two post-fire years in this study (e.g., CMD ~30-50 mm higher than the 1971-2000 average). This suggests that the warmest and driest forested sites could transition toward ecosystems where exotic annual grasses are dominant or co-dominant following severe fire as found in this study even under moderate climate change scenarios. In contrast, under the more extreme scenario (Hadley model; increases in CMD of 150-200 mm), even currently relatively moist sites (e.g., CMD of 600 mm), which had high native perennial cover in this study and low exotic cover, could be susceptible to increasing invasion by conversion exotic annual grasses following severe wildfire. Conversion from native forests to communities dominated or co-dominated by exotic annual grasses could have a myriad of ecosystem consequences, including reduced native diversity and forage for wildlife (Davies and Svejcar 2008), reduced carbon storage (Bradley et al. 2006), altered water and nutrient cycling (D'Antonio and Vitousek 1992) and increased fire frequency (Balch et al. 2013). These effects may have important long-term ramifications for climate change feedbacks and diversity. For example, increased fire frequency may preclude forest re-establishment as young conifers in dry forests are easily killed by fire (Harrington 1993), often establishing during longer fire-free periods (Meunier et al. 2014). Reduced carbon storage in conversion from forested to non-forested or sparsely forested ecosystems (Kashian et al. 2006) could provide positive feedback to climate change. Further study is needed to better understand the potential for a changing climate to alter ecosystem recovery, including experimental studies to gain a more mechanistic understanding of ecosystem responses to a changing climate after severe disturbances such as wildfire.

Acknowledgements

We would like to thank Dr. Richard Halse from the Oregon State University Herbarium for helping with identification of unknown species. Ethan and Ernest Dodson assisted with field data collection and the Puettmann lab at Oregon State helped make this study possible. The comments of Dave W. Peterson and two anonymous reviewers helped improve this manuscript.

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Supporting Information:

Table S1: Characteristics of the 31 plots sampled in the Eyerly Fire.

Figure S1: Relationship between climatic moisture deficit and a) mean annual temperature, b) growing season precipitation and c) elevation at the 31 plots on the Eyerly Fire. R^2 values are from simple linear regression with a quadratic term for each of the three predictors.

Figure S2: Modeled values (from logistic regression) of the probability of sampling regenerating conifer seedling cover (seedlings did not have to be rooted in to contribute cover) on at least one of the 10 quadrats (1 m²) per plot across the 31 plots on the Eyerly wildfire as a function of climatic moisture deficit and topographic heat load index.

Figure S3: Exotic annual grasses growing under perennial native shrubs at a relatively mesic site 11 years after the Eyerly Fire.

Table 1: Type III tests of fixed effects for regression models of native and exotic cover 11 years following stand-replacing wildfire.

Effect	Effect Size	F-value	<i>P</i>	R ²
Native perennial cover				0.83
CMD	-0.26	92	<.001	
HLI	-113.97	22	<.001	
Native short-lived cover				0.28
CMD	0.01	11	0.002	
Exotic cover				0.53
CMD	0.01	20	<.001	
HLI	5.42	6	0.018	
Relative exotic cover				0.64
CMD	0.01	32	<.001	
HLI	6.68	9	0.006	

Figure 1: Map of study plot locations within the Eyerly Fire (a) and representative photographs showing exotic annual grasses at a high climatic moisture deficit (CMD) site (b), native perennial shrubs at a relatively low CMD site (c), and a mixture of exotic annual grasses and perennial native species at a moderate CMD site (d).

Figure 2: Relationship between climatic moisture deficit (CMD) and a) perennial native cover and b) short-lived native cover 11 years following the Eyerly wildfire. Scatterplot

points show values from field data with sizes scaled by heat load index (larger for higher heat load). Lines are fitted values from regression at the median heat load. Native short-lived species cover was natural log transformed prior to analysis.

Figure 3: Relationship between climatic moisture deficit (CMD) and a) exotic cover and b) relative exotic cover 11 years following the Eyerly Wildfire. Scatterplot points show values from field data with sizes scaled by heat load index (larger for higher heat load). Lines are fitted values from regression at the median heat load. A natural log transformation was applied prior to analyses.

Figure 4: Changes from the 1971-2000 normal period in a) mean annual temperature(MAT), b) growing season (May-September) precipitation and c) climatic moisture deficit (CMD) for the Eyerly fire study sites for the factorial combination of two emission scenarios and two climate models predicted using ClimateWNA (Wang et al. 2012).







