

1 **Disequilibrium of fire-prone forests sets the stage for**  
2 **a rapid decline in conifer dominance during the 21<sup>st</sup>**  
3 **century.**

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## 30 Abstract

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As trees are long-lived organisms, the impacts of climate change on forest communities may not be apparent on the time scale of years to decades. While lagged responses to environmental change are common in forested systems, potential for abrupt transitions under climate change may occur in environments where alternative vegetation states are influenced by disturbances, such as fire. The Klamath mountains (northern California and southwest Oregon, USA) are currently dominated by carbon rich and hyper-diverse temperate conifer forests, but climate change could disrupt the mechanisms promoting forest stability— regeneration and fire tolerance— via shifts in the fire regime in conjunction with lower fitness of conifers under a hotter climate. Understanding how this landscape will respond to near-term climate change (before 2100) is critical for predicting potential climate change feedbacks and to developing sound forest conservation and management plans. Using a landscape simulation model, we estimate that 1/3 of the Klamath could transition from conifer forest to shrub/hardwood chaparral, triggered by an enhanced fire activity coupled with lower post-fire conifer establishment. Such shifts were more prevalent under higher climate change forcing (RCP 8.5) but were also simulated under the climate of 1950-2000, reflecting the joint influences of early warming trends and historical forest legacies. Our results demonstrate that there is a large potential for loss of conifer forest dominance—and associated carbon stocks and biodiversity-- in the Klamath before the end of the century, and that some losses would likely occur even without the influence of climate change. Thus, in the Klamath and other forested landscapes subject to similar feedback dynamics, major ecosystem shifts should be expected when climate change disrupts key stabilizing feedbacks that maintain the dominance of long-lived, slowly regenerating trees.

## 67 INTRODUCTION

68

69 Climate change is expected to cause significant changes in forest carbon (C) cycling and  
70 species composition, with potentially profound effects given that forests globally harbor the  
71 majority of Earth's terrestrial biodiversity and store ~45% of terrestrial organic C (Bonan, 2008;  
72 Pan *et al.*, 2011). How and when these shifts will manifest and how they will interact with land-  
73 use legacies and other mesoscale dynamics, is, however, not well understood. While statistical  
74 associations between species distributions and climate suggest the potential for rapid shifts in  
75 forests species ranges due to shifts in their associated suitable habitats (Iverson *et al.*, 2008;  
76 Serra-Diaz *et al.*, 2014), there is also mounting evidence of lagged responses (Bertrand *et al.*,  
77 2011; Svenning & Sandel, 2013) that the literature has characterized as "debts" or borrowed  
78 time (Hughes *et al.*, 2013): climate change debt when species do not track their climatic  
79 environment fully (Bertrand *et al.* 2011), or resilience debt when species are not adapted to a  
80 given disturbance regime (Johnstone *et al.* 2016). Overall, these debts reflect that the current  
81 state of the forest communities may not readily reflect species climatic fitness, or equilibrium,  
82 but is rather a product of the past. Because of these lagged effects, predicting the actual  
83 responses of forests to near-term climate change (i.e. < 100 years) is thus an urgent priority for  
84 global change ecology.

85

86 Rapid changes to forest communities are likely when climate change induces shifts in  
87 disturbance regimes and extreme events, including changing patterns and occurrence of forest  
88 pests, the frequency and severity of drought mortality events (Allen *et al.*, 2010; Clark *et al.*,  
89 2016), large-scale recruitment failures (Turner, 2010; Feddema *et al.*, 2013; Clark *et al.*, 2016;  
90 Johnstone *et al.*, 2016; Tepley *et al.*, 2017) or shifts in biotic interactions rendering shifted  
91 fitness of forest species in the community (Carnicer *et al.*, 2014). Alternatively, forest  
92 communities could be resilient, resistant, or simply experience gradual and delayed responses  
93 to climate change due to the long generation times of trees. These buffering mechanisms  
94 include demographic stabilization, CO<sub>2</sub> fertilization, microclimatic buffering and landscape  
95 heterogeneity (Keenan *et al.*, 2011; Lloret *et al.*, 2012; De Frenne *et al.*, 2013; Bertrand *et al.*,  
96 2016; Seidl *et al.*, 2016). Interactions between all these phenomena are complex and are an  
97 active focus of global change research (Franklin *et al.*, 2016).

98

99 In the view of forests as complex systems of multiple interacting mechanisms, rapid forest  
100 declines (<100 years) should be expected when key reinforcing feedbacks that maintain a stable  
101 community state are disrupted (Bowman *et al.*, 2015). For instance, both empirical and  
102 theoretical studies recognize that there is a range of climatic conditions in which tropical and  
103 subtropical forest and savanna may exist as alternative stable states modulated by vegetation-  
104 fire feedback dynamics (Staver & Levin, 2012). The persistence of these feedbacks is also a  
105 major concern in fire-prone temperate forests (Paritsis *et al.*, 2015; Johnstone *et al.*, 2016;  
106 Kitzberger *et al.*, 2016; Tepley *et al.*, 2016), and, under climate change, such feedbacks could  
107 either be expected to increase the frequency, size and/or severity of wildfires (Flannigan *et al.*,  
108 2000; Westerling *et al.*, 2006), or reduce fire activity via negative feedbacks (Parks *et al.*, 2016;  
109 McKenzie & Littell, 2017). In addition, these new climate-change shifted fire regimes could

110 interact with large-scale mortality with recruitment failures for some forest species (Enright *et al.*, 2015), and/or hamper potential re-colonization (Caughlin *et al.*, 2016; Tepley *et al.*, 2017).  
111  
112 Therefore, a wide array of outcomes may be expected under climate change due to several  
113 mechanisms acting in concert.

114  
115 Here we investigate the potential for rapid large-scale and fast transitions in forest communities  
116 due to interacting mechanisms due to climate change. We use the Klamath forest landscape  
117 (northern California and southern Oregon, USA) to portray potential shifts between high  
118 biomass conifer temperate forests (CON) and Mediterranean sclerophyll shrub, chaparral, and  
119 hardwood communities (SCH). The Klamath is a major carbon reservoir and an internationally  
120 recognized hotspot of botanical biodiversity (Briles *et al.*, 2005; Sawyer, 2007; Fig 1a). These  
121 vegetation types (conifer forests vs. hardwood-chaparral) are suggested to function at local  
122 scales as alternative stable states due to their self-stabilizing feedbacks involving biotic  
123 interactions and climate-fire (Petraitis & Latham, 1999; Odion *et al.*, 2010; Airey Lauvaux *et al.*,  
124 2016) (Fig.1b). There are concerns about conifer regeneration failure in the Klamath, typically  
125 stemming from clear-cut logging (*sensu* Hobbs & Huenneke, 1992), and high severity wildfire,  
126 potentially exacerbated by climate change (Tepley *et al.*, 2017). The SCH state is comprised of  
127 highly pyrogenic SCH species (Brown & Smith, 2000) that inhibit conifer regeneration (Hobbs &  
128 Huenneke, 1992). Consequently, the SCH communities promote fire at a regime that hampers  
129 conifer regeneration (Thompson & Spies, 2010). Only when the fire-free interval is sufficiently  
130 long can conifers overtop the shrub layer and begin to dominate the site (Shatford *et al.*, 2007a).  
131 Indeed, mature conifer forests include (*Pseudotsuga menziesii*, *Calocedrus decurrens*, etc.) with  
132 fire-resistance adaptations that strengthen with age (e.g. bark thickening, crown base height,  
133 canopy shading; Agee, 1996; Shatford *et al.*, 2007b). At the mature conifer stage, a low severity  
134 fire regime is generally promoted, wherein surface fuels that affect only the understory and  
135 hamper ladder fuel development, reducing fire risk to the mature conifer overstory (Sensenig *et al.*, 2013).

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139 It is difficult to assess whether observations and local studies are only context dependent (e.g.  
140 post fire legacy effects (Johnstone *et al.*, 2016)), or if they could represent a major regional shift  
141 towards SCH. Because large-scale experimentation in forest is unrealistic, mechanistic models  
142 with explicit representation of species and adaptations to wildfire offer a tool to explore the  
143 individual and interacting effects of multiple climate change drivers as well as feedback  
144 mechanisms; and allow consideration of a breadth of spatial and temporal scales in forest  
145 community dynamics. The aim of this study is to test the hypothesis that a warming climate and  
146 increased fire activity will drive rapid conifer decline in the Klamath. We expected that,  
147 compared to forest dynamics driven by the current climate (baseline conditions), climate change  
148 would (1) increase fire activity (decrease fire rotation period), (2) slow conifer growth, and (3)  
149 trigger major declines of conifer dominance.

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151

## 152 METHODS

### 153 Study area and species

154

155 The Klamath ecoregion is situated in the Pacific Northwest region of the United States (Figure  
156 1) at the convergence of major North American floristic zones (Whittaker, 1960), and includes  
157 an exceptionally diverse flora, with strong components of sclerophyll broadleaf hardwood,  
158 coniferous, and herbaceous vegetation. Topography is mountainous and complex; elevation  
159 ranges from 100m to 2000 m asl. The climate is Mediterranean, with dry, warm summers and  
160 wet, mild winters. Mean January temperature is 6°C. Mean July temperature is 16°C. Mean  
161 annual precipitation is 2900 mm, with greater than 90% occurring in winter (Daly *et al.*, 2002,  
162 2008). Before the onset of effective fire suppression (c. 1945) wildfire return intervals ranged  
163 from 6 to 60 years (Taylor & Skinner, 2003; Sensenig *et al.*, 2013), although the regionally the  
164 Klamath has supported various fire regimes and return intervals in the last 2000 years  
165 (Colombaroli & Gavin, 2010).

### 166 Modeling framework

167 Our approach consists of modeling vegetation succession interactions with climate change to  
168 integrate both slow (e.g. forest stand development) and fast processes (e.g. disturbances) into  
169 projections of potential vegetation transitions at a regional scale (Walker & Wardle, 2014).

170

171 We simulated vegetation dynamics using the forest community model LANDIS-II v 6.1 (Scheller  
172 *et al.*, 2007); <http://www.landis-ii.org/>). This process-based model includes biophysical (climate  
173 and soils) and ecological processes (species interactions, dispersal) to simulate growth,  
174 mortality and regeneration at the species level. Different life history traits enable modeling inter-  
175 and intra- specific interactions (e.g. competition, facilitation) integrated with disturbance  
176 responses (e.g. resprouting). Species are simulated as age-cohorts that compete for and  
177 modify aboveground and belowground resources within each cell; disturbances and dispersal  
178 are spatially-explicit processes. The model has been widely used in both temperate forests and  
179 Mediterranean type ecosystems to investigate climate-fire-forest interactions (Syphard *et al.*,  
180 2011; Loudermilk *et al.*, 2013; Liang *et al.*, 2016). We ran 9 model replications for each climate  
181 change and baseline climate scenarios, thus a total of 45 simulations. Simulation were run in a  
182 cluster for 25 days. We classified each cell as conifer state or shrubland-chaparral-hardwood  
183 state according to the most dominant species in each cell. Dominance classification was based  
184 on the functional identity (e.g. SCH or conifer) of the species with the highest biomass.

185

### 186 Initial species distribution

187

188 Initial distribution of vegetation types was obtained from nearest neighbor imputation of forest  
189 inventory plots (Ohmann & Gregory, 2002; <https://lemma.forestry.oregonstate.edu/data>) and

190 they were constant among replications and scenarios. This methodology assigns each cell  
191 within the study area a forest inventory and analysis plot (FIA; United States Forest Service,  
192 2008) based on the similarity of environmental data and remote sensing image spectral  
193 properties. We pooled cells of initial resolution of 30 m in to cells of 270 m to align with the  
194 assumptions associated with modeling cohorts, though still retaining the capacity to identify  
195 species distributions (Franklin *et al.*, 2013). We chose to model the most prevalent target  
196 species as well as grouped shrubs species into functional groups according to their seed vs.  
197 resprouting behavior, as well as their N-fixation availability (see Succession section).  
198

## 199 Input geophysical data

200 Weather data was extracted from the United States Geological Service data portal  
201 (<http://cida.usgs.gov/gdp/>; June 2016). We used Maurer historical weather data for baseline  
202 conditions for the period 1949-2010 (Maurer *et al.*, 2002) and bias corrected constructed  
203 analogs v2 daily for climate change projections climate change projections. We chose four GCM  
204 - RCP that portray the breadth of climate change conditions modeled for the Klamath region—  
205 i.e. those spanning the widest range of average annual temperature and precipitation--predicted  
206 for the study area (ACCESS 8.5 (Ac85, hotter and drier); CNRM-CM5 8.5 (Cn85 hotter and  
207 wetter); CNRM-CM5 4.5 (slightly hotter and slightly wetter), MIROC5 2.6 (slightly hotter and  
208 slightly drier; Fig.S1).  
209

210 Soil characteristics were obtained through the web soil survey  
211 (<http://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm>) from the STATSGO2 database.  
212 We used the measures of soil organic matter content, and physical characteristics of soils that  
213 drive water balance dynamics and biogeochemistry in the model (e.g. drainage class,  
214 percentage of sand). Nitrogen deposition was obtained from the National Atmospheric  
215 Deposition Program database (<http://nadp.sws.uiuc.edu/>).  
216

217 In order to harmonize different scales and data types among physical inputs we parsed the  
218 study area into ecoregions with similar environmental conditions (Serra *et al.*, 2011). We  
219 grouped different cells in environmental space according to their soil and climate characteristics  
220 through cluster analysis, using the *clara* function in the 'cluster' package (v 2.0.4) in R 3.3.3 (R  
221 library core team, 2017). We used soil drainage characteristics, field capacity, percentage of  
222 clay, percentage of sand, wilting point and soil organic content to define five soil regions. For the  
223 climate regions we defined 5 regions using precipitation, minimum temperature and maximum  
224 temperature. The final set of twenty-five ecoregions is derived from the combination of climate  
225 and soil regionalization sets (5x5).

## 226 Succession

227 Vegetation succession is generated by competition for light and water within each cell, and is  
228 represented via C and N cycling through leaf, wood, fine and coarse roots by species and age  
229 cohorts using the LANDIS-II Century Extension (Scheller *et al.*, 2011). The succession model  
230 operates at a monthly scale and simulates growth as a function of water, temperature, and



231 available nitrogen, while accounting for inter-cohort competition for light and space. Mortality is  
232 caused by disturbances (see next section), senescence (ongoing loss of trees and branches),  
233 and age (higher mortality rate when approaching species longevity). Regeneration and  
234 establishment are characterized by probabilities based on species-specific life history attributes  
235 that consider dispersal distances, sexual maturity, post-fire behavior (e.g. serotiny, resprouting),  
236 light, and water availability.

237  
238 Tree and shrub species species-level parameters and functional type parameters. Functional  
239 groups were created by combining growth forms (e.g. hardwood, conifer, shrub),  
240 biogeochemical behavior (e.g. N-fixing) and seasonality in growth (e.g. evergreen, deciduous)  
241 (following (Loudermilk *et al.*, 2013) and (Creutzburg *et al.*, 2016a). Species and functional group  
242 parameters determine growth in response to climate and soil properties. We calibrated species'  
243 cohort growth using two parameters: maximum monthly aboveground productivity, and large  
244 wood mass [g C/m<sup>2</sup>] at which half of the theoretical maximum leaf area is attained, using 950  
245 Forest Inventory Analysis (FIA) plots representative of the different community types and  
246 climate gradients present in the study area. Full list of input parameters are available in Table  
247 S1-S9.

248  
249 We calibrated the growth model to represent the biomass of the selected FIA plots. Accuracy  
250 assessment indicated that the model was able to capture species-specific biomass with an  
251 average deviation of 10% of the biomass in a plot for each species (Figure S3).

## 252 Fire

253 Wildfire was simulated using the Dynamic Fires and Fuel extensions (Sturtevant *et al.*, 2009).  
254 This extension simulates the landscape-scale fire regime given input parameters of topography,  
255 fuel type, fuel condition and daily fire weather (see full model description and fuel  
256 implementation in Sturtevant *et al.*, 2009 and Syphard *et al.*, 2011) . Weather changes the  
257 probability of ignition and fire spread rates according to fuel type, fuel condition and the  
258 probability of a sustained flame via fire weather indices (Beverly & Wotton, 2007). Fire causes  
259 mortality in tree cohorts according to their age and the difference between species' fire  
260 tolerance and fire intensity. Higher fire intensity is required to kill older cohorts whereas younger  
261 cohorts are killed by less intense fire. Such fire intensity is related to the topography, the climate  
262 conditions and vegetation (via fuel types). For instance, shrub fuel type enhance fire severity  
263 whereas adult mature conifer decrease the potential for high intensity fire.

264  
265 We calibrated the fire regime using three attributes: fire rotation period, fire size distribution, and  
266 fire severity - (Keeley *et al.*, 2011). We calculated fire attributes through LANDSAT imagery and  
267 products derived from the Monitoring Trends in Burned Severity program (Eidenshink *et al.*,  
268 2007). We chose the period 2000-2010 excluding the 2002 Biscuit Fire (ca. 202,000ha),  
269 because we wanted to discount the effect of one outlier fire that had a large influence over the  
270 fire regime (Fig S4 and Table S11). However, the targeted fire rotation period still portray the  
271 1984-2010 period including such big fire. Fire severity was calculated as percent crown  
272 damage, and was approximated by using the relationship built in the study area between  
273 percent crown damage and the difference Normalized Burned Ratio Index (Thompson *et al.*,

274 2007). Recent patterns of fires size, severity and frequency were reproduced by the model  
275 (Table S12; input parameters in Table S13 and S14).

276  
277 We accounted for spatial differences in fire regimes by dividing the study area into three regions  
278 reflecting differences in contemporary ignition rates and fuel moisture (Fig S5 and Fig S6).  
279 These regions were identified by combining remote sensing estimates of the fog belt  
280 (Torregrosa *et al.*, 2016) and density estimators of fire occurrence as a distance from roads and  
281 human settlements (Figure S5). Fuel classifications were species and age specific and were  
282 derived from similar Mediterranean ecosystems studies (Syphard *et al.*, 2011).

283  
284

## 285 RESULTS

286

### 287 **Climate change scenarios and forest development under climate change**

288

289 The climate change scenarios predicted consistent warming throughout the seasons ranging  
290 from 1.18 to 2.9 °C on average (Fig. 2a), whereas seasonal precipitation patterns varied  
291 between scenarios, GCMs, and seasons (Fig. 2b). Precipitation generally increased during the  
292 winter, with increases between 8 and 60 mm/month depending on the climate change scenario.  
293 Spring and fall had the highest temperature increase (rcp 8.5; Fig. 2). Conversely, summers  
294 were predicted to be hotter – ranging from 1.2 to 4.9 °C/month – with slightly lower precipitation  
295 – between 0 and 10 mm/month, depending on the scenario. These changes became more  
296 evident towards the latter half of the 21<sup>st</sup> century simulation period.

297

298 Modeled forest growth rates reflected changes in soil water availability, which varied spatially  
299 depending on precipitation, temperature and soil characteristics (Fig. 2c and 2d). We selected  
300 two ecoregions that bound the gradient of water balance conditions in the area and thus show  
301 different responses to environmental conditions. In these ecoregions, modeled forest  
302 productivity ranged between 0.11 gC m<sup>-2</sup>yr<sup>-1</sup> and 104 gC m<sup>-2</sup>yr<sup>-1</sup>. The model projected shifts in  
303 growth, with strong growth limitation during summer under climate change (Fig 2c and 2d). The  
304 model also projected a lengthening of the growing season, with greater growth enhancement at  
305 the beginning of the growing season (late winter/ early spring) than at the end (Fig 2c and d). It  
306 is important to note that these growth behavior – earlier growth in winter-spring and reduced  
307 growth in summer – across climate change scenarios are most apparent later in the 21<sup>st</sup> century  
308 (Fig 2).

309

310 The model projected a decline in the probability of establishment under climate change (Table  
311 1) due to increased summer drought. The decline ranged from 26- 39% depending on the  
312 climate change scenario for the conifer species and between 7- 20% for the SCH group (Table  
313 1). In general, probability of establishment was lower for the higher temperature forcing  
314 scenarios (Ac85 and Ca85 vs. Mi26 and Cn45). The probability of establishment was higher in



315 Mi26 vs Cn45, which we attribute to the compensating factor of water in this case (water  
316 availability is higher in Cn45 than in Mi26; Table 1 and Fig. S1).

317

### 318 **Increased fire activity**

319

320 Climate change enhanced fire activity (Figure 3). Fire rotation periods (FRP) were lowered by  
321 approximately 20 years on average for the highest forcing climate change scenarios (i.e. Ca85  
322 and Ac85 Fig. 3a), whereas there was little change in the FRP under milder forcing scenarios  
323 (Cn4.5 and Mi2.6). There was high variability among simulations within each climate change  
324 scenario, especially for those climate change scenarios with the least forcing. Simulations  
325 suggest that, while averaged FRP may not be statistically different from baseline conditions in  
326 100 years, the result was much higher risk of conditions conducive to higher fire conditions (fire  
327 weather indices) that can lead to a large shift in FRP.

328

329 Average fire sizes increased under climate change (Fig. 3b), particularly under the warmest  
330 scenarios (Ca85 and Ac85). The model projected a maximum average increase of 1,011 ha and  
331 1,222 ha between baseline conditions and Ca85 and Ac85 scenario, respectively. More  
332 importantly, climate change was projected to increase the severity of fires (Fig. 3c), especially in  
333 the last part of the century.

334

335 The number of megafires – above 100,000 ha (Fig. 4). Baseline conditions predicted the  
336 occurrence of large-scale fires of approximately 200,000 ha, while under the warmest climate  
337 change scenarios (Ac85 and Ca85) fires reached between 200,000 ha and 500,000 ha in  
338 several years. Only in the highest forcing scenarios did a fire reached a size beyond the half  
339 million hectares (1 out of 9 repetitions per scenarios in Ca85 and Ac85).

340

341 Mean fire return intervals maps highlight the spatial variability of fire recurrence (Fig. 5). Fire  
342 was more prevalent in the eastern side of the study area, consistent with the west to east  
343 gradient of increasing water deficit (Fig. 1a). The total area with mean fire return intervals under  
344 25 years only increased between 1% and 5% of the study area depending on the climate  
345 change scenario (Fig. 5)

346

### 347 **Dominance shifts**

348

349 Compared to the current vegetation dominance pattern, simulations of both baseline and  
350 climate change conditions resulted in large-scale shifts in vegetation dominance, particularly  
351 within the drier eastern half of the study area (Fig. 6a). Major shifts were thus located where the  
352 model projected the highest fire activity. The most pronounced spatial disagreement between  
353 baseline and climate change simulations was concentrated in the center of the study area,  
354 coinciding with higher elevations and topographic complexity (Fig. 6b).

355

356 The model estimated a conifer dominance loss of more than half million hectares in areas  
357 affected by fire during 85 years of simulation, even under current (e.g. baseline; dominance loss  
358 579,000 ha) conditions. That approximately represents 31% of the initial forest dominated by

359 conifers in the study region. Climate change increased the area of conifer forest lost by an  
360 average of 7,000 ha when forced by the Mi26 scenario and 60,000 ha with the Ac85 scenario  
361 (Fig. 6c). Once more, the stochasticity of wildfire is highlighted in climate change scenarios that  
362 present higher precipitation under climate change (Fig 6c, height of boxplot in Cn45 and Ca85).  
363  
364

## 365 DISCUSSION

366  
367 Our results demonstrate a large potential for rapid vegetation shifts in the Klamath region during  
368 the 21<sup>st</sup> century. Some of these shifts are driven by climate change, but simulations with current  
369 climate conditions also produced major shifts. Climate change, in the 100 year interval, may  
370 cause a decrease in the fire rotation period in the area and an increase in fire size.

371  
372 These results concur with empirical and modeling studies that suggest that disturbances can  
373 rapidly accelerate vegetation shifts during climate change (De Frenne *et al.*, 2013; Serra-Diaz *et*  
374 *al.*, 2015; Stevens *et al.*, 2015) and suggest that rapid vegetation dominance shifts are likely to  
375 occur when strong feedbacks between co-existing species are present in the community (e.g.  
376 conifer forests and shrublands), as in the case of the Klamath with vegetation-fire interactions  
377 create alternative stable states. In our case, this synergy is reflected in the increase in fire  
378 severity along the simulation time, especially at the end of the 21<sup>st</sup> century, coinciding with the  
379 expansion of shrubs and hardwoods (Fig 3c). Such potential for rapid shifts are likely to be  
380 found at biome transitions, such as the conifer forests and Mediterranean hardwoods of the  
381 Klamath, where several functional types and traits adapted to fire regimes coexist and climate  
382 conditions can lead to different vegetation community states. Our work suggests that the local  
383 empirical studies by Odion *et al.* (2010) and Tepley *et al.* (2017) can be generalized to a  
384 regional context, and portray a regional trend of increasing vulnerability of conifer forests to  
385 altered fire regimes along a west to east gradient with increasing aridity (Fig. 1a and Fig. 4b).

386  
387

### 388 **Shifts in the 21<sup>st</sup> century even under current climate conditions**

389  
390 One of the most striking results of the modeling experiment is that, on average, current baseline  
391 conditions (1949-2010) largely lead to the loss of almost 1/3 of the initial conifer forest extent.  
392 Several mechanisms could explain such results, but we argue that these stem from the  
393 combination of (i) disequilibrium of vegetation with disturbance dynamics.

394  
395 Disequilibrium with climate refers to the lag between changes in abiotic conditions and the  
396 response of communities or species to such changes. Several lines of evidence suggest that  
397 species distributions and communities reflect past environmental changes rather than current  
398 environments (Sprugel, 1991; Donato *et al.*, 2012; Hughes *et al.*, 2013; Svenning & Sandel,  
399 2013; Odonez & Svenning, 2017). This emphasizes the need to stress the temporal scope of  
400 100 years climate change projections. For instance, in a climate change model experiment,

401 García-Valdés *et al.* (2013) found that forest species in Spain are predicted to increase their  
402 range and abundance under current climate as a result of last glacial maximum dynamics that  
403 pushed many species southwards in Europe. Specifically, in their study climate change would  
404 only affect that inertia in 3 out of 10 species. In our case, we cannot rule out the idea of the  
405 influence of the fire shortage during the Little Ice Age may have increased the dominance of  
406 forests of our region via fire shortage (Colombaroli & Gavin, 2010); and that legacy may be  
407 playing out today in a remarkably warmer climate after 1949-2010 (our climate baseline climate  
408 input). Such longer term dynamics may indeed obscure the short-term predictions of the  
409 consequences of climate change in forests.

410

411 In addition, the potential effects of recent historical fire suppression by humans, which has  
412 promoted conifer dominance in many forests (Parsons, & DeBenedetti, 1979; McIntyre *et al.*,  
413 2015) may have exacerbated positive fire–vegetation feedbacks in certain landscapes, thereby  
414 facilitating extensive vegetation transformation (McWethy *et al.*, 2013; Tepley *et al.*, 2016).  
415 Indeed, empirical data indicate that such afforestation process may increase subsequent fire  
416 risk due to fuel continuity and exposure to high severity fires (Foule 2003, Miller 2009,  
417 Westerling 2016), at least at early stages of conifer development before negative forest  
418 feedbacks with fire arise. These un-intended effects together with rapid increases in  
419 temperature have led to an increase in fire sizes and the number of megafires in many regions  
420 (Adams, 2013), as simulated here in our study.

421

422

### 423 **Climate change signal at the end of the century: mechanisms acting in concert for rapid** 424 **shifts coupled with long-term transitions**

425

426 The interaction of several processes included in our modeling experiment indicated a low  
427 potential for maintaining the current level of conifer dominance in forests in the region,  
428 concurring with other mixed conifer forests in western United States that showed or predict  
429 major vegetation shifts (McIntyre *et al.*, 2015; Harvey *et al.*, 2016). Despite similarity to baseline  
430 conditions for half of the simulation our study, several projections suggest potential for longer  
431 term transitions. First, fire severity and fire sizes were projected to increase under climate  
432 change. Second, species probability of establishment decreased, particularly for conifer  
433 species; and third, the model suggests growth limitation, hampering post-fire regeneration.

434

435 The interaction of fire size and fire severity and fire return interval are key to understand post-  
436 disturbance and recolonization, and may have a strong bearing on the capacity of forest to  
437 recolonize burned patches (Harvey *et al.*, 2016; Johnstone *et al.*, 2016; Tepley *et al.*, 2017). Our  
438 simulations projected increased fire size, concurring with empirical work (Westerling *et al.*, 2006;  
439 Westerling, 2016). Particularly interesting is that the model suggested potential for an increase  
440 in megafires under climate change, surpassing the historical maximum fire sizes recorded in the  
441 area (Biscuit fire 202,000 ha). Similar projections based on statistical correlations also project  
442 an increase of megafires in North California (Barbero *et al.*, 2015). Interestingly, both fire size  
443 and severity seem to start differentiating from baseline at the end of the 21<sup>st</sup> century, and the  
444 ‘slightly wetter’ scenario (Ca 85) produced higher fire activity in terms of size and severity (Fig.

445 3) than the 'slightly dryer' scenario (Ac85). We can't rule out the possibility that this effect may be  
446 due to the relatively low number of replications, but we argue that this is likely the effect of  
447 increased fuel build up due to wetter conditions in concert with a much warmer summer. Indeed,  
448 this may represent an early signal that under much dryer conditions negative feedbacks of  
449 vegetation with fire may arise in the future.

450  
451 In addition to potential limitation of conifer re-colonization via dispersal, establishment  
452 probabilities were projected to decrease under climate change. This is reflected in the model  
453 through lower soil moisture and higher temperatures. Such influences appear to have played  
454 out after recent fires in the Klamath Mountains. Following high-severity fire, the trend of  
455 decreasing density of regenerating conifers with reductions in seed-source availability becomes  
456 steeper as climatic water deficit increases (Tepley et al. 2017). Thus, if climate change drives  
457 increases in the patch sizes for high-severity fire while also creating a more arid post-fire  
458 environment, dry portions of the landscape could face a substantial lengthening of the time to  
459 forest recovery after high-severity fire, increasing the probability that the post-fire SCH  
460 vegetation is perpetuated by repeated fire before it has a chance to return to forest cover  
461 (Coppoletta *et al.*, 2016). Similar decreases in opportunities for seedling establishment under  
462 drier conditions have been observed in western US forests (Davis *et al.*, 2016; Welch *et al.*,  
463 2016), especially following high severity fires (Savage & Mast, 2005; Feddema *et al.*, 2013).  
464 Interannual climatic variation, which was large during the 21<sup>st</sup> century, in the future may provide  
465 opportunities for species establishment even if average climatic conditions are not conducive to  
466 seedling establishment (Serra-Diaz *et al.*, 2016). However, high inter-annual climatic variation  
467 may also come at the cost of cohort mortality due to extreme dry conditions. On balance, the  
468 rate at which conifers successfully establish and persist for a decade or more in the Klamath  
469 declines with increasing aridity, with seed source proximity as a key interactive variable.

470  
471 The model does not simulate drought-related cohort mortality due to processes of hydraulic  
472 failure, carbon starvation or a combination of both. It is thus likely that our results represent a  
473 conservative estimate of vegetation shifts. First, data shows an ongoing recurrence of tree  
474 mortality events in forests affected by drought (Allen *et al.*, 2010; Carnicer *et al.*, 2011),  
475 including the recent (2012-2015) major drought in the region (Asner *et al.*, 2016), and  
476 projections show that the probability of such droughts will increase in this region in the future. In  
477 addition, empirical data shows that larger trees may be more vulnerable to drought related  
478 mortality (Bennett *et al.*, 2015), which could further reinforce the transitions via fuel dryness  
479 enhancement (e.g. less shading) and increased seedling mortality due to less canopy shading.

480  
481 Our model predicted an overall reduction in annual tree cohort growth, although there is high  
482 variation depending on the species, climate, and soils. Overall, and particularly for the drier  
483 regions in the landscape, summer growth is predicted to decline in both our model and across a  
484 network of tree-ring chronologies (Restaino *et al.*, 2016). But there is potential for additional  
485 growth in spring and to a lesser extent in the fall (Fig. 2b; see also Creutzburg *et al.*, 2016b).  
486 Indeed, earlier springs and overall extended growing seasons are important and could increase  
487 growth and thus the ability of conifers to recover after a fire (see Chmura *et al.*, 2011 and  
488 references therein) especially for the higher elevations in our study region. Using a combined

489 measurements of flux tower and satellite information, Wolf *et al.* (2016) found that earlier spring  
490 could reduce the impact of a subsequent summer drought in 2012. However, the model outputs  
491 suggest that this effect may be transient and compensation may not hold during summer.  
492 Our results regarding growth should be interpreted with caution. Our model assumes full  
493 phenological adaptation, and it is likely that growth can be further constrained by  
494 maladaptations to the new phenological cycle (Morin *et al.*, 2009). The model also does not  
495 incorporate the potential effects of CO<sub>2</sub> fertilization (Keenan *et al.*, 2011, 2013) that could speed  
496 up forest development and growth as well as alter successional dynamics (Anderson-Teixeira *et*  
497 *al.*, 2013; Miller *et al.*, 2016). The effects of CO<sub>2</sub> on growth in this forest are subject to further  
498 scrutiny, and potential growth is likely to be limited by the low N deposition in the region (0.12  
499 Kg N/ha annual average, NADP; <http://nadp.sws.uiuc.edu/>).

500  
501 Our various model components highlight that different processes may hamper current conifer  
502 dominance. Indeed, the fire regimes that emerge from the interaction of vegetation, climate and  
503 soils show the high potential for developing long-term shrubland states (Lindenmayer *et al.*,  
504 2011): Mean fire rotation intervals and higher fire severity projected in some areas are certainly  
505 too short ( $\leq 40$  years) to fully develop a mature conifer forest, concurring with the hypothesis of  
506 a general interval squeeze that may hamper the development of conifers (Enright *et al.*, 2015).  
507 Accordingly, empirical data show that broadleaf trees and shrubs typically comprise the majority  
508 of aboveground woody biomass for at least the first three decades following high-severity fire  
509 (Tepley *et al.* 2017), and when stands reburn before conifers regain dominance, fire-severity  
510 tends to be high (Thompson and Spies 2010, Lauvaux *et al.* 2016). Thus, successive high-  
511 severity fires on the order of decades could potentially preclude the recovery of conifer forests  
512 almost indefinitely.

513

514

### 515 **Average projections vs. Risk in disequilibrium systems.**

516

517 The differences in potential for conifer decline between simulations driven by baseline climatic  
518 conditions and those driven by climate change scenarios were, on average, somewhat less than  
519 might be anticipated (Fig. 4). Nevertheless, we argue that main differences between climate  
520 change and baseline conditions are better interpreted using the potential for extreme scenarios  
521 of shift rather than average conditions.

522

523 Some of the processes that have been analyzed may be of limited relevance in short time  
524 frames. For instance, lower probabilities of establishment in conifers will have a large  
525 repercussion on mature conifer forest abundance, but it is likely that they play a major role  
526 beyond the 21<sup>st</sup> century given that forest development times operate at larger time scales. Also,  
527 the length of our simulations (85 years) comprises only about one complete fire rotation under  
528 each of the future climate scenarios. If high-severity fire is the mechanism that converts conifer  
529 forests to SCH, and repeated severe fire (possibly facilitated by positive fire–vegetation  
530 feedbacks) is the mechanism that perpetuates SCH once the conversion occurs, we may need  
531 a longer timeframe before we see these transitions play out extensively across the landscape.  
532 In a single fire rotation, some portions of the landscape burn more than once and others remain



533 unburned, but the fire–vegetation feedbacks would have to be very strong to see large areas of  
534 conifer forest that are converted to SCH and then perpetuated in that state by repeated burning  
535 within a single fire rotation. Individual fire events are fast processes that can transform forests  
536 rapidly and may have major impacts at finer spatial scales and shorter temporal frames.  
537 However, the degree to which these effects persist may depend on slower processes of  
538 vegetation regrowth and the timing and severity of subsequent fires. Therefore, at this temporal  
539 span (~100 years, potentially one generation of trees), projections of vegetation shifts are more  
540 useful when interpreting the risk of such fires' transformations rather than by averaged outputs.

541  
542 Our modeling experiment projects a high potential for the loss of nearly one-third of the existing  
543 mature conifer forest across the Klamath region in the coming century, warning that there is  
544 potential for fast transitions in forests. Baseline model projections of widespread forest loss (Fig.  
545 4 a,c) suggest that current widespread distribution of conifer forests are not in equilibrium with  
546 the late-20<sup>th</sup> or early 21<sup>st</sup>-century conditions. Given this disequilibrium, the projected fire  
547 dynamics, and the increasingly challenging conditions for conifer to regenerate during climate  
548 change, this study highlights that current conifer forests may be holding a considerable amount  
549 of resilience debt (*sensu* Johnstone et al. 2016), likely to be paid during the 21<sup>st</sup> century. Further  
550 research still needs to unveil to what extent local forest management aimed at reducing the  
551 vulnerability of conifer forests to severe fire, or facilitating their post-fire recovery could buffer  
552 against our projected forest loss, and to better understand how and to what degree we need to  
553 learn to adapt to the changing landscapes and disturbance regimes where preventing such  
554 changes may no longer be possible.

555  
556  
557

558



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560

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564

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## 816 SUPPORTING INFORMATION

817

818 Figure S1 Climate change scenarios considered.

819 Figure S2 Species specific biomass calibration

820 Figure S3 Plot level accuracy assessment

821 Figure S4. Total burned area for the period 1984-2010.

822 Figure S5 Cumulative ratio of fire ignitions from distance to road

823 Figure S6 Fire regions encompassing spatial variability in ignitions and spread rates.

824 Figure S7 Mean fire rotation thresholds on predictions of conifer dominance in forests.

825 Table S1 LANDIS-II general species parameters.

826 Table S2 Available light biomass table.

827 Table S3. Light establishment table.

828 Table S4. Century succession species parameters.

829 Table S5. Century succession functional group parameters.

830 Table S6. Initial ecoregion parameters.

831 Table S7. Ecoregion parameter table.

832 Table S8. Monthly maximum above-ground net primary productivity (ANPP) table (g m<sup>-2</sup>).

833 Table S9. Maximum biomass table.

834 Table S10 Fire statistics according to different time periods

835 Table S11 Fire regime calibration: Fire Size distributions and Severity.

836 Table S12 Shape parameters for fire size distributions for all climate models by fire region.

837 Table S13 Fuel types description and parameters for the Dynamic Fire and Fuel extension of  
838 LANDIS-II.

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## 845 FIGURES

846

847

848 Figure 1. (a) Study area temperature, precipitation and initial forest dominant type (left to right),  
849 and (b) feedback loops that maintain the two forest community states (adapted from Odion et al  
850 2010).

851

852 Figure 2. Climate seasonal regimes and the simulated effects on forest productivity.  
853 Temperature (a) and precipitation (b) under baseline and climate change conditions for the  
854 whole landscape. Effects of climate on forest net primary productivity (NPP) in two locations  
855 chosen to highlight the model's response to environmental gradient under all climate scenarios:  
856 (c) warm-wet and (d) warm-dry. See Table 1 for climate change scenario acronyms

857

858 Figure 3. Fire regime model outputs: (a) Fire return period – time to burn an area of the same  
859 size of the area of study; (b) Fire Size for different simulation repetitions under baseline and  
860 climate change scenarios; (c) High fire severity area for different classes. Boxplot represent  
861 different the distribution of values across 9 simulation repetitions. See Table 1 for climate  
862 change scenario acronyms

863

864 Figure 4. Time series of maximum fire size for different model simulation. Horizontal solid line  
865 indicates the historical maximum fire size recorded in the area (Biscuit fire 202,000 ha). See  
866 Table 1 for climate change scenario acronyms

867

868

869 Figure 5. Spatial distribution of mean fire return intervals (MFRI) in the area. MFRI above 85  
870 indicates that no fire was recorded in the area for the simulations analyzed. See Table 1 for  
871 climate change scenario acronyms

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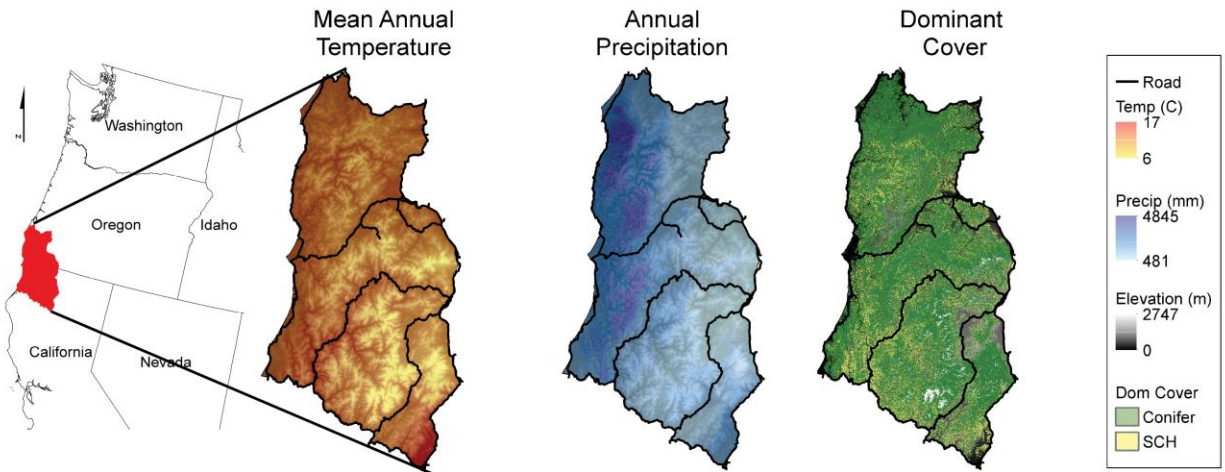
874 Figure 6. Shifts in forest type as determined by species dominance: (a) Forest dominance shifts  
875 compared to initial conditions; (b) Similarity index between climate change scenarios and  
876 baseline conditions. The index informs how many climate change scenarios agree with baseline  
877 (e.g. matches, 4 = maximum agreement, 0 = maximum disagreement); and (c) Area of conifer  
878 forest transitions remaining as conifer (CON) or shifted to shrubland-hardwood (SCH). See  
879 Table 1 for climate change scenario acronyms

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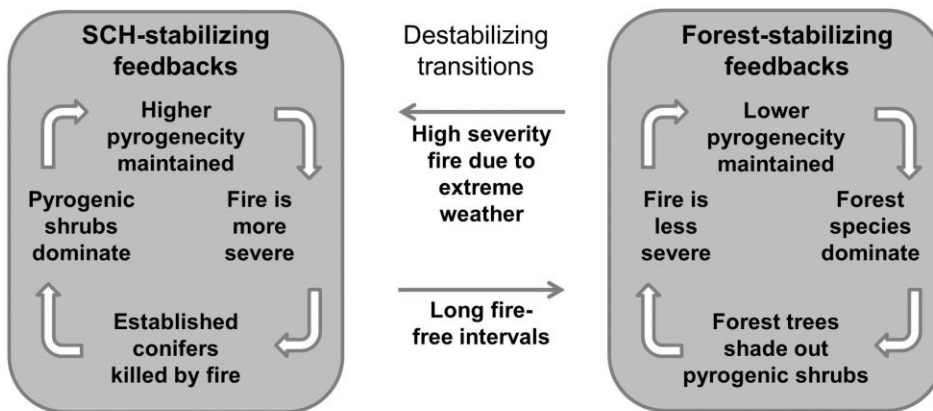
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882 Figure 1.  
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(a) Study area



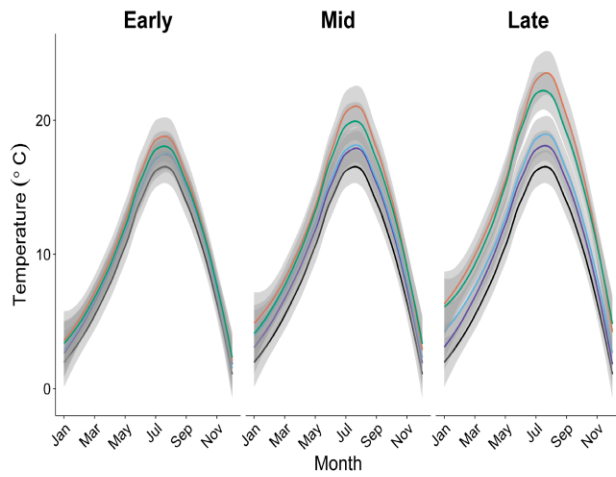
(b) Feedback loops



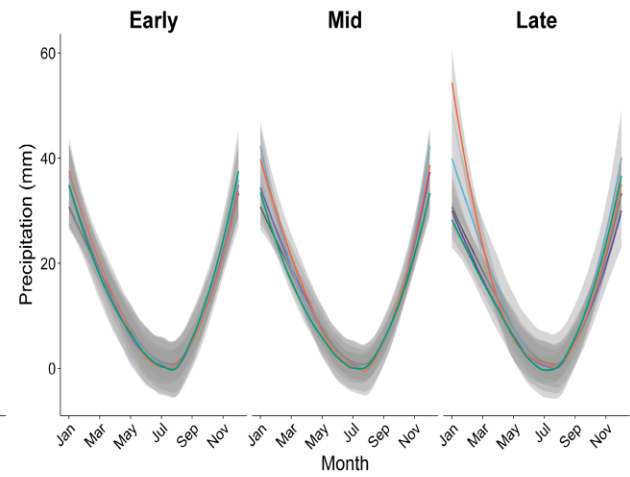
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890 Figure 2

(a) Temperature

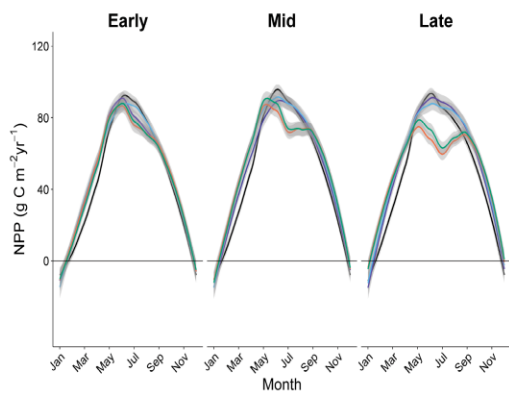


(b) Precipitation

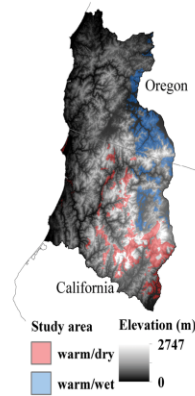
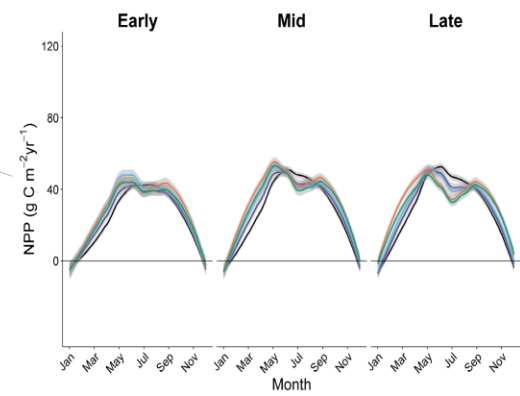


— Base — Mi26 — Cn45 — Ca85 — Ac85

(c) NPP - warm/wet



(d) NPP - warm/dry



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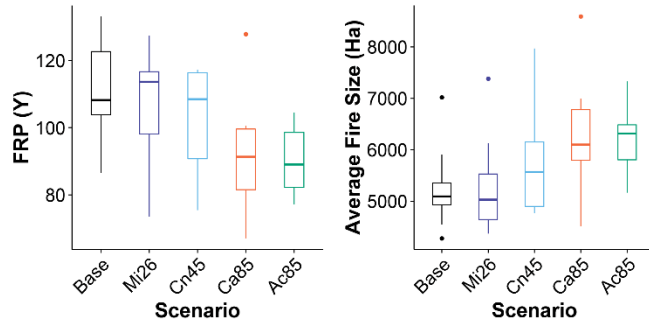
906 Figure 3

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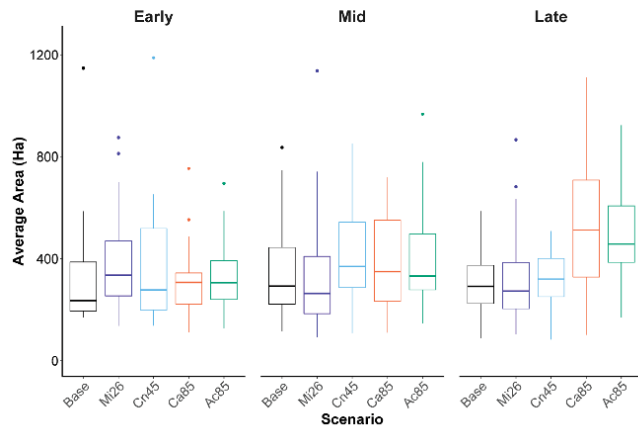
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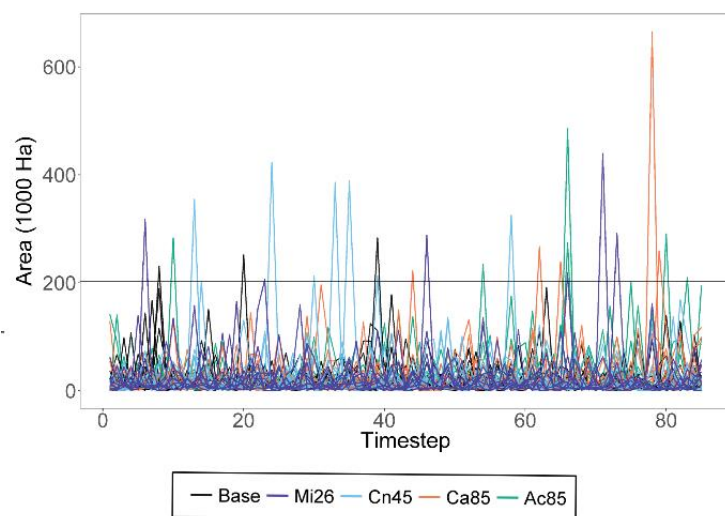
(a) Fire return period (b) Fire size



(c) Area of maximum fire severity



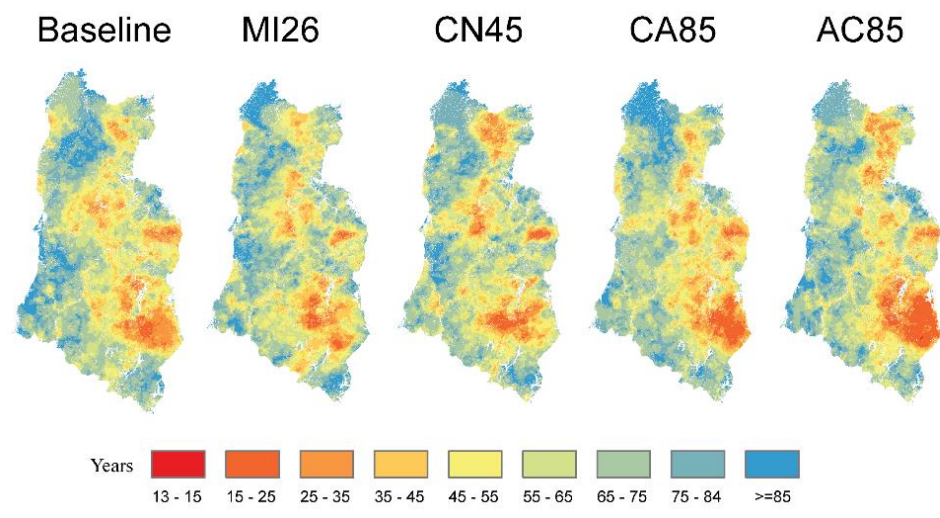
910 Figure 4



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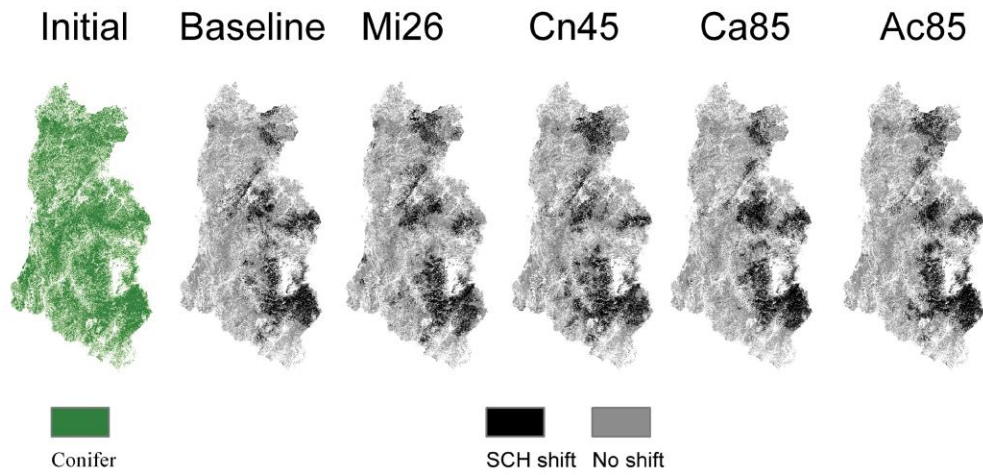
914 Figure 5  
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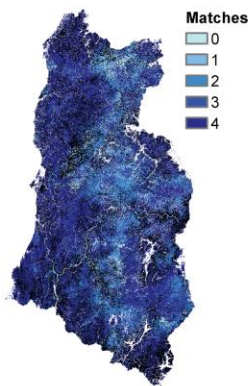
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917 Figure 6  
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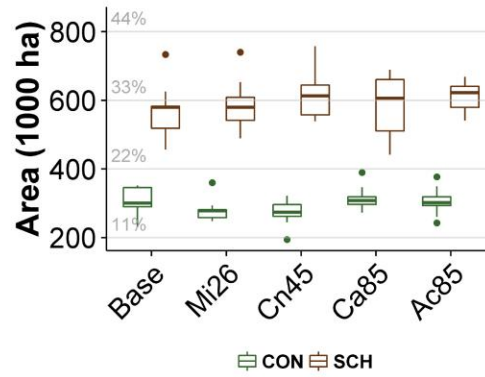
(a) Dominance shift from initial conditions



(b) Similarity to baseline



(c) Area change



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921 Table 1. Baseline and climate change scenario projections. Relative projections represent a  
922 qualitative analysis of Fig S1 for the purpose of synthesis. These labels are based on average  
923 annual statistics over the course of the simulation (85 years) for mean annual temperature and  
924 annual precipitation. Annual probability of establishment shifts across species in conifer and  
925 shrubland-chaparral-hardwood (SCH) species under different climatic conditions. These values  
926 represent averages across species and time. Percentages in brackets indicate the percentage  
927 of probability of establishment loss with respect to baseline conditions.  
928

Climate Scenario	Emissions scenario (RCP)	Climate model	Relative projections *	Fire Rotation Period * <sup>1</sup>	Annual establishment probability	
					Conifers	SCH
Baseline				104-123	0.23	0.3
Mi26	2.6	MIROC5	Mild hot – wetter	98-117	0.17 (26 %)	0.28 (7 %)
Cn45	4.5	CNRM-CM5	Hotter – wetter	91-116	0.18 (22 %)	0.29 (3 %)
Ac85	8.5	ACCESS	Much hotter - drier	82-100	0.15 (35 %)	0.25 (17 %)
Ca85	8.5	CanESM2	Much hotter - wetter	82-99	0.14 (39 %)	0.24 (20%)

929

930 \*See Fig. S1 for quantitative outputs.

931 \*1 Range indicates 25<sup>th</sup> -75<sup>th</sup> percentile

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