Received Date : 25-Jul-2016
Revised Date : 06-Nov-2016
Accepted Date : 22-Nov-2016
Article type : Articles

Running title: Feedback between pine invasions and fire

Title: *Pinus contorta* invasions increase wildfire fuel loads and may create a positive feedback with fire

Kimberley T. Taylor[1*], Bruce D. Maxwell[1], David B. McWethy[2], Aníbal Pauchard[3,4], Martín A. Nuñez[5], and Cathy Whitlock[2]

[1] Land Resources and Environmental Sciences Department, Montana State University, Bozeman, MT 59717, USA
[2] Earth Sciences Department, Montana State University, Bozeman, MT 59717, USA
[3] Laboratorio de Invasiones Biológicas (LIB). Facultad de Ciencias Forestales. Universidad de Concepción, Victoria 631, Casilla 160-C, Concepción, Chile.
[4] Institute of Ecology and Biodiversity (IEB), Las Palmeras 3425, Casilla 653, Santiago, Chile.
[5] Grupo de Ecologia de Invasiones, INIBIOMA, CONICET, Universidad Nacional del Comahue, Quintral 1250, San Carlos de Bariloche, CP 8400, Argentina
* Corresponding author; Current address: Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA

Emails:
KTT Kimberley.Taylor@umontana.edu

BDM Bmax@montana.edu
DBM DMcwethy@montana.edu
AP Pauchard@udec.cl
MAN Nunezm@gmail.com
CW Whitlock@montana.edu

Abstract

Invasive plant species that have the potential to alter fire regimes have significant impacts on native ecosystems. Concern that pine invasions in the Southern Hemisphere will increase fire activity and severity and subsequently promote further pine invasion prompted us to examine the potential for feedbacks between *Pinus contorta* invasions and fire in Patagonia and New Zealand. We determined how fuel loads and fire effects were altered by *P. contorta* invasion. We also examined post-fire plant communities across invasion gradients at a subset of sites to assess how invasion alters the post-fire vegetation trajectory. We found that fuel loads and soil heating during simulated fire increase with increasing *P. contorta* invasion age or density at all sites. However, *P. contorta* density did not always increase post-fire. In the largest fire, *P. contorta* density only increased significantly post-fire where the pre-fire *P. contorta* density was above an invasion threshold. Below this threshold, *P. contorta* did not dominate after fire and plant communities responded to fire in a similar manner as uninvaded communities. The positive feedback observed at high densities is caused by the accumulation of fuel that in turn results in greater soil heating during fires and high *P. contorta* density post-fire. Therefore, a positive feedback may form between *P. contorta* invasions and fire, but only above an invasion density threshold. These results suggest that management of pine invasions before they reach the invasion density threshold is important for reducing fire risk and preventing a transition to an alternate ecosystem state dominated by pines and novel understory plant communities.

Keywords: Biological invasion, fire, fuel load, invasion impact, invasion threshold, pine invasion, *Pinus contorta*, positive feedback

Introduction

Invasive plants can lead to abrupt shifts in fire regimes that increase the potential for invasions to impact native ecosystems (Brooks et al. 2004, Pausas and Keeley 2014). Invasions that alter fire regimes may endanger native plants that are well adapted to one fire regime but may be threatened in another (Keeley et al. 2011). Invasive plants can influence fire regimes by altering fuel loads (Dibble and Rees 2005, Pauchard et al. 2008), fire frequency (Balch et al. 2013), fire spread (Balch et al. 2013), fire intensity (van Wilgen and Richardson 1985, Stevens and Beckage 2009, Setterfield et al. 2010), and flammability (Dibble et al. 2007). Impacts of woody invasive plants on fuel loads are highly variable (Mandle et al. 2011) suggesting that it is necessary to examine each species or group of species on a case-by-case basis to fully understand the potential effects of woody invasions on fire regimes.

Invasion impacts on native communities can be exacerbated when invasive plants create positive feedbacks with fire, altering fire regimes in ways that promote their own success over native plants. Positive feedbacks can cause rapid shifts in the frequency and severity of fire activity. Hence, identifying invasive species capable of causing positive feedbacks is essential to predict which species will be high impact invaders and to prioritize management efforts (Gaertner et al. 2014). For example, the grass-fire cycle is a well described phenomenon in which non-native grasses increase fine fuel loads and/or fine fuel continuity thus promoting more frequent, larger, or more intense fires (Setterfield et al. 2010, Balch et al. 2013, Wagner and Fraterrigo 2015), which in turn promote their own dominance over native plants (D'Antonio and Vitousek 1992). Feedbacks between woody invasive plants and fire are less well studied and can either promote or discourage fire (Pauchard et al. 2008, Stevens and Beckage 2009).

There is concern that invasions by fire-adapted pine species (genus *Pinus*) may increase fuel loads and overall landscape flammability, promoting a more fire-prone plant community to the detriment of native species (Simberloff et al. 2010, Veblen et al. 2011, Raffaele et al. 2016). However, even though pine invasions are widespread across the Southern Hemisphere due to pine introduction for forestry (Richardson and Higgins 1998), few studies have examined evidence for the formation of a positive feedback between pines and fire. *Pinus contorta* (lodgepole pine) is one of the most invasive pine species (Rejmanek and Richardson 1996), and is rapidly invading the Patagonian steppe (Langdon et al. 2010, Taylor et al. 2016a), Chilean Araucaria forests (Peña et al. 2008, Taylor et al. 2016a), and both North and South Island, New

Zealand (Ledgard 2001, Taylor et al. 2016a). While *P. contorta* is known to accumulate high fuel loads in its native range (Baker 2009), it grows faster in its introduced than native range (Taylor et al. 2016a) thus potentially resulting in more rapid fuel accumulation. Furthermore, fire is widely considered to enhance *P. contorta* regeneration in western North America by causing prolific recolonization of burned areas, even in non-serotinous populations (Baker 2009).

Although evidence suggests a positive feedback between fire and pine invasions, this idea has not been well tested with empirical data. To our knowledge, only one study has examined changes in fuel loads due to pine invasions. Córbar-Carranza et al. (2014) found that in a forested ecosystem fuel quantities did not change with *P. contorta* invasion but fuel structure was altered causing a potential switch from a surface- to canopy-fire dominated regime. Several studies have looked at regeneration and other post-fire effects in areas with and without exotic pine species. In South Africa, soil properties under burned pine canopies and native fynbos suggested that fire severity was higher in pine plantations than in fynbos (Scott and Van Wyk 1990). In Patagonia, post-fire *Pinus ponderosa* plantations created novel conditions that prevented regrowth of native matorral (shrubland), despite the fact that matorral is well adapted to surface fire (Nuñez and Raffaele 2007). Whether the post-fire vegetation trajectories differed due to pre-fire species composition or changes in fire severity in this study is unclear. In the Argentine pampas and the South African fynbos, fire caused a rapid expansion of introduced *Pinus halepensis* (Richardson 1988, Zalba et al. 2008).

Post-fire successional trajectories can be altered by exotic pines, yet the mechanisms causing the observed changes in community structure and function are still poorly understood. The goal of this study is to better understand the relationship between *P. contorta* invasions and fire activity in locations where *P. contorta* has invaded open habitat (grasslands and shrublands) in the Southern Hemisphere. We addressed this objective by first, assessing changes in fuel loads across a *P. contorta* invasion gradient at four sites in three countries in the introduced range (Argentina, Chile and New Zealand). Specifically, we determined if the abundance of each type of fuel was related to pine invasion age or invasion density. Second, we used our fuel data from across the invasion gradient to model soil heating during a simulated fire. Third, we assessed the response of the vegetation and, in particular, *P. contorta* to fire in a subset of sites that had recent fires. We expected that increasing pine density would be associated with increasing fuel loads and thus greater soil heating during fire, which in turn may reduce recovery of some native species. We hypothesized that pines would dominate burned areas. The results of our study provide new information about the mechanisms that may cause changes in fire regimes as a result of pine invasions in Southern Hemisphere plant communities.

Methods

Study Sites

Sampling occurred at four sites in Argentina (AR) (1), Chile (CL) (1), and New Zealand (NZ) (2) (Appendix S1: Table S1). Each of these sites has been invaded by *P. contorta* over the past 24 to 53 years. The sites were either dominated by native and introduced grasses (CL, first NZ site) or native shrubs (AR, second NZ site). The site in Bariloche, Argentina (AR) was a shrub steppe community (dominated by *Mulinum spinosum*, *Acaena* spp., and *Stipa* spp.). The *P. contorta* plantations at AR were on average 34 years old. An area of the study site (plantations and native steppe) burned at moderate to high severity in a 300 ha human-caused fire in December 2006. The Chilean site, located in Coyhaique Alto, was a grass steppe community (*Festuca* spp.; Langdon et al. 2010). *Pinus contorta* plantations at CL were an average of 24 years old. A 7 ha human-caused fire burned at moderate to high severity through a patch of *Nothofagus* spp. and dense shrubs at this site in November 2011. The two NZ sites were in the Canterbury region on the South Island. NZ1 was dominated by introduced grasses and forbs (e.g. *Agrostis capillaris, Hieracium* spp.) and native *Festuca novae-zelandiae*. The more diverse Craigieburn Forest Park site (NZ2) contained areas dominated by introduced grasses and forbs, native grasses, the tall shrub manuka (*Leptospermum scoparium*), and shorter shrubs (*Discaria toumatou*). At NZ2 there was a very small (1 ha) human-caused fire in 1986, that appeared to have killed all shrubs at the site (shrubs have since begun to regenerate). Plantations were originally planted 45 years ago at NZ1 and 53 years ago at NZ2. New Zealand sites were sampled in January and February 2013 and Patagonian sites in January and February 2014.

Fuel Loads

To collect fuel data across the gradient of invasion levels, 10 m wide transects were randomly placed at the edge of *P. contorta* plantations and ran perpendicular to the plantation edge into natural vegetation. Transects started at least 50 m from other transects. Due to different invasion ages and topographic and anthropogenic barriers, transects were not the same length at all sites. At NZ1 transects were 3.5 km, at AR 2 km, at CL 800 m, and at NZ2 100-600 m. At NZ2, 2 additional 200 m transects were added at random start points along the 1986 fire boundary that crossed the fire and continued for 100 m into adjacent unburned vegetation. Due to the fire's small size these transects started 25 m from each other but ended 200 m apart. Sample fuel plots were randomly selected (*n* = 1-5 every 100 m) for a total of 44 plots at AR, 35 at CL, 73 at NZ1 and 128 at NZ2. Within each plot, basal diameter, diameter at breast height, height to crown base, and height were measured for each *P. contorta* individual. Age of each tree was estimated based on whorl counts or tree cores. One thousand-hour fuel loads were also collected within the entire 100 m^2 plot. In four one-m^2 subplots, one hour, ten hour, 100 hour, herbaceous, and shrub fuels were recorded using the Photoload method and averaged for each plot (Keane and Dickinson 2007). All of the biomass in 12 subplots at AR and 17 subplots at NZ2 was clipped, sorted into fuel type (one hour, ten hour, 100 hour, herbaceous, and shrub fuels), dried, and weighed to calibrate field Photoload estimates. Species composition at the two New Zealand sites and the two Patagonian sites was similar (besides greater shrub dominance at AR and NZ2) so the calibrations from NZ2 and AR were also applied to NZ1 and CL, respectively. Two measurements of litter and duff depth were taken in each subplot. Percent litter cover and litter type (e.g. grass, pine, shrub, *Nothofagus* spp.) were also recorded. Samples of each litter type were collected, dried, and weighed to determine the bulk density of each type. Depth, cover and bulk density values were used to determine litter fuel loads in each subplot. *Pinus contorta* biomass was calculated using separate allometric equations for trees with heights > 1.37 m (Jenkins et al. 2004) and < 1.37 m (Turner et al. 2004). *P. contorta* biomass < 2 m in height was added to the shrub stratum fuel loads (which includes all live woody biomass < 2 m in height).

To examine the relationship between *P. contorta* and fuel loads, total fuel and fuel of each fuel type were modelled with multiple linear regression as a function of time since invasion of the plot (TSI; age of oldest tree in plot) and *P. contorta* density. At NZ2, the model included management as a predictor because some plots were in areas where pines had been cut or hand pulled and left on the site in the past year. Where necessary, fuel loads were log-transformed to meet normality assumptions. All statistical analysis was performed in R (R Core Team, 2014).

Fire Effects

The impact of *P. contorta* invasion on soil heating was determined with the First Order Fire Effects Model (FOFEM; Reinhardt 2003). FOFEM assumes that all herbaceous and litter fuels will be consumed and uses the Burnup model to consume woody fuels in each plot (Albini & Reinhardt, 1997). Soil heating is modeled as a function of fire intensity, duration, and soil properties. Although this model was created in North America, it uses actual fuel loads for each fuel type to simulate fire rather than predetermined "fuel models" specific to North America so we feel it is appropriate to use in a different setting. Fuel data for each plot were input into the batch processing function of FOFEM. Log-transformed soil temperature was modeled using linear regression as a function of TSI, *P. contorta* density, and management (at NZ2).

Plant Community Response to Fire

We examined the response of *P. contorta* to fire (e.g., regeneration density) and the effect of invasion on the response of the rest of the vegetation community to fire (e.g., composition, abundance) at a subset of sites with recent fire activity. We determined *P. contorta* density continuously in 10 x 10 m plots along the transects described above at AR, CL, and NZ2 where the transects passed through recent burns (CL burned in 2011; AR in 2006; NZ2 burned in 1986). Where the plots were burned at AR and CL, we recorded the density of trees pre-fire, most of which died during the fire, and live regeneration density. We only recorded live regeneration density at NZ2 because the fire was older and we could not reliably count pre-fire density. We used the densities from these burned plots and all unburned plots on the transects that were within 100 m of the fire edge, to control for environmental variability, in the comparison of *P. contorta* invasion density in burned versus unburned plots (n=347 at AR; n=68 at CL; n=27 at NZ2). We modeled density in the selected plots as a function of fire, plot vegetation type (shrub or grass dominated), and their interaction using a negative binomial mixed model to account for overdispersion and spatial autocorrelation (Fournier et al. 2012, Skaug et al. 2013). Where vegetation type was not significant (P>0.05) it was not included in the final model. Correlograms showed that the maximum distance of density correlation was 50 m. Including 50 m clusters as a random effect in the model significantly reduced the spatial autocorrelation.

Further analysis was conducted for the AR site given the larger extent of the fire and the variety of vegetation types that burned (*P. contorta* plantations, *P. contorta* invaded areas, uninvaded steppe). At AR, we plotted the density of *P. contorta* that had colonized burned plots as a function of the number of dead, burned *P. contorta* in each plot to determine the invasion level at which *P. contorta* density is higher after fire than before. This relationship was non-linear and suggested a threshold (1000 trees/ha) above which post-fire *P. contorta* density was much higher than pre-fire density (Fig. 1). We divided the pre-fire invasion level for each density plot into categories (low invasion burned, high invasion burned) based on this threshold and then modeled the density data from AR as a function of the fire-invasion category (unburned, uninvaded burned, low invasion burned, high invasion burned) using a negative binomial mixed model as described above. We could not repeat this process at CL because only two plots were invaded by *P. contorta* prior to burning.

In order to further examine *P. contorta* and understory plant community response to fire at AR, we surveyed the species composition of burned and unburned plots located in plantations, invaded areas (invaded pre-fire), and uninvaded areas. Hereafter, we refer to these different areas of sampling as “conditions” which include the six categories: uninvaded unburned, uninvaded burned, invaded unburned, invaded burned, plantation unburned, and plantation burned. We randomly placed five plots in each category except the plantation burned category, which had 7 plots (32 plots total). The plots were 5 x 5 m and in each we recorded the percent cover of all species and the number of *P. contorta* individuals and their ages, as well as total *P. contorta* cover. We used principal coordinates analysis based on Morista-Horn distances between plots to examine differences in species composition (excluding *P. contorta*) between plots. We used permutational multivariate analysis of variance (PERMANOVA) to determine if plot condition affected plot level species composition (Oksanen et al. 2013). We also modeled total native plant cover and log transformed exotic plant cover as a function of condition with linear regression.

Results

Changes in Fuel Loads

P. contorta invasion was associated with increased overall fuels at all sites (Fig. 2, Appendix S1: Fig. S1, and Table 1). Metrics of *P. contorta* invasion explained more of the variation in fuel loads at the grassland sites (CL, NZ1) than the shrubland sites (AR, NZ2; Table 1). Time since invasion (TSI; oldest tree in plot) was generally more important than *P. contorta* density in explaining fuel loads at CL, NZ1 and NZ2, while invasion density was more important than TSI at AR (Table 1). In all cases except one, the significant relationships between invasion age or density and fuel loads were positive.

Changes in Fire Effects

Overall, simulated soil heating increased most with invasion into grass-dominated sites CL and NZ1, and TSI and/or *P. contorta* invasion density generally explained more of variation in these responses than at the shrub-dominated AR and NZ2 sites (Table 1). TSI was generally the best predictor of simulated soil temperatures, although there was some variation by site and response (Table 1). At NZ2, including management in the models improved their explanatory power (e.g. R^2 of 0.28 versus 0.03 for surface temperature, with and without management respectively). Management resulted in a steeper increase in soil heating with increasing TSI (Fig. 3D). At CL1, soil heating appears to have a threshold (around TSI 10 years) below which soil temperature did not change with increasing invasion age and after which there is a rapid increase in soil temperatures (Fig. 3A).

Pinus contorta Response to Fire

At AR, *P. contorta* density depended on fire-invasion class (high invasion pre-fire, low invasion pre-fire, no invasion pre-fire, unburned; $\chi^2 = 32.2$, df = 3, $P<0.0001$). Density was much higher in burned plots with pre-fire invasion densities above the 1000 trees/ha threshold than in any other category (Fig. 4A), although there were statistically significant differences ($P<0.05$ for pairwise comparisons) between all groups except the unburned and low-invasion pre-fire plots.

At CL, we sampled 32 plots in the 2011 burn, of which only two had *P. contorta* trees growing in the plot and these trees had survived the fire. No other plots in the burned area had been invaded prior to the fire. Consequently, plots in the burned area had significantly lower *P. contorta* density than unburned plots at this site ($\chi^2 = 15.7$, df = 1, $P<0.0001$; Fig. 4B).

At NZ2, there was a significant vegetation by fire interaction ($\chi^2 = 8.7$, df = 1, $P = 0.0031$) whereby there was no difference in *P. contorta* density between burned and unburned plots in grasslands; however, unburned shrublands had significantly lower *P. contorta* density than burned shrublands (Fig. 4C).

Plant Community Response to Fire at AR

At AR, we found that fire altered plant species composition in uninvaded and lightly invaded sites but that in plantations and highly invaded sites (greater than 50% pre-fire *P. contorta* cover or 800 trees/ha), plant composition changed little with fire (Fig. 5). The principal coordinates analysis identified three main groups of plots: (1) plots that had high cover of *P. contorta* before or after fire (Fig. 5, dash-dot line circle), (2) plots that burned and were either uninvaded or had low densities of *P. contorta* (<200 trees/ha pre-fire; Fig. 5, dashed line circle), and (3) plots that were unburned and either uninvaded or very lightly invaded (Fig. 5, solid line circle). Condition (uninvaded unburned, uninvaded burned, invaded unburned, invaded burned, plantation unburned, plantation burned) was a significant predictor of species composition ($F_{5,31} = 3.5$, $P = 0.001$) with an R^2 of 0.40.

Condition was also a significant predictor of total native plant cover ($F_{5,26}$ = 9.6, $P<0.001$, R^2 = 0.65) and total exotic plant cover (not including *P. contorta*; $F_{5,26}$ = 5.6, P = 0.001, R^2 = 0.52) at AR. There was no difference in native plant cover between uninvaded unburned and uninvaded burned plots (t = -1.0, d.f. = 26, P = 0.31); however, plots in all other conditions had significantly lower native plant cover ($P<0.05$ for all pairwise comparisons) than uninvaded unburned plots. Exotic cover was higher in invaded burned plots (mean = 11.14%, t = 2.4, d.f. = 26, P = 0.03) and lower in plantation unburned plots (mean = 0.02%, t = -2.4, d.f.= 26, P = 0.02) than in the uninvaded unburned plots (mean = 0.66%).

Discussion

Our results highlight the potential for *P. contorta* invasions to modify fire regimes. Fuel loads and simulated fire effects were altered by invasion at all sites. Our analysis of changes in post-fire *P. contorta* density and plant communities at AR demonstrated that invasive plant impacts can have nonlinear threshold responses that result in regime shifts. The nonlinear increase in fuel loads at NZ1, NZ2, and CL suggest that threshold responses are also possible at these sites. We suggest that once *P. contorta* invasions cross a density threshold, a positive feedback with fire is likely to develop (Fig. 6). The positive feedback at high *P. contorta* densities is created by the accumulation of high fuel loads that in turn result in greater soil heating during the fire and thus altered plant communities and high *P. contorta* density post-fire.

As expected, overall fuel loads increased with increasing *P. contorta* invasion age or density. This increase in fuels likely has serious consequences for fire activity and behavior. Other studies have also found fuel loads to increase with woody invaders (Dibble and Rees 2005, Pauchard et al. 2008), which can lead to increased fire intensity (van Wilgen and Richardson 1985). Dead woody and duff fuel loads were low, due to the young age of the invasions but we expect both types of fuel to increase over time with litter accumulation and stand self-thinning.

Our results suggest that changes in fire behavior, and not just changes in pre-fire plant composition, likely contribute to differences in post-fire regeneration success. More severe soil heating with increasing levels of invasion may explain the different post-fire trajectories seen in sites dominated by pines compared to native-dominated sites in our study and others (Holmes et al. 2000, Nuñez and Raffaele 2007, Zalba et al. 2008). If seedbanks and resprouting plants are destroyed by fire, then native regeneration is more dependent on distance to nearest seed source. In invaded shrublands and grasslands, pines may have the advantage in seed dispersal over native shrubs and forbs because their greater height and winged seeds readily allow for long-distance dispersal (Ledgard 2001). We expect that soil heating will become more intense in older invasions once a duff layer and 1000-hour fuel loads develop, as smoldering of these types of fuels contributes greatly to soil heating (Baker 2009).

Soil heating also intensified at NZ2 where management practices cut trees and left them on site. Overall fuel loads were lower in managed plots but the distribution of the fuels (downed dead woody versus standing live woody fuels) affected soil heating. Similarly, in South Africa cutting and leaving invasive pines on site followed by burning led to more negative impacts on native plant communities compared with strategies that burned standing pine trees, likely due to sterilization of the upper soil layers (Holmes et al. 2000). Managers should consider the impact of control actions on potential fire behavior to avoid undesirable vegetation trajectories post-fire.

Overall, we saw more impact of *P. contorta* invasion on fuel loads and fire effects in grasslands than shrublands. Shrublands had higher live woody and litter biomass prior to invasion. Some shrublands already have enough fuel present to burn at moderate to high severities without *P. contorta* invasion, such as manuka in NZ (Perry et al. 2014) and tall shrublands and *N. antarctica* stands in Patagonia (Mermoz et al. 2005). Identifying combinations of plant life-forms and ecosystems most likely to result in a regime shift is important to predict high-impact invaders (Gaertner et al. 2014). We suggest that trees invading into grasslands are most likely to significantly alter fire severity and post-fire vegetation communities.

The changes that we observed in fuel loads and simulated fire effects likely contribute to the different post-fire trajectories of plant communities in areas with different levels of *P. contorta* invasion. At AR, *P. contorta* density increased after fires in areas that were highly invaded (>1000 trees/ha) or plantations (prior to fire). Conversely, in some sites, fire in low-density invaded plots actually resulted in lower *P. contorta* density. This threshold response supports the theoretical model of Buckley et al. (2007) who posit that there is a tension between disturbance promoting invasion and disturbance killing the seed source necessary for invasion. Native plant communities at AR also appeared to have a threshold response to fire based on the level of *P. contorta* invasion. Plant community composition in areas without dense *P. contorta* invasion at AR shifted after fire compared with the composition in unburned plots; however, post-fire plant communities were still dominated by native species in uninvaded as well as in lightly invaded plots. Highly invaded plots (>800 trees/ha) at AR had a different species composition than uninvaded burned or unburned plots, and this composition did not shift after fire (Fig. 5). The maintenance of similar species composition in burned and unburned highly invaded plots, as well as the creation of high *P. contorta* densities post-fire, suggest that dense invasions lead to a new and relatively stable state that is resistant to disturbances such as fire. Thus, these highly invaded communities exhibit “unhelpful resilience” (Standish et al. 2014), which maintains them in an undesirable invaded state. Once communities cross the density threshold it is unlikely that they will return to a native-dominated state without significant management intervention (Cuevas and Zalba 2010). Therefore, management of pine invasions before they reach this threshold is necessary to prevent a new fire regime and vegetation state that may be undesirable.

The observed threshold effect at AR could result from differences in native and *P. contorta* propagule supply due both to differences in pre-fire plant abundance and differences in fire behavior caused by high fuels in older and denser invasions. The more severe fires could hamper herbaceous or shrub regeneration by harming native plant seeds or reproductive organs (Holmes et al. 2000, Zalba et al. 2008), whereas *P. contorta* regenerates well after severe surface fire (Baker 2009) and has seeds that are resistant to higher temperatures than two native Patagonian tree species (Cóbar-Carranza et al. 2015). Additionally, *P. contorta* seedlings do not compete well with grass (Ledgard 2006) and thus more severe fires may create favorable conditions for seedling survival and growth by reducing herbaceous competition. Furthermore, highly invaded areas have lower native plant cover and species richness than uninvaded areas pre-fire (Ledgard and Paul 2008, Taylor et al. 2016b), resulting in fewer native plants to contribute to the seedbank or to resprout after fire.

Although the nature of the studied fires prevented us from thoroughly investigating if a threshold response exists at CL and NZ2, several results are consistent with the potential for a threshold at these sites as well. First, fire did not result in an increase in invasion density in either site. At CL, the burned area was largely uninvaded prior to fire and thus below a potential invasion threshold. Given the older age of the fire at NZ2, the pre-fire invasion density is unknown, however the lack of downed dead *P. contorta* trees at this site suggests that the area was not dominated by a dense mature *P. contorta* stand prior to burning and was thus likely below a potential invasion threshold. Second, fuel loads and soil heating generally increased in a non-linear fashion at all sites, highlighting the potential for abrupt changes in fire behavior and, consequently, *P. contorta* density and plant community composition post-fire. Further study is necessary to determine if the threshold for a positive feedback between pine invasion and fire indeed exists at other sites, how it varies between ecosystems with different historical fire regimes and plant communities, and if it depends on fire properties (e.g. season, duration).

Overall our study shows the strong potential for invasive pines to alter fuel loads, fire effects, and post-fire plant communities, particularly when invasion densities cross a threshold and where woody species represent a novel life form. Although it has been suggested that a positive feedback between pines and fire is inevitable, our data suggest that there is a threshold density below which a positive feedback is unlikely. Above this threshold, fires will likely be more intense and may facilitate a conversion to pine domination. Given the widespread nature of pine invasions and the tendency of these invasions to create dense stands in open habitat that exceed the threshold identified here (Appendix S1: Fig. S2), the interaction between pine invasions and fire will be significant in the future. The implications for management are clear, in areas vulnerable to pine invasions (especially grasslands and sparse shrubland/steppe), the removal of propagule pressure is likely necessary to prevent invading pine densities from crossing thresholds at which increased fuel loads lead to more fire-prone landscapes.

Acknowledgements

We thank Hannah Funke, Maria Theresa Jessen and Sam Wall for field assistance and Pablo Bravo, Jonathan Urrutia and Jorgelina Franzese for help with species identification. KTT, BDM, DBM, and CW were funded by NSF-WildFIRE PIRE, OISE 09667472. AP funded by Fondecyt 1140485, Ministry of Economy ICM P05-002 and CONICYT PFB-23. MAN funded by BioSilva #5 of the MAEyP of Argentina.

References

Albini, F. A., and E. D. Reinhardt. 1997. Improved calibration of a large fuel burnout model. International Journal of Wildland Fire **7**:21-28.

Baker, W. L. 2009. Fire Ecology in Rocky Mountain Landscapes. Island Press, Washington D.C.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gomez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). Global Change Biology **19**:173-183.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. Bioscience **54**:677-688.

Buckley, Y. M., B. M. Bolker, and M. Rees. 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. Ecology Letters **10**:809-817.

Cuevas, Y. A., and S. M. Zalba. 2010. Recovery of native grasslands after removing invasive pines. Restoration Ecology **18**:711-719.

Cóbar-Carranza, A. J., R. A. Garcia, A. Pauchard, and E. Peña. 2014. Effect of *Pinus contorta* invasion on forest fuel properties and its potential implications on the fire regime of *Araucaria araucana* and *Nothofagus antarctica* forests. Biological Invasions **16**:2273-2291.

Cóbar-Carranza, A. J., R. A. García, A. Pauchard, and E. Peña. 2015. Effects of high temperatures in the germination and seed survival of the invasive species *Pinus contorta* and two native species of South Chile. Bosque **36**:53-60.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics **23**:63-87.

Dibble, A. C., and C. A. Rees. 2005. Does the lack of reference ecosystems limit our science? A case study in nonnative invasive plants as forest fuels. Journal of Forestry **103**:329-338.

Dibble, A. C., R. H. White, and P. K. Lebow. 2007. Combustion characteristics of north-eastern USA vegetation tested in the cone calorimeter: invasive versus non-invasive plants. International Journal of Wildland Fire **16**:426-443.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods & Software **27**:233-249.

Gaertner, M., R. Biggs, M. Te Beest, C. Hui, J. Molofsky, and D. M. Richardson. 2014. Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. Diversity and Distributions **20**:733-744.

Holmes, P. M., D. M. Richardson, B. W. Van Wilgen, and C. Gelderblom. 2000. Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. Austral Ecology **25**:631-639.

Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2004. Comprehensive Database of Diameter-based Biomass Regressions for North American Tree Species Page 45. USDA Forest Service Northeastern Research Station, Newtown Square, PA.

Keane, R. E., and L. J. Dickinson. 2007. The photoload sampling technique: estimating surface fuel loadings from downward-looking photographs of synthetic fuelbeds. General Technical Report RMRS-GTR-190. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station. 44 p.

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science **16**:406-411.

Langdon, B., A. Pauchard, and M. Aguayo. 2010. *Pinus contorta* invasion in the Chilean Patagonia: local patterns in a global context. Biological Invasions **12**:3961-3971.

Ledgard, N. 2001. The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. Forest Ecology and Management **141**:43-57.

Ledgard, N. J. 2006. Determining the effect of increasing vegetation competition through fertiliser use on the establishment of wildings in unimproved high country grassland. New Zealand Journal of Forestry **51**:29-34.

Ledgard, N. J., and T. S. H. Paul. 2008. Vegetation successions over 30 years of high country grassland invasion by *Pinus contorta* New Zealand Plant Protection **61**:98-104.

Mandle, L., J. L. Bufford, I. B. Schmidt, and C. C. Daehler. 2011. Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. Biological Invasions **13**:1815-1827.

Mermoz, M., T. Kitzberger, and T. T. Veblen. 2005. Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. Ecology **86**:2705-2715.

Nuñez, M. A., and E. Raffaele. 2007. Afforestation causes changes in post-fire regeneration in native shrubland communities of northwestern Patagonia, Argentina. Journal of Vegetation Science **18**:827-834.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Pauchard, A., R. A. Garcia, E. Peña, C. Gonzalez, L. A. Cavieres, and R. O. Bustamante. 2008. Positive feedbacks between plant invasions and fire regimes: *Teline monspessulana* (L.) K. Koch (Fabaceae) in central Chile. Biological Invasions **10**:547-553.

Pausas, J. G., and J. E. Keeley. 2014. Abrupt climate-independent fire regime changes. Ecosystems **17**:1109-1120.

Perry, G. L. W., J. M. Wilmshurst, and M. S. McGlone. 2014. Ecology and long-term history of fire in New Zealand. New Zealand Journal of Ecology **38**:157-176.

Peña, E., M. Hidalgo, B. Langdon, and A. Pauchard. 2008. Patterns of spread of *Pinus contorta* Dougl. ex Loud. invasion in a Natural Reserve in southern South America. Forest Ecology and Management **256**:1049-1054.

R Core Team. 2014. R: A Language and Environment for Statistical Computing version 3.1.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Raffaele, E., M. A. Nuñez, J. Eneström, and M. Blackhall. 2016. Fire as mediator of pine invasion: evidence from Patagonia, Argentina. Biological Invasions **18**:597-601.

Reinhardt, E. D. 2003. Using FOFEM 5.0 to estimate tree mortality, fuel consumption, smoke production and soil heating from wildland fire. Page P5.2 *in* Proceedings of the Second International Wildland Fire Ecology and Fire Management Congress and Fifth Symposium on Fire and Forest Meteorology. American Meteorological Society, Orlando, Florida, USA.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**:1655-1661.

Richardson, D. M. 1988. Age structure and regeneration after fire in a self-sown *Pinus halepensis* forest on the Cape Peninsula, South Africa. South African Journal of Botany **54**:140-144.

Richardson, D. M., and S. I. Higgins. 1998. Pines as invaders in the southern hemisphere. Pages 450-473 *in* D. M. Richardson, editor. Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge.

Scott, D. F., and D. B. Van Wyk. 1990. The effects of wildfire on soil wettability and hydrological behavior of an afforested catchment. Journal of Hydrology **121**:239-256.

Setterfield, S. A., N. A. Rossiter-Rachor, L. B. Hutley, M. M. Douglas, and R. J. Williams. 2010. Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. Diversity and Distributions **16**:854-861.

Simberloff, D., M. A. Nuñez, N. J. Ledgard, A. Pauchard, D. M. Richardson, M. Sarasola, B. W. Van Wilgen, S. M. Zalba, R. D. Zenni, R. Bustamante, E. Peña, and S. R. Ziller. 2010. Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. Austral Ecology **35**:489-504.

Skaug, H., D. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2013. Generalized Linear Mixed Models using AD Model Builder.

Standish, R. J., R. J. Hobbs, M. M. Mayfield, B. T. Bestelmeyer, K. N. Suding, L. L. Battaglia, V. Eviner, C. V. Hawkes, V. M. Temperton, V. A. Cramer, J. A. Harris, J. L. Funk, and P. A. Thomas. 2014. Resilience in ecology: Abstraction, distraction, or where the action is? Biological Conservation **177**:43-51.

Stevens, J. T., and B. Beckage. 2009. Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). New Phytologist **184**:365-375.

Taylor, K. T., B. D. Maxwell, A. Pauchard, M. A. Nuñez, D. A. Peltzer, A. Terwei, and L. J. Rew. 2016a. Drivers of plant invasion vary globally: evidence from pine invasions within six ecoregions. Global Ecology and Biogeography **25**:96-106.

Taylor, K. T., B. D. Maxwell, A. Pauchard, M. A. Nuñez, and L. J. Rew. 2016b. Native versus non-native invasions: similarities and differences in the biodiversity impacts of *Pinus contorta* in introduced and native ranges. Diversity and Distributions **22**: 578-588.

Turner, M. G., D. B. Tinker, W. H. Romme, D. M. Kashian, and C. M. Litton. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems **7**:751-775.

van Wilgen, B. W., and D. M. Richardson. 1985. The effects of alien shrub invasions on vegetation structure and fire behavior in South African fynbos shrublands: A simulation study. Journal of Applied Ecology **22**:955-966.

Veblen, T. T., A. Holz, J. Paritsis, E. Raffaele, T. Kitzberger, and M. Blackhall. 2011. Adapting to global environmental change in Patagonia: What role for disturbance ecology? Austral Ecology **36**:891-903.

Wagner, S. A., and J. M. Fraterrigo. 2015. Positive feedbacks between fire and non-native grass invasion in temperate deciduous forests. Forest Ecology and Management **354**:170-176.

Zalba, S. M., Y. A. Cuevas, and R. M. Boo. 2008. Invasion of *Pinus halepensis* Mill. following a wildfire in an Argentine grassland nature reserve. Journal of Environmental Management **88**:539-546.

Table 1. Coefficients, *P*-values and the variation explained by the best model (either *P. contorta* density and time since invasion (TSI) or only one explanatory variable where the other is not significant) for fuel overall, each fuel class, and simulated soil temperatures at each site. Density was included in NZ2 models but was not significant in any. TSI signifies the coefficient for time since invasion, Den for total *P. contorta* density, and Mgt for management at NZ2. “-“ signifies no significant relationship between the predictor and response variable (fuel loads or soil heating).

		All fuel	Shrub fuel	Herb fuel	Litter fuel	Dead woody fuel	Surface soil heating	2 cm soil heating
AR - shrubland	Den	0.01	0.02	-	0.07	-	-	-
	P den	0.02	<0.01	-	0.06	-	-	-
	TSI	-	-	-	-	-	-	-
	P TSI	-	-	-	-	-	-	-
	R^2	0.12	0.17	-	0.09	-	-	-
CL - grassland	Den	-	-	-0.001	-	-	-	-
	P Den	-	-	0.02	-	-	-	-
	TSI	0.2	0.32	-	0.18	-	0.13	0.07
	P TSI	<0.01	<0.01	-	<0.01	-	<0.01	<0.01
	R^2	0.55	0.66	0.15	0.30	-	0.47	0.53

NZ1 - grassland	Den	-	-	-	-	-	-	0.004
	P Den	-	-	-	-	-	-	0.03
	TSI	0.26	0.38	0.13	0.24	-	0.11	0.07
	P TSI	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01
	R^2	0.49	0.34	0.29	0.29	-	0.28	0.65
NZ2 - shrubland	Mgt	-0.76	-	-	-0.67	-2.11	-0.78	-0.37
	P Mgt	<0.01	-	-	<0.01	<0.01	<0.01	0.01
	TSI	0.26	0.63	-	0.14	0.28	-0.09	0.05
	P TSI	<0.01	<0.01	-	<0.01	<0.01	<0.01	0.01
	Mgt*TSI	-	-	-	-	0.54	0.28	0.07
	P Mgt*TSI	-	-	-	-	<0.01	<0.01	0.03
	R^2	0.43	0.26	-	0.18	0.55	0.28	0.24

Figure 1. Post-fire *Pinus contorta* density (trees/ha) versus pre-fire *P. contorta* density (trees/ha) at the AR site for all burned 100 m^2 plots sampled. The dashed line shows the 1:1 line where post-fire density equals density pre-fire. The vertical line shows the threshold of 1,000 trees/ha above which post-fire *P. contorta* density was higher than pre-fire *P. contorta* density for all plots measured.

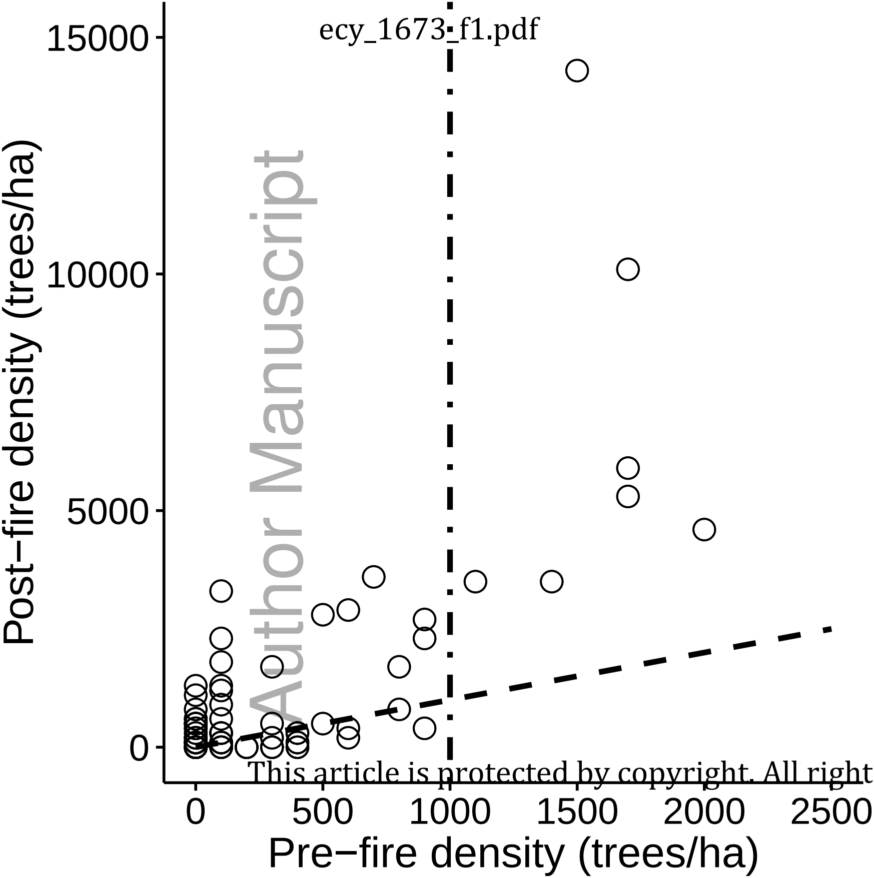
Figure 2. Total fuel (kg/m^2) as a function of time since invasion (CL, A; NZ2, D; NZ1, C) and *Pinus contorta* (PICO) density (AR, B) with the fitted line from the models of each site and the 95% confidence interval shown. The grayscale of the points represents the percent of the total fuel load that was accounted for by *P. contorta* biomass (Percent PICO), with darker points having a higher percent of *P. contorta* biomass relative to other types of fuels.

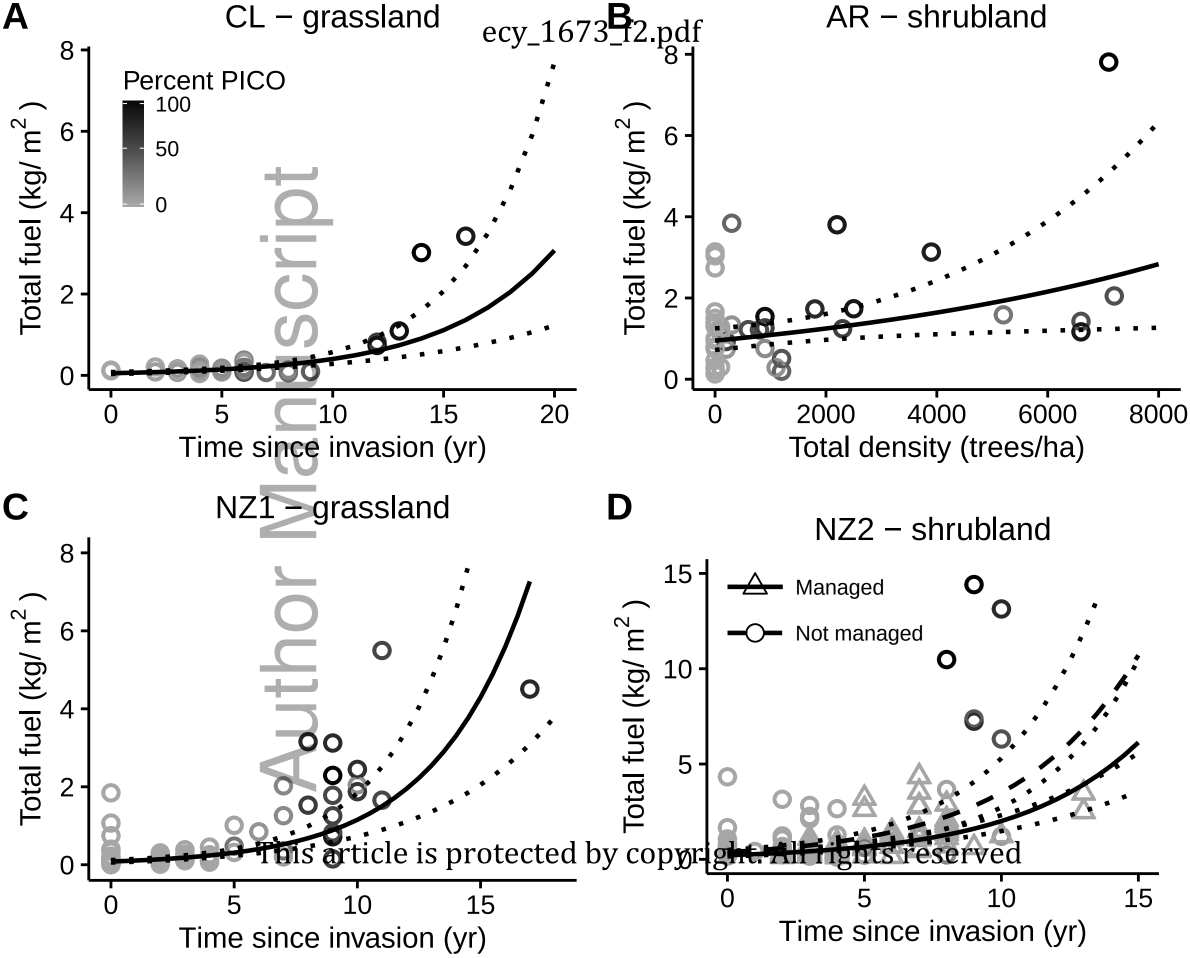
Figure 3. Simulated soil temperature at 2 cm depth as a function of time since invasion (yr) with the fitted line from the models of each site and the 95% confidence interval shown. The grayscale of the points represents the percent of the total fuel load that was accounted for by *Pinus contorta* biomass (Percent PICO), with darker points having a higher percent of *P. contorta* biomass relative to other types of fuels.

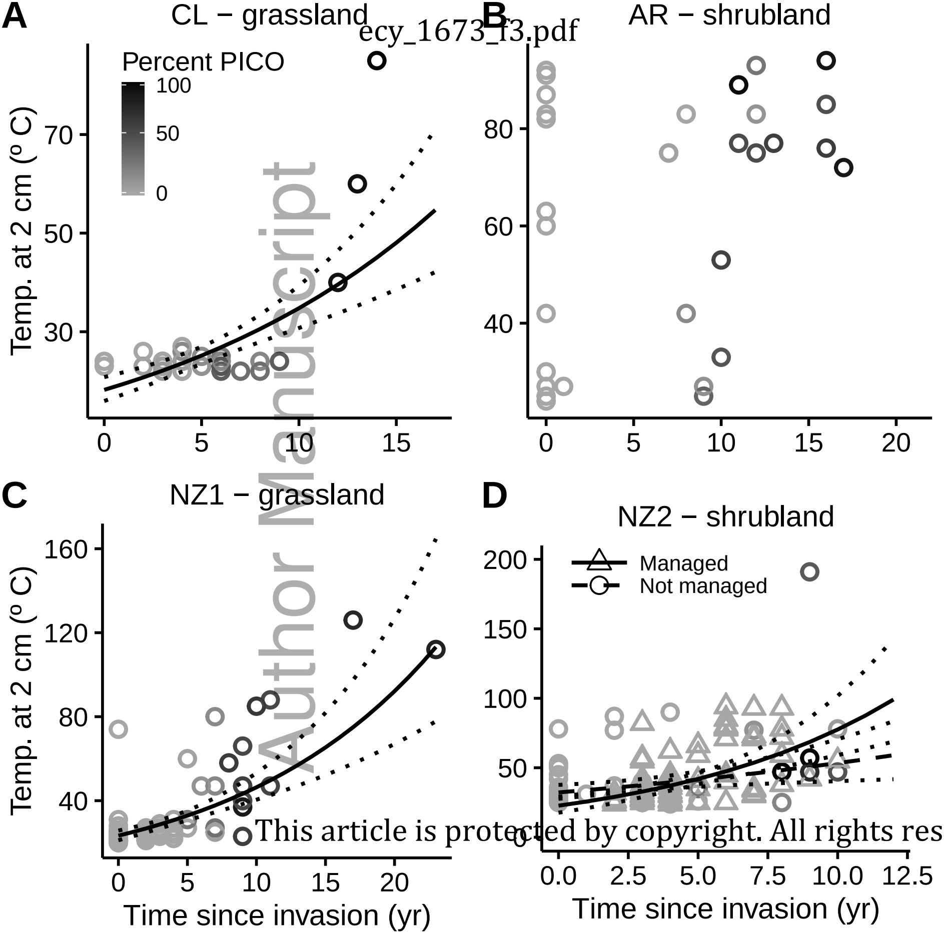
Figure 4. *Pinus contorta* density (trees/ha) in burned (gray fill) and unburned (white fill) 100 m^2 plots at AR (A), CL (B), and NZ2 (C). HIB = high invasion burned, LIB = low invasion burned, NIB = not invaded burned. "Grass" and "shrub" in (C) refer to whether the plot was dominated by grass or shrub pre-fire at NZ2. The older age of the fire at NZ2 prevented us from classifying pre-fire invasion level at this site. Vegetation type was not a significant predictor of *P. contorta* density at AR or CL and thus is not shown.

Figure 5. Principal coordinates analysis of understory plant communities based on the Morista-Horn distance between species compositions of each plot. Filled points represent burned plots and hollow points represent unburned plots. Triangles are plantation plots, squares are invaded plots, and circles are uninvaded plots. Dash-dot line encircles plots that had high cover of *Pinus contorta* before or after fire, dashed line encircles plots that burned and were either uninvaded or had low *P. contorta* densities (a maximum of 200 *P. contorta* individuals per hectare pre-fire as judged by dead stems and aerial photos), and the solid line encircles plots that were unburned and either uninvaded or very lightly invaded (*P. contorta* cover 6 to 12%). The point not in a circle was uninvaded and burned and still had no *P. contorta* when sampled after fire.

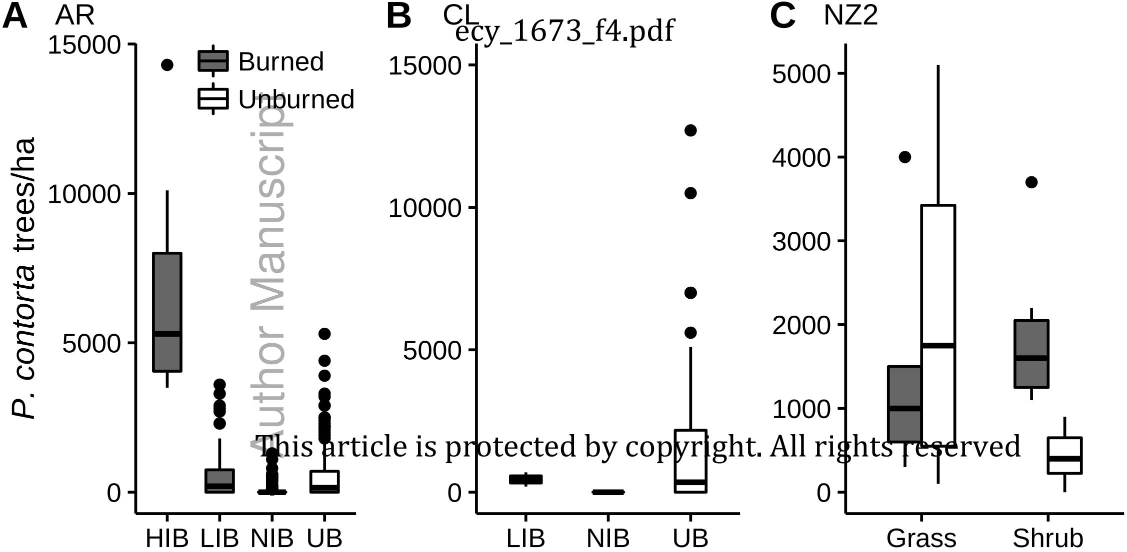
Figure 6. Conceptual diagram demonstrating the effects of *Pinus contorta* invasion and fire on native plant communities, based on data collected in Bariloche, Argentina (AR). The percent cover of each plant type in each ecosystem state is shown in the pie charts (data are means from 5x5 m vegetation plots). Invasion level increases going down through the diagram and the dotted line represents the invasion threshold. As *P. contorta* invasion increases, fuel loads also increase.


15000
10000
5000
0
0
500
1000
1500
2000
2500
Post−fire density (trees/ha)
Pre−fire density (trees/ha)

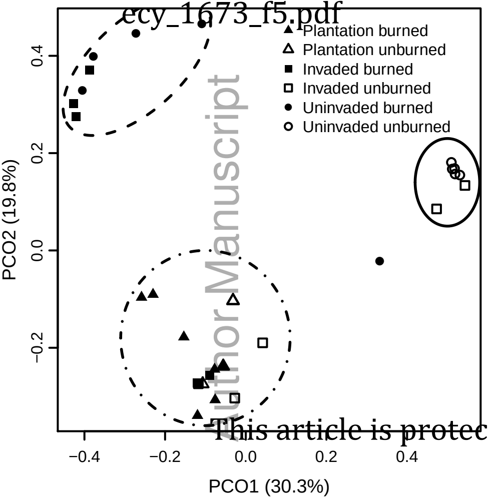

A
CL − grassland
Percent PICO
100
50
0
Total fuel (kg/ m^2)
8
6
4
2
0
0
5
10
15
20
Time since invasion (yr)
B
AR − shrubland
Total fuel (kg/ m^2)
8
6
4
2
0
0
2000
4000
6000
8000
Total density (trees/ha)
C
NZ1 − grassland
Total fuel (kg/ m^2)
8
6
4
2
0
0
5
10
15
Time since invasion (yr)
D
NZ2 − shrubland
Managed
Not managed
Total fuel (kg/ m^2)
15
10
5
0
0
5
10
15
Time since invasion (yr)


A
CL − grassland
Percent PICO
100
50
0
Temp. at 2 cm (º C)
30
50
70
0
5
10
15
B
AR − shrubland
40
60
80
0
5
10
15
20
C
NZ1 − grassland
Temp. at 2 cm (º C)
40
80
120
160
0
5
10
15
20
Time since invasion (yr)
D
NZ2 − shrubland
Managed
Not managed
0
50
100
150
200
0.0
2.5
5.0
7.5
10.0
12.5
Time since invasion (yr)

ecy_1673_f4.pdf



ecy_1673_f5.pdf



ecy_1673_f6.pdf