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Title: Simulation model suggests that fire promotes lodgepole pine (*Pinus contorta*) invasion in Patagonia

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Abstract

To best understand plant invasions and predict unexpected outcomes it is necessary to integrate information on disturbance, the local environment, and demography. Disturbance by fire has been shown to promote invasions worldwide, but precise interactions between fire, native and invading species remain unclear. Indeed, trade-offs exist between fire-induced mortality of seed sources and increased establishment, driving invasion outcomes. A positive feedback between lodgepole pine (*Pinus contorta*) invasions and fire has been identified but only above a certain pine density. Above this threshold, fire resulted in increased pine dominance at the plot level, however below this threshold establishment rates did not change. We used a spatially explicit invasion simulation model modified to include fire to explore the implications of these complex interactions between pine invasions and fire. We asked if fire promoted *P. contorta* invasion across a Patagonian steppe site and if this depended on the age of the invasion when it burned. Our simulations indicated that, although fire was not necessary to initiate invasion, fire in communities where pine invasions were at least 10 years old resulted in increased spatial extent and maximum invasion density compared to unburned simulations. Fire through younger invasions did not alter the progression of the invasion compared to unburned simulations. Pine invasions should be managed before they reach an advanced stage where positive feedbacks between fire and pine invasion could lead to dramatic increases in invasion rate.

Keywords: biological invasion, fire, *Pinus***,** positive feedback, simulation model, tree invasion

Introduction

Plant invasions that have the capacity to alter fire regimes and create positive feedbacks with fire have the potential to cause significant impacts on native ecosystems (Mack and D'Antonio 1998; Brooks et al. 2004; Gaertner et al. 2014). Although many studies have examined how invasive plants alter fire regimes (e.g. van Wilgen and Richardson 1985; Rossiter et al. 2003; Pauchard et al. 2008; Balch et al. 2013), few have integrated information on invasion-fire feedbacks to study the effects of these complex interactions on invasion extent. Integrating feedbacks and population dynamics is necessary to determine how fire across a landscape will alter invasion spread and consequently invasion impacts on native communities.

Disturbance is widely believed to increase invasion success for many plant species by creating an invasion window with increased resource availability (Johnstone 1986; Sher and Hyatt 1999; Davis et al. 2000). For pine species (genus *Pinus*) introduced to the Southern Hemisphere, invasion is often correlated with human-caused or natural disturbances (Richardson and Bond 1991; Richardson et al. 1994). In particular, fire has been found to promote the invasion of *Pinus radiata*, *P. pinaster*, and *P. halepensis* into South African fynbos (Richardson and Cowling 1992) and *P. halepensis* into the Argentine Pampas grasslands (Zalba et al. 2008). Additionally, areas dominated by tall shrubs that are generally resistant to invasion by *Pinus contorta* (Taylor et al. 2016a) were significantly more vulnerable after fire (Taylor et al. 2017). Other studies suggest that when disturbance is more likely in invaded than uninvaded areas it may actually decrease the likelihood of further invasion, due to tradeoffs between increased invader habitat quality in disturbed areas and disturbance-induced invader mortality (Buckley et al. 2007). Therefore, it is necessary to consider both the negative and positive effects of disturbance on invasion when predicting landscape-level changes in invasion as a result of disturbance. Examining these interactions may be best achieved through simulation modeling

72 (Higgins et al. 1996). Several invasion simulation models have incorporated disturbance into
73 their simulations and found that the effects of disturbance on invasion depends on the vegetation
74 type and the disturbance regime (e.g. Higgins and Richardson 1998; Pausas et al. 2006; Stevens
75 and Beckage 2009; Shackelford et al. 2013). Such modeling efforts have also shown that
76 including feedbacks between fire and vegetation in models can lead to abrupt non-linear state
77 changes (Stevens and Beckage 2009).
78 Invasive pine species introduced to the Southern Hemisphere are thought to create a
79 positive feedback with fire whereby they alter some aspect of the fire regime which then
80 promotes their own success over native plants (Veblen et al. 2011). Recent work has shown that
81 one of the commonly invading pine species, *Pinus contorta*, alters fuel loads and structure
82 compared to uninvaded communities and that this likely increases fire spread and severity
83 (Cóbar-Carranza et al. 2014; Taylor et al. 2017; Paritsis et al. 2018). The effect of disturbance on
84 invasion success varies when the likelihood of disturbance differs between uninvaded and
85 invaded areas (Buckley et al. 2007), as is the case for *P. contorta* invasions into previously fuel-
86 limited steppe systems (Veblen et al. 2011; Paritsis et al. 2013). *Pinus contorta* experiences high
87 levels of fire-induced mortality (Baker 2009), and it recovers rapidly following fire in its native
88 range in western North America (e.g. Turner et al. 1997; Pierce and Taylor 2011; Kemp et al.
89 2016). However, we have found that in the introduced range, fire only promotes *P. contorta*
90 establishment when the invasion density prior to the fire was high (Taylor et al. 2017). In other
91 words, a positive feedback between pine invasions and fire is likely to form above an invasion
92 density threshold (Taylor et al. 2017).
93 Given the potential for *P. contorta* to alter fire behavior in invaded systems and to
94 respond differently to fire depending on pre-fire invasion density, it is unknown how fire will

affect invasion success across a site. For example, although fire through a dense invasion will increase the quality of the seedbed and the rate of pine establishment, it may also destroy a large part of the invasion seed source. Given the threshold effect we found, we may expect that fires through a young, low density invasion would reduce post-fire invasion rates, whereas fire through an older, high density invasion would increase invasion rates. Additionally, the invasion threshold at which a positive feedback forms with fire likely depends on the native vegetation. To explore the interactions between *P. contorta* invasions and fire we created a spatially explicit invasion-fire simulation model. This study aims to answer two questions through simulations with the invasion-fire model. First, will fire through an invaded system promote further invasion and does this depend on the age of the invasion when it burns? Second, will changes in the invasion density threshold that results in increased post-fire *P. contorta* establishment alter invasion density and extent?

We hypothesized that fire early in an invasion would reduce *P. contorta* occupied cells (invasion extent) and mean densities by killing invading trees but not promoting high post-fire establishment rates (due to low pre-fire invasion densities and reproductive output). We expected that fire through older invasions (>10 years, mainly reproductive trees) would result in higher invasion densities, but reduced spatial extent in the short term.

Methods

Study Species

Pinus contorta is native to western North America where its range extends from Yukon Territory, Canada (64°N) to Baja California, Mexico (31°N) (Lotan and Critchfield 1990). It is a is a shade-intolerant and fast-growing tree species that first reproduces at 3 to 15 years and produces small seeds capable of long-distance wind dispersal (Richardson et al. 1994; Despain

2001; Ledgard 2001). There are four varieties of *P. contorta* in its native range that vary morphologically and in their level of serotiny, although serotiny also varies widely within and between populations of the same variety (Lotan and Critchfield 1990). For example, *P. contorta* var. *latifolia* generally has higher levels of serotiny than other varieties but the percent of serotinous trees per stand still varies from zero to 100 (Turner et al. 1997; Harvey et al. 2016). *P. contorta* is an obligate seeder with thin bark that experiences high levels of fire-induced mortality (Baker 2009). Stands with high levels of serotiny tend to regenerate with the highest density following fire (Turner et al. 1997), however even non-serotinous *P. contorta* can regenerate abundantly following fire (Pierce and Taylor 2011; Harvey et al. 2016), likely because *P. contorta* germinates best on bare mineral soil, is a prolific seed producer, exhibits high germination and establishment rates, and benefits from reduced competition with herbaceous species and lower canopy cover following fire (Lotan and Critchfield 1990; Despain 2001; Ledgard 2001). Most *P. contorta* seed germinates in the first year and seeds are likely not viable in the seedbank beyond three to four years (Ledgard 2001).

Study Site

Our model simulates a well-studied site in Coyhaique Alto, Chile (CA) (Langdon et al. 2010; Taylor et al. 2016a). CA is a Patagonian steppe site with a cold dry climate dominated by *Festuca* sp. and cushion plants such as *Baccharis* sp., *Mullinum* sp., and *Acaena* sp. Pine plantations (*P. contorta* and *P. ponderosa*) were planted in this area in the late 1980's and *P. contorta* but not *P. ponderosa* has invaded the surrounding native vegetation (Langdon et al. 2010; Taylor et al. 2016a). It is unclear which variety of *P. contorta* was planted at this site, but we did not observe serotinous cones on any *P. contorta* individuals. The probability of fire in

similar Patagonian steppe sites is low due to limited fuel continuity, however historically there has been anthropogenic burning in the region (Paritsis et al 2013).

Simulation Model

We created a spatially explicit cellular automata simulation model in the modeling environment Netlogo (Wilensky 1999) based on the general tree invasion model created by Caplat et al. (2014; Fig. 1). We adapted the tree dynamics of the Caplat et al. (2014) model so that the demographic and dispersal characteristics matched observations for *P. contorta* (Table 1). We also added fire to the model as described below (Table 2). The dimensions of the modeled landscape (CA) were 1800 m by 1430 m, divided into 10 m x 10 m cells. Simulations ran for 35 years. When run without fire to simulate actual conditions at CA, the model performed well compared to field data collected in 275 10x10 m plots in 2012 (Taylor et al. 2016a) and 289 10x10 m plots in 2014 (Davis unpublished data; Table 3). Mean observed (in 2014) and simulated (30 model runs) *P. contorta* density was 11 and 12.9 trees per 100 m^2 respectively.

Tree Dynamics. The model is composed of a grid where each cell is a cellular-automaton and population dynamics occur within the cell. Each cell was assigned a vegetation type (grass, *Nothofagus antarctica*, or *P. contorta* plantation) based on a map previously created at CA (Langdon et al. 2010; Taylor et al. 2016a). The plantation started with 15 three-year-old *P. contorta* per cell. Cells outside of the plantation contained no *P. contorta* at time zero. At each time step (annual) we calculated the number of trees in each individual age class, from the seedbank through 9 years old, within each cell (10 m x 10 m; see Table 1 for all demographic parameters and their sources). Once trees reached the age of 10 years, they were added to the adult stage class and the total number of adults was tracked. Demographic parameters driving population dynamics were derived from emergence experiments (Langdon 2011), 5 years of monitoring all *P. contorta* individuals in 3 hectares at the Coyhaique Alto site (Pauchard

164 unpublished data), and a large observational data set from the site (Taylor et al. 2016a).
165 Emergence was lowered by 90% in cells in which *N. antarctica* was present, based on the
166 extremely low levels of invasion observed in this vegetation type despite its proximity to the
167 plantation (Taylor et al. 2016a). Emergence and survival were also subject to density dependence
168 based on our data and supported by the lack of *P. contorta* regeneration observed beneath *P.*
169 *contorta* canopies elsewhere in the introduced range (Howell and McAlpine 2016).
170 Seed production was calculated separately for adult trees (age 10 and older) and for trees
171 between the ages of 5 and 9 (hereafter subadults) based on field observations (Table 1). Seed
172 production was determined separately for each cell by drawing a random number of cones per
173 tree from the measured distribution at the Coyhaique Alto site (Taylor et al. 2016a) and
174 multiplying by 20 seeds per cone (Davis unpublished data). For subadults, it was first determined
175 if they were reproductive in a given year or not, based on the proportion of subadults that
176 contained cones in each sampling year at CA; then, the number of cones per tree was drawn from
177 the sampled distribution for subadults.
178 Seeds were dispersed from a cell based on two exponential functions, one for normal
179 dispersal and one for long distance dispersal (Higgins and Cain 2002; Caplat et al. 2008). Each
180 seed had a probability P_{LDD} of being dispersed by the long-distance dispersal function. The
181 majority of seeds were dispersed within 100 meters of the parent tree (Ledgard 2001). We
182 included a separate function for long distance dispersal in the model because long distance
183 dispersal of up to 40 kilometers has been found for *P. contorta* (Ledgard 2001), a simple
184 exponential model does not capture this long distance dispersal (Nathan and Muller-Landau
185 2000), and long distance dispersal is important in explaining plant invasions and range
186 expansions (Shigesada et al. 1995; Higgins and Richardson 1999). CA experiences consistent

187 strong winds and frequent wind events, suggesting that long distance dispersal is important at
188 this site. Our dispersal kernel allowed occasional long-distance dispersal farther than 1 km,
189 although the majority of our long-distance dispersal occurred between 200 and 600 m from the
190 parent tree. The appropriate parameters for the dispersal functions were determined with a
191 sensitivity analysis that compared the resulting invasion metrics (mean invasion density,
192 maximum invasion density, and mean density at different distances from the plantation edge) to
193 known values sampled at CA. Although we captured mean densities and densities at each
194 distance fairly well, we were less successful in capturing the rare long-distance events that led to
195 establishment of lone trees farther than 500 m from the plantation edge (Table 3).

196 Fire Dynamics. A maximum of one fire per simulation occurred and was started in the
197 same cell for each simulation. Given our simulation time of 35 years it is unlikely that more than
198 one fire would burn our study site. Fire spread probabilistically to surrounding cells (Fig. 1) and
199 continued to spread until no new cells were ignited (Perry et al. 2012; Perry et al. 2015). The size
200 of the fires was not fixed but emerged as a function of fire-vegetation-invasion feedbacks.
201 Probability of spread between cells depended on the vegetation type in each cell and was based
202 on the literature for native vegetation (*Nothofagus antarctica* and steppe; Paritsis et al. 2013) and
203 prior measurements of fuel loads and bareground with different levels of *P. contorta* invasion at
204 CA for invaded cells (Table 2; Taylor et al. 2017). We did not include the effects of topography
205 or wind on fire spread. Given the flat nature of our study site, we do not expect that excluding
206 topography greatly influenced fire spread, however the lack of wind effects in the model could
207 result in smaller fires than might naturally occur.

208 All *P. contorta* individuals were killed in burned cells (Baker 2009). *Nothofagus*
209 *antarctica* generally survives and resprouts following fire (Burns 1993). After fire, the

probability of *P. contorta* establishment increased in *N. antarctica* cells to match the level in the steppe for five years, after which point competition from resprouting *N. antarctica* would likely prevent high *P. contorta* establishment (Burns 1993). *Pinus contorta* generally establishes well post-fire in its native range (e.g. Turner et al. 1997; Kemp et al. 2016), even where it is not serotinous (e.g. Pierce and Taylor 2011). However, a steppe site in Northern Patagonia showed high post-fire densities only in plots with older, dense pre-fire invasions (Taylor et al. 2017). Given that those *P. contorta* populations (and those at Coyhaique Alto) are not serontinous, we presume the increase in establishment was due to reduced competition with native plants (Taylor et al. 2016b) and enhanced seed bed conditions due to higher fire severity in highly invaded plots (Taylor et al. 2017; Paritsis et al. 2018). Based on these observations that (1) native vegetation seemed to recover and become dominant where pre-fire densities of *P. contorta* were low, and (2) invasion was enhanced when pre-fire pine densities were high, we increased post-fire *P. contorta* establishment in model cells that had a pre-fire invasion density of subadult and adult *P contorta* greater than a threshold value (Taylor et al. 2017). We found that 10 trees per 100 m^2 was the threshold density at a site in Northern Patagonia (Taylor et al. 2017) but we varied the value in the model simulations as described below. The elevated establishment rate in the model, based on pre- and post-fire densities in a steppe site in Northern Patagonia (Taylor et al. 2017), persisted for three years post-fire. We also reduced the seedbank by 50% in model cells with maximum *P. contorta* age of >= 15 years based on modeled soil temperatures during fire in different age invasions (Taylor et al. 2017) and the known temperature tolerances of *P. contorta* seeds (Knapp and Anderson 1980).

231 ***Model Scenarios and Statistical Analysis***

232 To test the effects of fire at different stages of invasion on invasion density and spread,
233 we ran simulations with a single fire ignition for each simulation at five-year intervals (no fire,
234 fire in year 5, year 10, year 15, and year 20). We crossed this fire year treatment with an invasion
235 threshold treatment. We estimated the invasion threshold that increased rates of post-fire *P.*
236 *contorta* establishment was 10 trees per 100 m^2 at a shrub steppe site in Argentinian Patagonia
237 (Taylor et al. 2017). We assessed the effect of changing the *P. contorta* density threshold on
238 invasion density and extent by including simulations with the invasion threshold set at 5, 10, or
239 15 trees per 100 m^2. We included an invasion threshold treatment because we expect that this
240 threshold may vary by site. Adjusting fire year and invasion threshold left us with a total of 15
241 treatment combinations (5 fire year levels x 3 threshold levels). We ran simulations for 35 years
242 with 100 replicates for each treatment combination (1,500 model runs). We recorded outputs at
243 the end of 35 simulation years for each scenario. Model output included number of burned cells,
244 number of pine-occupied cells, mean pine density in pine-occupied cells, maximum pine density,
245 and maximum distance from the plantation to an invaded cell.

246 To better explain patterns that emerged from the initial model runs, we also ran the model
247 with each fire year and threshold treatment combination for 35 years and obtained output for
248 each year so that we could determine changes in pine density and number of cells occupied by
249 pine over time. This process was replicated 12 times for each treatment combination.

250 Model output was analyzed in R (R Core Team 2017) with generalized linear models
251 with fire year and pre-fire invasion density threshold as the explanatory variables and the output
252 as the response. Where necessary (e.g., for number of pine-occupied cells, maximum pine
253 density), a Poisson error distribution fit with quasi-likelihood was used for the models. To

examine trends over time we used generalized additive mixed models to model mean and maximum pine density, pine-occupied cells and maximum distance from a plantation as a function of the threshold value and the interaction between year and fire year, with model simulation (run) as a random effect. When necessary (e.g., for number of pine-occupied cells, maximum pine density) we used a Poisson error distribution.

Results

Burned Area

Fires that burned in simulation year 5 remained small (<2000 cells; Fig. 2) due to the low fuel loads associated with low density pine invasions. Fires in year 10 or 15 had a trimodal distribution with some fires remaining extremely small, while others entered the pine plantation and/or flammable *Nothofagus antarctica* stands and grew large (>2000 cells; Fig. 2). All fires in year 20 became much larger (>4000 cells) than the fires in year 5 (Fig. 2) due to the presence of large, connected areas of fuel resulting from the high-density of *P. contorta*.

Effect of Fire Year and Invasion Density Threshold on Invasion

Overall, the fire year caused significant differences in *P. contorta* invasion response metrics (Fig. 3). In general, fires that occurred late in invasion had the most impact on invasion metrics, causing increases in pine occupancy, maximum pine density, and distance from plantation. Contrary to our expectations, invasion parameters did not decline compared to unburned simulations when fire burned early in the invasion (fire year 5; Fig. 3); fuels were insufficient to carry the fire (Fig. 2) and small fires had little effect on *P. contorta* mortality. Differences in the pre-fire invasion density threshold that resulted in increased *P. contorta* establishment post-fire were less important than fire year in explaining invasion density and extent.

277 Specifically, fire year, threshold, and their interaction were significant predictors of pine-
278 occupied cells ($\chi^2 = 1656.14$, df = 4, $P<0.001$; $\chi^2 = 39.8$, df = 2, $P<0.001$; and $\chi^2 = 54.49$, df = 8,
279 $P<0.001$ respectively), mean pine density of pine-occupied cells ($F_{4,1485} = 1307.3$, $P<0.001$;
280 $F_{2,1485} = 320.6$, $P<0.001$; and $F_{8,1485} = 276.9$, $P<0.001$ respectively), and maximum distance of a
281 pine-occupied cell from the plantation ($F_{4,1485} = 362.2$, $P<0.001$; $F_{2,1485} = 16.4$, $P<0.001$; and
282 $F_{8,1485} = 7.1$, $P<0.001$ respectively) after 35 simulation years (Fig. 3). While the number of pine-
283 occupied cells and maximum distance from plantation both increased with increasing fire year,
284 mean density declined. Different pre-fire invasion density thresholds only resulted in different
285 post-fire invasion rates when the fire burned at later invasion stages (Fig. 3). Maximum pine
286 density increased with increasing fire year ($\chi^2 = 24125.8$, df = 4, $P<0.001$; Fig. 3), but was not
287 related to invasion density threshold or the interaction between threshold and fire year ($\chi^2 = 2.7$,
288 df = 2, $P = 0.25$; and $\chi^2 = 5.5$, df = 8, $P = 0.70$, respectively). The large variability in invasion
289 responses for simulations with fires in year 10 (Fig. 3) can be explained by the size of the fire,
290 with more pine-occupied cells and greater maximum distance from the plantation in the
291 simulations with larger fires (Supplemental information Fig. S1).

292 ***Trends Over Time***

293 The trends over time for all responses (pine-occupied cells, mean pine density, maximum
294 pine density, and maximum distance to plantation) differed between the unburned simulations
295 and those burned in years 10, 15, and 20 ($P<0.001$ for all comparisons); however, trends over
296 time did not differ between unburned and burned in year 5 ($P>0.05$ for all responses; Fig. 4).
297 Mean pine density was the only response variable where the invasion density threshold was
298 significant: lower mean densities occurred in simulations with a threshold of 15 than in those
299 with a threshold of 5 ($P<0.001$).

In all treatment combinations, the number of pine-occupied cells jumped significantly in year 8 when the plantation trees matured and increased seed production (Fig. 4). The unburned and fire year 5 simulations indicated that pine-occupied cells and maximum distance to plantation increased steadily after year 8. With fires in years 10, 15 and 20, pine-occupied cells briefly declined the year following fire (Fig. 4). In simulations with fire in years 10 and 15, some runs showed that the fire grew large whereas in others fire size remained small. In runs where the number of burned cells was large, a large jump in pine-occupied cells and maximum distance to plantation occurred as soon as the post-fire cohort became mature and started dispersing seeds (Fig. 4). All fires burned in year 20 became large, due to more continuous pine fuels, and the number of pine- occupied cells and the maximum distance to plantation increased when the post-fire cohort matured (Fig. 4). In all cases, in the years that the number of pine-occupied cells and maximum distance to plantation increased, mean density declined due to lower densities in the front of the invasion wave. Maximum densities peaked at simulation year 17 for the unburned and the fire year 5 simulations. For the other simulations (fire years 10, 15 and 20) the maximum density peaked 11 years after fire (Fig. 4) before declining due to the density-dependent feedback on establishment included in the model.

Discussion

To best understand the ecology of plant invasions and predict unexpected outcomes, it is necessary to integrate information on disturbance, the local environment, invasive plant traits, and demography (Higgins and Richardson 1998; Buckley et al. 2007; Stevens and Beckage 2009). The model developed in this study is unique in that it combined a mechanistic explanation for feedbacks (altered fuel loads and fire spread) with a population model (Gaertner et al. 2014) to examine the complexity and potential for non-intuitive outcomes resulting from the interaction

between fire and pine invasions. Although fire was not necessary to initiate a *P. contorta* invasion, simulated fire through invasions that were at least 10 years old increased the spatial extent of pine and its maximum invasion density.

The age of the invasion when the fire occurred proved to be an important parameter, because it affected both the size of the fire and the ability of *P. contorta* to recruit successfully post-fire. The model suggests that the probability of an ignition becoming a large fire increases greatly in older invasions compared with uninvaded steppe sites. Empirical studies show that steppe vegetation is generally fuel limited (Paritsis et al. 2013; Taylor et al. 2017), and pine invasions increase the fuel loads (Taylor et al. 2017; Paritsis et al. 2018), likely resulting in more continuous fire spread. Once fuel levels are sufficient for fire to spread, the pine invasion is generally above the density threshold necessary to cause an increase in *P. contorta* establishment post-fire. This interaction sets up a positive feedback: older, dense invasions promote larger fires which in turn promote denser post-fire invasions that eventually spread more rapidly than invasions in unburned simulations. It is difficult to disentangle the effects of pine density and pine age, given that in the sites used to calibrate the model invasion age and density are strongly positively correlated. However, we would expect the feedback to be weaker where invasions are older but not dense and thus less likely to influence fire behavior due to lower fuel loads. A similar positive feedback between flammable native shrubs and fire occurs in Patagonia (Mermoz et al. 2005), and increasing fire could promote further shifts from fire-sensitive *Nothofagus pumilio* forests to fire-prone shrublands (Paritsis et al. 2015). Flammable pine plantations (Paritsis et al. 2018), which are often located on the forest-steppe ecotone, and pine invasions, could exacerbate this positive fire feedback and further contribute to losses of fire sensitive *Nothofagus* species. The situation is particularly acute when plantations are placed

346 adjacent to the fire-sensitive *Nothofagus pumilio* forest, as occurs frequently in the Chilean
347 Aysén Region.

348 When disturbance is more likely in invaded areas than in uninvaded areas it was
349 predicted that disturbance would decrease invasion rates (Buckley et al. 2007). In contrast, even
350 though fires spread more readily through invaded than uninvaded areas in our simulations, fire
351 increased invasion rates. We attribute this finding to several factors. First, the inherently patchy
352 nature of fires ensures that some mature seed trees survive fires and promote recolonization of
353 the burned area (Pierce and Taylor 2011). Second, *P. contorta* seeds can withstand high
354 temperatures in the soil (Knapp and Anderson 1980; Cóbar-Carranza et al. 2015), and these
355 temperatures generally exceed modeled soil temperatures in fire simulations that are based on
356 fuel loads recorded at four sites with *P. contorta* invasions (Taylor et al. 2017). For that reason,
357 rapid regeneration of pine could come from an in-situ post-fire seedbank (although *P. contorta*
358 seeds generally only survive one to three years in the soil seedbank (Ledgard 2004)). Third, *P.*
359 *contorta* reproduces at a young age, particularly in its introduced range (Taylor et al. 2016a).
360 We found that invasion was only slowed for 5 years post-fire until a new cohort became
361 reproductive. The post-fire cohort was denser than invasions in unburned simulations, allowing
362 the invasion to proceed more quickly than in the unburned simulations.

363 In general, the benefits of disturbance for establishment rates outweighed the negative
364 effects of disturbance on tree survival in our model experiment. However, the tradeoff between
365 pine mortality and increased post-fire establishment rates can be seen by comparing the number
366 of occupied cells when fire burned in year 10 versus year 20 (Figs. 3 & S1). The highest number
367 of pine occupied cells occurred when a large fire burned in year 10 (Fig. S1). These fires tended
368 to be smaller than fires burned in year 20, thus the adult mortality rate was lower, but enough

369 cells burned that had high invasion densities to also result in increased establishment rates at
370 some locations on the landscape. Therefore, a slight effect of reducing the adult population that
371 provides a seed source was observed. The fires in our simulation were fairly patchy leaving
372 enough adults on the landscape to provide a seed source. We expect that where large patches of
373 complete adult mortality occur, seed limitation may slow recolonization of the burned area as has
374 been observed for non-serotinous populations of *P. contorta* in its native range (Harvey et al.
375 2016).

376 It has long been known that fire and other disturbances promote pine invasions,
377 particularly for serotinous species (Richardson and Bond 1991; Richardson and Higgins 1998);
378 however, it has also been recognized that the effects of disturbance are context specific
379 (D'Antonio 2000). In the case of invasive species, disturbance must be understood in light of
380 the native vegetation and disturbance regime as well as the plant traits of the invader (Higgins
381 and Richardson 1998). We suggest that *P. contorta* invasion will be promoted by fire across
382 much of the world, based on several factors: first, changing the pre-fire invasion pine density
383 (threshold) necessary to promote establishment of pine after a fire had a minimal effect on model
384 outcomes. Thus, even if critical levels of pine density vary by site, the response of pine invasion
385 after fire will not show significant variation. Second, our intermediate threshold level (1000
386 trees/ha) was estimated from a site with fire-adapted species that readily resprout after fire
387 (Nuñez and Raffaele 2007). We would expect the threshold to be even lower in sites with less
388 fire-adapted vegetation (e.g., New Zealand, Perry et al. 2014) because reduced recovery of native
389 vegetation after fire would decrease competition with pine seedlings. Additionally, sites with less
390 fire-adapted vegetation are particularly vulnerable to human-induced changes in fire regimes
391 (Perry et al. 2014; Whitlock et al. 2015). Third, *P. contorta* growth is slower at the Chilean

392 Coyhaique Alto site than at other sites in Argentina and New Zealand where *P. contorta* is also
393 currently invading (Taylor et al. 2016a). Thus, fuel accumulation with invasion is more rapid in
394 these other sites suggesting that a positive feedback could form earlier in the invasion. Fourth, *P.*
395 *contorta* individuals also have higher fecundity at a younger age at other sites in Argentina and
396 New Zealand than at Coyhaique Alto (Taylor et al. 2016a). Therefore, the post-fire cohort of
397 pine will become reproductive sooner and produce more seeds, promoting an even larger
398 increase in post-fire invasion spread rates. Finally, the *P. contorta* at the study sites used to
399 parameterize the model were not serotinous (Taylor et al. 2016a; Taylor et al. 2017). We would
400 expect *P. contorta* to be even more abundant following fire where there are serotinous
401 individuals (Turner et al. 1997).
402 Our study site in Coyhaique Alto was relatively homogenous in terms of suitable habitat
403 for *P. contorta* but in sites with more heterogeneous habitat, spread rates will depend on other
404 factors, including density dependence (Pachepsky and Levine 2011) and background habitat
405 suitability for establishment, survival, and reproduction. Furthermore, interactions with other
406 invasive species that also respond positively to fire may reduce *P. contorta* establishment rates
407 post-fire. For example, initial observations following a fire that burned dense *P. contorta*
408 invasions in New Zealand suggest that abundant regrowth of several invasive European pasture
409 grasses, and potentially post-fire climate conditions, may have limited *P. contorta* establishment
410 in the first three years following fire (Davis unpublished data). Abiotic conditions may also
411 affect feedbacks. For example, high densities of pines were found after fire in Northern
412 Patagonia in wet but not dry sites (Raffaele et al. 2016). Thus, the potential for fire to promote
413 pine invasions will likely depend strongly on the response of the dominant vegetation to fire, as
414 well as other site-specific factors such as climate.

415 The trends seen in pine-occupied cells and their density over time (Fig. 4) explained
416 several patterns seen in the snapshot results from year 35 (Fig. 3). Mean density declined when
417 the number of pine- occupied cells increased due to an increase in low-density cells at the
418 invasion front. Density dependence caused the overall mean density to remain fairly constant
419 between fire year treatments, after an initial brief increase in mean pine density post-fire in the
420 later year burns. However, the maximum density was significantly higher in simulations with
421 large fires. High maximum pine densities will likely result in strong declines in native plant
422 cover and richness, which are both negatively correlated with *P. contorta* cover (Taylor et al.
423 2016b). Therefore, synergies between disturbance and invasion may accelerate impacts due to *P.*
424 *contorta* invasion on native ecosystems.
425 Our modeling experiments indicate that high maximum densities of *P. contorta* after fire
426 abruptly increased the number of pine-occupied cells and the maximum distance of invasion
427 from plantations. This stepwise invasion process with rapid and nonlinear increases in spread
428 rates contrasts with unburned and small fire (fire year 5 and some fire year 10) simulations where
429 the increase in occupied cells was linear after the initial jump in year 8 (Fig. 4). Other studies
430 have also found that feedbacks between tree invasions and fire led to nonlinear behavior (Stevens
431 and Beckage 2009) and thus rapid increases in tree invasions may be expected in other systems
432 that also have feedbacks between invasion and fire.
433 Our results highlight the necessity of managing pine invasions before they reach an
434 advanced stage where positive feedbacks between fire and pine invasion could lead to dramatic
435 increases in invasion rate. The increasing density and extent of post-fire pine will exacerbate
436 non-fire driven invasion impacts, such as declines in native biodiversity (Ledgard and Paul 2008;
437 Pawson et al. 2010; Taylor et al. 2016b), changes in soil microbial communities and nutrient

cycling (Dehlin et al. 2008; Dickie et al. 2014), and altered hydrological regimes (Farley et al. 2005; Fernandez et al. 2009). Pine plantations in Patagonia became widespread beginning in the 1970s, while pine plantations were already widespread by that point in South Africa, Australia, and New Zealand (Simberloff et al. 2010). Therefore, many pine invasions across the Southern Hemisphere are likely at the stage where fire will promote invasion. Fires in the study region, and other parts of the Southern Hemisphere with introduced pines (South Africa, southeast Australia, and New Zealand), are predicted to increase in the future given climate trends and changes in land use (Veblen et al. 2008; Holz and Veblen 2011; Veblen et al. 2011; Moritz et al. 2012). Large fires in pine plantations in the study region (near Coyhaique, Chile in 2016) and in other regions invaded by *P. contorta* (Craigieburn, New Zealand 2015) occurred during recent warmer-than-average summers, which underpins the need to seriously consider the potential impact of wildfires on pine plantations and invasions. While fire is not necessary to promote pine invasions, it could certainly increase the invasion rate and further complicate management efforts going into the future.

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634 Table 1. Model demographic parameters and their sources.

Parameter	Value	Description & Source
Plantation density	15 trees per 100 m^2	Pauchard communication with forestry company that owns plantation
Dispersal	Alpha = 3.5; beta = 0.0035; C = 50; pLDD = 0.1	Alpha, beta, C are dispersal parameters and pLDD is probability of long distance dispersal (LDD). Sensitivity analysis described in methods
pEst	0.01	Probability of establishment Langdon 2011
pEst in NOAN	0.1*pEst	pEst in *N. antarctica* (NOAN) plots Taylor et al. 2016a
S_{12}	0.9	Survival year 1 to 2 Pauchard unpublished data
S_{23}, S_{34}, S_{45}, S_{56}	0.97	Survival year 2 to 3 up to survival year 5 to 6 Pauchard unpublished data
S_{67}, S_{78}, S_{89}, S_{9A}, S_{AA}	0.99	Survival year 6 to 7 up to adult survival Pauchard unpublished data
Seedbank survival	0.2	Proportion of seeds surviving each year Ledgard 2004
Seed predation	0.03	Proportion of seeds removed by predators Davis unpublished data
Adult cones per tree	Mean: 38; sd: 20	Adult cones per tree mean and standard deviation Taylor et al. 2016a
P_{repro}	0.28	Probability a subadult (ages 5-9) has cones in given year Taylor et al. 2016a
Subadult cones per tree	Mean: 9.5; sd: 8	Subadult cones per tree mean and standard deviation Taylor et al. 2016a
f_A, f_{SA}	Cones * 20	Seeds per cone for adult and subadult trees Davis unpublished data

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642 Table 2. Fire-related model parameters and their sources.

Parameter	Value	Description & Source
Invasion density threshold (*P. contorta* per 100 m^2)	5, 10, 15	Pre-fire density above which *P. contorta* establishment is increased post-fire for 3 years. Taylor et al. 2017
Post-fire establishment in plots above invasion density threshold	0.043 for 3 years post-fire	Taylor et al. 2017
Post-fire establishment in *N. antarctica* plots	pEst (0.01) for first 5 yrs post-fire	Same as steppe plots because fire reduces competition with *N. antarctica* until it recovers Burns 1993
Seedbank (sb) response to fire	Sb=sb*0.5 if maximum tree age > 15 years Sb=sb otherwise	Taylor et al. 2017 Knapp & Anderson 1980
Probability fire spread in *P. contorta*	If density > 40 or oldest tree > 10 years spread prob. = 0.8 Otherwise = spread in that vegetation type (steppe or *N. antarctica*)	Taylor et al. 2017
Probability fire spread in *N. antarctica*	0.61	Paritsis et al. 2013
Probability fire spread in *N. antarctica* with steppe neighbors	0.71	Higher probably of burning due to drying effect of edge with steppe
Probability fire spread in *N. antarctica* with *P. contorta* neighbors older than 10 years	0.71	Higher probably of burning when next to mature lodgepole
Probability fire spread in steppe	0.3	Paritsis et al. 2013 Taylor et al. 2017

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649 Table 3. Observed (Taylor et al. 2016a) and simulated (30 runs, no fire) pine invasion metrics for
650 the Coyhaique Alto site. For the simulation the mean and the standard deviation (SD) from the
651 30 runs for each invasion metric is shown. Densities are in units of trees per 100 m^2. "Occupied
652 plots 0-100 m" refers to plots with at least one *P. contorta* individual at distances of 0-100 m
653 from the plantation edge.

	Observed 2012	Observed 2014	Simulation Mean	Simulation SD
Plantation age	24	26	26	-
Mean density of pine-occupied cells	10.1	11.0	12.86	0.10
Mean adult pine density in cells with adults	-	5.0	4.88	0.08
Farthest invaded cell (m from plantation)	901	901	459.02	18.83
Mean density in *Nothofagus* cells occupied by at least one *P. contorta*	1.6	2.0	2.24	0.22
Maximum *P. contorta* density	83	67	36.43	1.68
Mean pine density occupied plots 0-100 m	28.1	19.9	22.29	0.15
Mean pine density occupied plots 100-200 m	16.6	25.2	10.79	0.13
Mean pine density occupied plots 200-300 m	4.1	5.9	7.13	0.52
Mean pine density occupied plots 300-400 m	3.6	4.9	4.02	0.45
Mean pine density occupied plots 400-500 m	1.8	2.8	1.31	0.24

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Figure captions

Figure 1. Diagram of the model flow. Abbreviations are explained in Tables 1 and 2, except n(adults) which signifies the number of adults in a cell. This variable affects establishment and survival at some stages through density dependence.

Figure 2. Frequency of fire size (number of burned cells) by fire year treatment (unburned and burned in years 5, 10, 15, or 20 of the invasion) during *P. contorta* simulated invasion. The number of simulations run for each fire year treatment was constant (300).

Figure 3. Simulation results for (A) number of *P. contorta* occupied cells; (B) mean pine density in occupied cells (100 m^2); (C) maximum pine density (trees per 100 m^2); and (D) maximum distance of a pine-invaded cell from the plantation for the five fire year treatments (unburned and burned in years 5, 10, 15, or 20 of the invasion). Number of pine-occupied cells and their densities exclude cells in the plantation. Colors show three different threshold densities for *P. contorta* (number of trees per 100 m^2 cell) prior to fire. Exceeding these threshold densities was required to increase *P. contorta* establishment post-fire.

Figure 4. Time series show changes in plot parameters over the course of the model simulation: (A) Change in *P. contorta* occupied cells; (B) mean density of pine-occupied cells: (C) maximum (max) pine density; and (D) maximum distance of an invaded cell from the plantation over simulation time. Densities are in units of trees per cell (100 m^2). Smooth lines are predicted trends from the GAMM model. There was no statistical difference in the relationship between year and occupied cells for the unburned and fire year 5 simulations so only one line is shown (black). Colored lines and points represent simulations burned in year 10 (blue), 15 (yellow), and 20 (green) of the invasion. Note that the line for fire year 10 does not appear to match the data because some points from fire year 10 simulations are hidden behind other points and represent the simulations where fires remained small.

685 Figure 1.

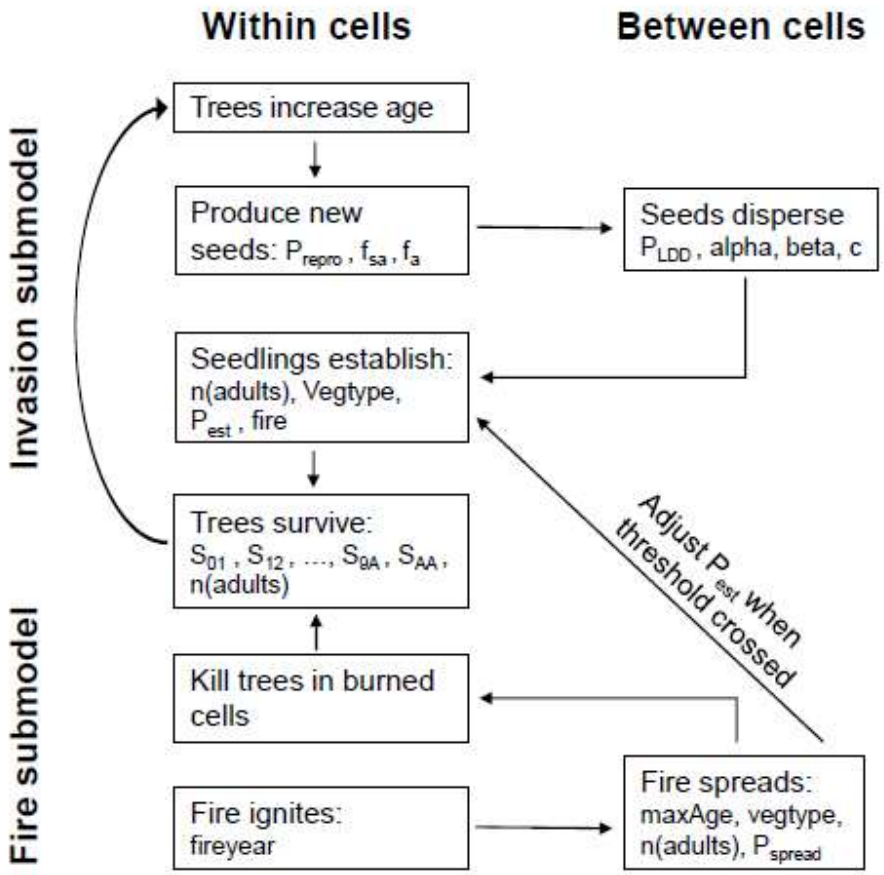

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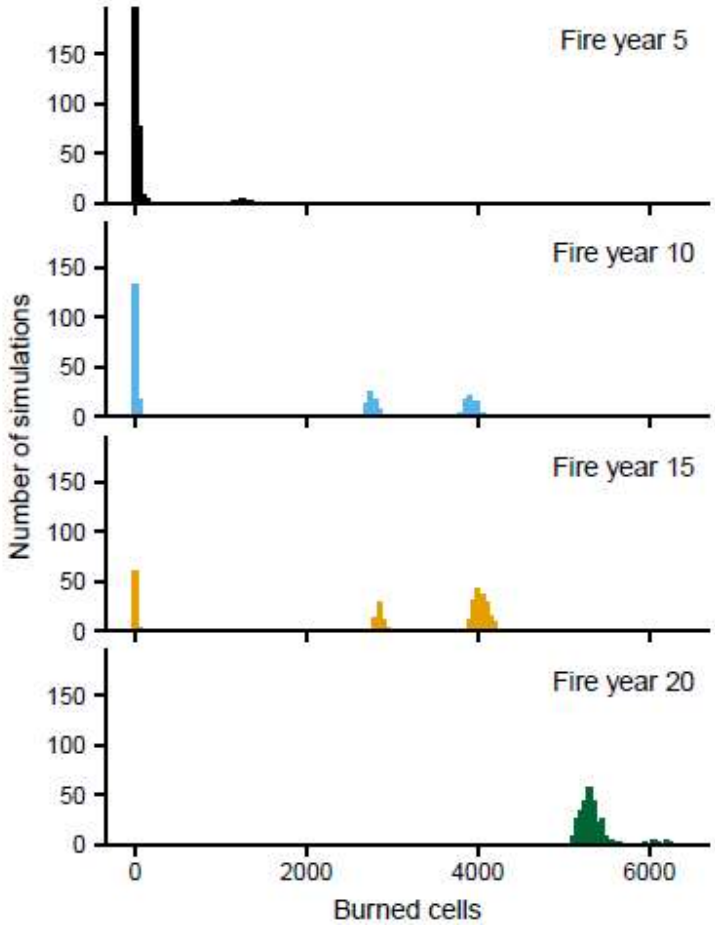
Figure 2.


Fire year 5
Fire year 10
Fire year 15
Fire year 20
Number of simulations
0
50
100
150
0
2000
4000
6000
Burned cells

707 Figure 3.

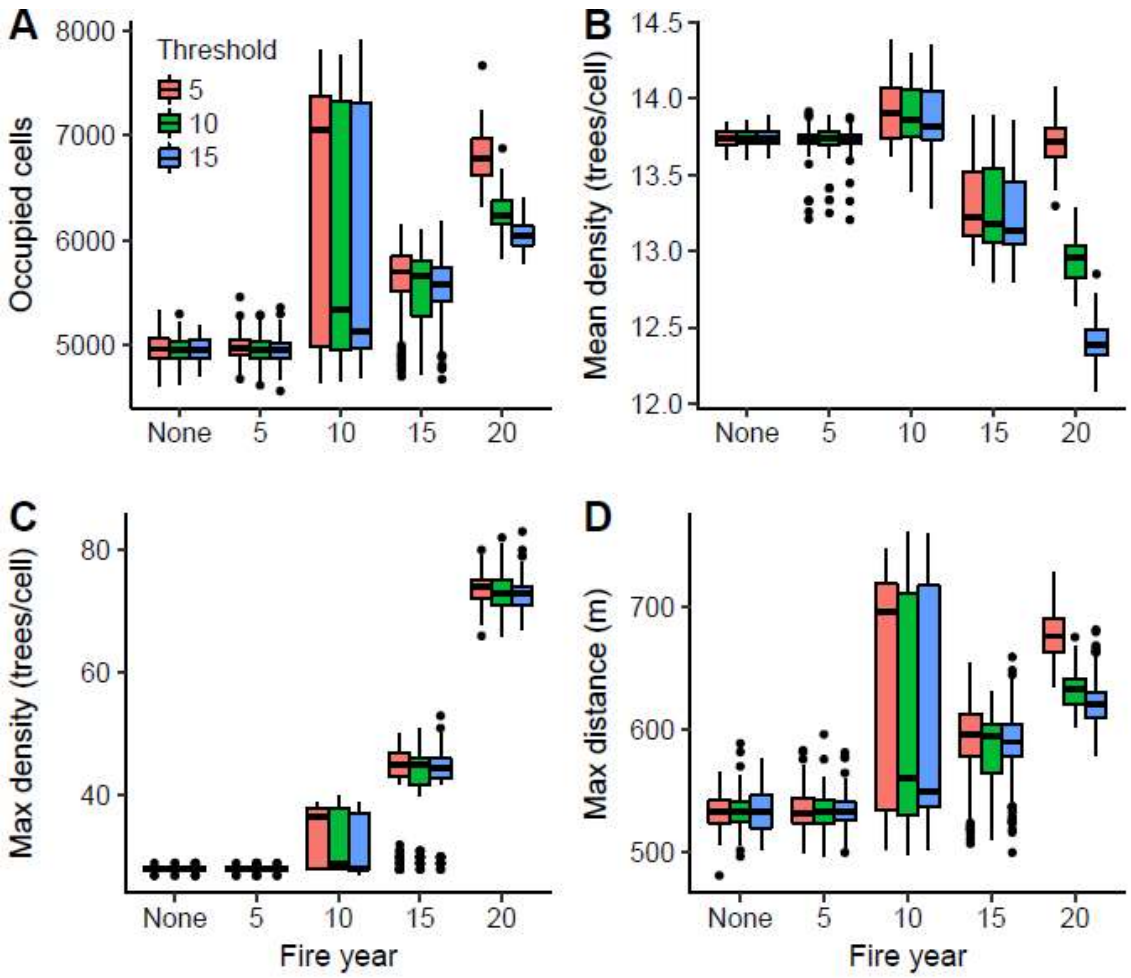


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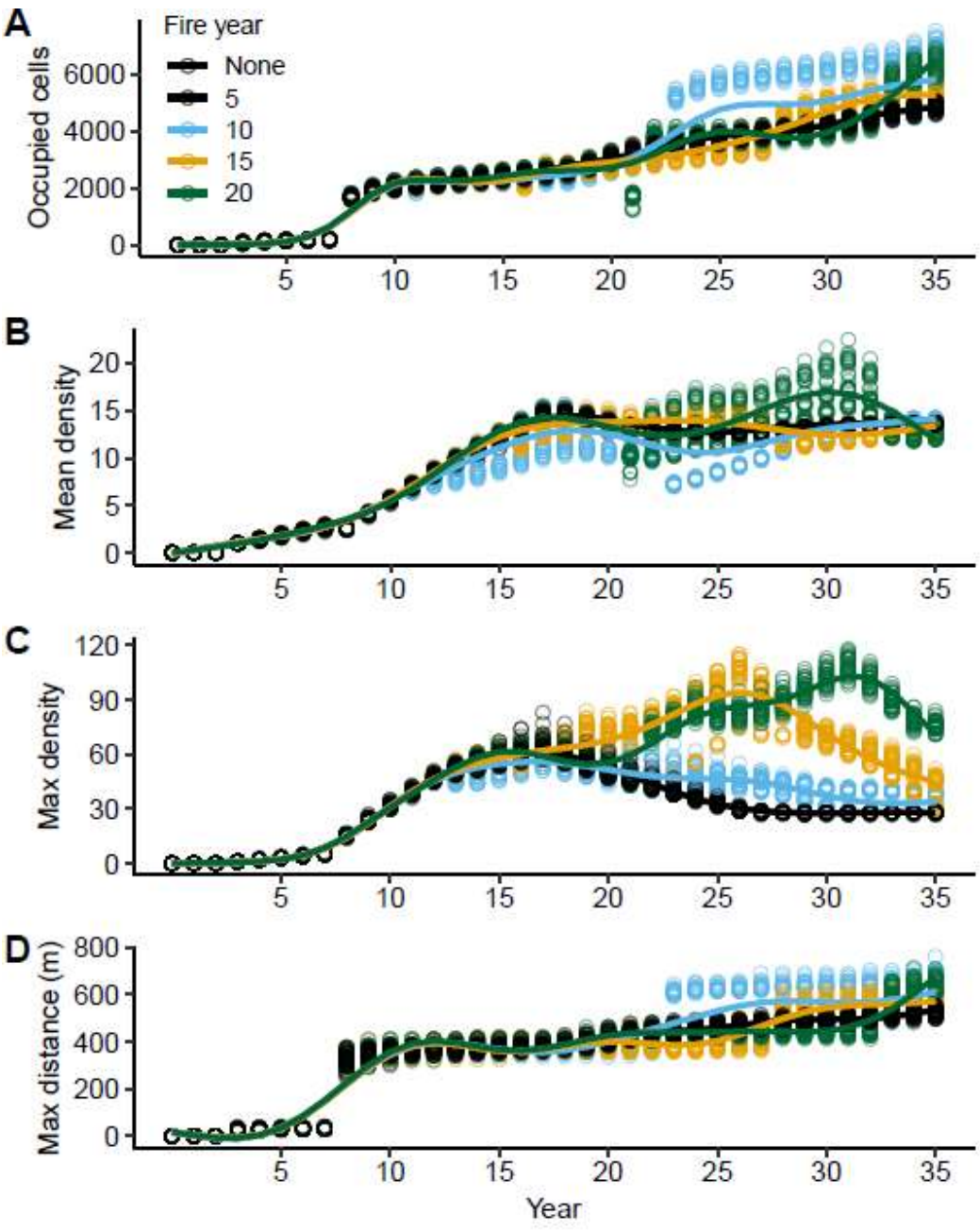
Figure 4.


A
Fire year
None
5
10
15
20
Occupied cells
6000
4000
2000
0
B
Mean density
20
15
10
5
0
C
Max density
120
90
60
30
0
D
Max distance (m)
800
600
400
200
0
5
10
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Year