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Native versus non-native invasions: similarities and differences in the biodiversity impacts of *Pinus contorta* in introduced and native ranges

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ABSTRACT

Aim To determine whether one of the most invasive pine species introduced to the Southern Hemisphere, *Pinus contorta*, has changed plant species richness, composition, diversity, and litter depth where it has invaded into native open forest, shrub steppe and grassland communities and to assess whether changes were similar in its native and introduced ranges.

Location Río Negro Province, Argentina; Aysén and Araucanía Regions, Chile; Greater Yellowstone Ecosystem, USA.

Methods We measured changes in plant species richness, species composition and cover, diversity, and litter depth associated with increasing *P. contorta* tree cover along the invasion front at three sites in the introduced range (Argentina and Chile) and one in the native range (Montana, USA).

Results Plant species richness and cover generally declined with increasing *P. contorta* canopy cover, at similar rates in both the introduced and native ranges. However, plant cover was not affected by *P. contorta* in a forested setting in the introduced range. *P. contorta* invasion explained more of the decline in species richness in the introduced than native range. Native species composition changed more strongly across the invasion gradient in the introduced than native range. Litter depth increased more rapidly with *P. contorta* cover in the native than introduced range.

Main conclusions Our results highlight the potential of pines to alter plant communities whether encroaching from forests in the native range or from plantations in the introduced range. Species richness and plant cover declined in both settings; however, individual species abundance and species composition were more impacted in the introduced range than in the native range. We suggest that invading trees have a greater capacity to cause ecological impacts in their introduced than in their native range, particularly where they represent a novel life-form.

Keywords

biogeography, biological invasions, invasion impact, pine invasion, *Pinus contorta*, tree invasions.

INTRODUCTION

Invasive plants, particularly invasive trees, are well known to have significant impacts on native biodiversity (e.g. Gaertner *et al.*, 2009; Camarillo *et al.*, 2015; Constán-Nava *et al.*, 2015; Lazzaro *et al.*, 2015; Shackleton *et al.*, 2015). Less known, however, is whether the impact differs depending on whether the invasion occurs in an introduced range or in the species' native range. Many plant species grow larger and more densely in their introduced than in their native range (Parker *et al.*, 2013), which would suggest that the potential for negative impacts through competition would be greater

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in the introduced range (Blossey & Notzold, 1995). Invasive species can also alter ecosystems through the introduction of novel traits or life-forms (Levine *et al.*, 2003). When the introduction of a novel trait to the new system causes invader impacts, similar impacts would not be expected in the native range where the trait was not novel. Generally, native species are less likely to spread into adjacent habitats than introduced species (Simberloff *et al.*, 2012). However, few studies have compared the impacts of a species invading new areas in both its native and introduced range. Here, we examine the influence of *Pinus contorta* invasion on plant biodiversity in both its native and introduced ranges when it encroaches into adjacent habitat.

Biogeographic studies that have examined invasive plant impacts on biodiversity have found that the presence of the invader is negatively correlated with native plant species richness or biomass in the introduced range, but neutral or positive correlations were noted in the native range (Inderjit *et al.*, 2011; Callaway *et al.*, 2012; Kaur *et al.*, 2012; Shah *et al.*, 2014). With one exception (Shah *et al.*, 2014), these studies examined plants that were not actively invading adjacent communities in their native range. They also did not measure species richness along an abundance gradient of the study species, but instead compared areas with and without the species present.

Several mechanisms have been suggested to explain differences in invader impacts between the native and introduced ranges. These mechanisms include the following: stronger competitive effects of invading species in the introduced range than in the native range (Callaway & Aschehoug, 2000; Ni *et al.*, 2010); evolution of increased growth rates in the introduced range (Blossey & Notzold, 1995; Siemann & Rogers, 2001); differences in plant–soil feedbacks between ranges (Klironomos, 2002); allelopathy in the litter and soil (Callaway *et al.*, 2008; Thorpe *et al.*, 2009; Ni *et al.*, 2010; Kaur *et al.*, 2012); differences in volatile organic compounds that affect neighbouring plant mortality between ranges (Inderjit *et al.*, 2011); and altered soil nitrogen cycling (Thorpe & Callaway, 2011). Many invader impacts are caused by alteration of the microenvironment, changes in litter abundance or composition, or changes in soil microbial communities (Skurski *et al.*, 2014), although it is unclear how these processes differ between invasions of new habitat in the native versus in the introduced ranges. Other studies have suggested that invader impacts can increase when multiple invasive species facilitate each other (e.g. exotic fungus promoting growth of exotic pines), creating an 'invasional meltdown' (Simberloff & Von Holle, 1999; Nuñez *et al.*, 2013; Dickie *et al.*, 2014).

Pines (genus *Pinus*) are an ideal group to examine whether invasion impacts are similar in the native and introduced ranges. Pines are widely distributed across the Northern Hemisphere, but there are no native pines in the Southern Hemisphere outside of a small area in Indonesia (Rundel *et al.*, 2014). In the 19th and 20th centuries, pines were introduced throughout the Southern Hemisphere for forestry (Richardson & Higgins, 1998). Currently, in both the introduced and native ranges, pines are encroaching into grasslands and shrublands (Richardson & Bond, 1991; Jakubos & Romme, 1993; Simberloff *et al.*, 2010). Generally, pine seeds are widely dispersed by wind and the seedlings are good colonizers of grasslands and shrublands (Richardson, 1998). In areas where they have been introduced and escaped, pines have had measurable impacts on native biodiversity (Ledgard & Paul, 2008; Pawson *et al.*, 2010; Urrutia *et al.*, 2013), nutrient cycling and soil microbial communities (Dehlin *et al.*, 2008; Dickie *et al.*, 2011, 2014), and hydrological cycles (Farley *et al.*, 2005; Fernandez *et al.*, 2009). *Pinus contorta* Dougl. (lodgepole pine), which is native to western North America, has traits that lead to high invasive potential (low seed mass, short juvenile period, and short interval between large seed crops; Rejmánek & Richardson, 1996), and only three pine species introduced to the Southern Hemisphere have been found to invade more regions than *P. contorta* (of 24 species; Rejmánek & Richardson, 2013). *Pinus contorta* was initially introduced for soil erosion control in New Zealand and Patagonia and has since been planted for forestry purposes.

Pinus contorta and other exotic pine species have been associated with biodiversity declines in their introduced ranges both within plantations (Nilsson *et al.*, 2008; Paritsis & Aizen, 2008) and where they have invaded into surrounding natural habitat (Ledgard & Paul, 2008; Dickie *et al.*, 2011; Steers *et al.*, 2013; Urrutia *et al.*, 2013). Impacts have also been observed in the native range where conifer encroachment (hereafter called invasion) into meadows in western North America has altered soil biogeochemical cycles and microbial communities (Griffiths *et al.*, 2005) and lowered meadow plant species diversity (Haugo & Halpern, 2007). Increased density of native slash pines (*Pinus elliottii*) due to fire suppression in the south-east USA was also correlated with lower understorey plant diversity (Brewer, 1998).

Thus, examining *P. contorta* invasions into grassland and shrubland plant communities provides a unique opportunity to compare their impacts on plant diversity between the native and introduced ranges. While impacts have been observed in both ranges, *P. contorta* invades more densely and grows faster in the introduced than native range (Taylor *et al.*, 2016). In addition, Southern Hemisphere plants have no evolutionary history of interacting with species in the Pinaceae. Therefore, we expected that *P. contorta* invasions would have a greater impact on plant communities in the introduced than native range, especially where pines add new functional traits (deep litter with slow decay, continuous tree canopy, and unique mycorrhizal associations) to the community (Rundel *et al.*, 2014).

The consequences that invasive species have on communities vary (Hulme *et al.*, 2013) as a function of the existing species composition and environmental conditions (Ehrenfeld, 2003). Therefore, it is important to study invasion across various sites with different environmental characteristics (Hulme *et al.*, 2013; Kumschick *et al.*, 2015). Previous studies have not compared the biodiversity of plant communities across a gradient of pine invasion in both the native and introduced range, and few have examined how the influence of an invader relates to its abundance (Vilà *et al.*, 2011). In this paper, we examine changes in plant communities and litter depth across a range of invasion intensities (as measured by *P. contorta* cover) at three sites in Patagonia (Argentina and Chile) and one site in the native range (Montana, USA). The specific objectives of this study were as follows: (1) to determine the relationship between changes in *P. contorta* cover and plant species richness, cover, composition, and diversity in native and introduced regions; (2) to assess whether certain life-forms within the native communities were correlated with *P. contorta* invasion; (3) to determine whether litter depth (a potentially important transformative trait) differs across the *P. contorta* invasion gradients; and (4) to assess the relative importance of litter abundance versus *P. contorta* cover in explaining variation in species richness and plant cover. We hypothesized that species richness, plant cover, and diversity would decline with increasing *P. contorta* cover at a faster rate in the introduced range than in the native range. We also expected that litter depth would increase with increasing *P. contorta* cover at all sites and would additionally contribute to reduced native species cover.

METHODS

Study sites

Study sites included locations in Bariloche and El Bolsón, Argentina (AR); Coyhaique Alto, Chile (CL1); Malalcahuello, Chile (CL2; all introduced range); and south-western Montana, United States of America (USA; native range; see Fig. S1 and Table S1 in Supporting Information for climate and other environmental characteristics of all sites). The sites in Argentina (AR) were combined because they had similar shrub steppe communities, dominated by *Festuca pallescens*, *Mulinum spinosum* and *Acaena* spp. (see Table S2 for full species lists). Adjacent *P. contorta* plantations were established between 20 and 35 years ago. Coyhaique Alto, Chile (CL1), was a grass steppe community dominated by *Festuca pallescens, Baccharis magellanicum* and *Acaena intergerrima*. The source *P. contorta* plantations at CL1 were 17–26 years old. The second site in Chile was located in the Reserva Nacional Malalcahuello (CL2) and was dominated by sparse *Araucaria araucana* forest with areas of *Nothofagus antarctica* and an understorey composed of *Festuca scabriuscula*, *Chusquea culeou* and *Gaultheria* species. Here, the source populations were trial forestry plots planted 43 years ago (Peña *et al.*, 2008; Urrutia *et al.*, 2013). The site in Montana (USA) included sagebrush steppe dominated by *Artemisia tridentata*, *Festuca idahoensis* and *Stipa* species. Most of the *P. contorta* encroachment into the sagebrush steppe at this site has occurred in the last 50 years (Patten, 1969). *Pinus contorta* encroachment into nearby grasslands has been attributed to long-term climatic change (Jakubos & Romme, 1993), although encroachment is generally rare in this region. There was no evidence of recent fire in any site. Nomenclature follows Lesica (2012) for USA and Zuloaga *et al.* (2008) for Argentina and Chile.

Field sampling

Plots were randomly located within sites and stratified by *P. contorta* canopy cover. The *P. contorta* cover gradient was positively correlated with the age of invading trees and their distance from the seed source plantation or native forest. Non-invaded plots were constrained to areas dominated by vegetation types known to be invaded by *P. contorta* at these same sites (Peña *et al.*, 2008; Langdon *et al.*, 2010; Taylor *et al.*, 2016).

Ocular canopy cover data were collected for every vascular plant species in each plot (five by five metres); every species had the potential to account for 100 percentage cover. In the only site with native trees (CL2), we did not include cover of overstorey tree species (mainly *Araucaria araucana*) in the analyses. At each plot, we estimated mean litter depth from five depth measurements. *P. contorta* canopy cover was recorded in the centre of each plot with a spherical densiometer. Sample sizes were 13 in AR, 20 in CL1, 19 in CL2 and 21 in USA, across a *P. contorta* canopy cover gradient from zero to nearly 100 percentage.

Studies that experimentally add an invasive plant and record impacts on plant communities over time are superior to the chronosequence approach that we took, but the years required for this type of experiment made it logistically unfeasible. Our sites were relatively homogenous and the invasions progressed uniformly from the plantations (Fig. S1), so we are confident that the main difference between invaded and non-invaded plots in any study site was largely a result of *P. contorta* presence. The continuous wave of invasion, as demonstrated by the decreasing age of trees with increasing distance from the plantation/forest edge (rather than patchy invasion), suggests that *P. contorta* establishment was not influenced by minor differences in local species composition or abundance (Pauchard A., pers. comm.).

Statistical analysis

We used *P. contorta* percentage cover as the explanatory variable in all analyses (Pawson *et al.*, 2010). Relative species richness (percentage of maximum at that site) was modelled with linear regression as a function of *P. contorta* cover for each site individually. We used relative species richness to account for overall differences in richness between sites. Shannon diversity was calculated for each plot (Oksanen *et al.*, 2013) and then modelled with linear regression as a function of *P. contorta* cover for each site individually. Additionally, data from all sites were combined and relative species richness and diversity were modelled as a function of

P. contorta cover, site and their interaction to determine whether the rate of change of richness and diversity differed between sites.

Species composition at each site was examined by calculating the Bray–Curtis distance between plots based on all species cover (excluding *P. contorta*). Permutational multivariate analysis of variance (PERMANOVA) was used to determine whether *P. contorta* cover was significantly related to species composition as represented by the Bray–Curtis distances. Linear regression was used to model total plant cover, plant cover by life-form (cushion, grass, forb, shrub), exotic plant cover, and cover of each species individually in response to *P. contorta* cover for each site separately. A Poisson regression was used to model exotic species richness as a function of *P. contorta* cover for each site. Finally, total plant cover data from all sites were combined to test for differences in the relationship between *P. contorta* cover and total cover between sites. To control for differences between sites in overall productivity, relative total plant cover (cover of each plot divided by maximum plant cover at that site) was modelled with linear regression as a function of *P. contorta* cover, site and their interaction.

Two potential mechanisms by which *P. contorta* could influence plant communities are through an increase in shade (measured here as canopy cover) and an increase in persistent litter (measured as litter depth). To explore these possibilities, we first modelled litter depth as a function of *P. contorta* cover at each site individually and then in a model that combined data from all sites to determine differences in litter accumulation rates with *P. contorta* invasion between sites. We then modelled relative species richness (percentage of maximum), total plant cover and plant cover by life-form (grass, forb, shrub) as a function of both *P. contorta* cover and litter depth. We used commonality analysis (Ray-Mukherjee *et al.*, 2014) to improve our interpretation of the multiple regression results, given the collinearity between *P. contorta* cover and litter depth (R^2 between 0.16 and 0.62, Table 1). Commonality analysis separates the variance of the model R^2 into unique and shared effects of the predictors (Ray-Mukherjee *et al.*, 2014). Commonality analysis allowed us to determine how much of the variance in the responses was explained by only *P. contorta* cover, only litter depth or both due to collinearity. All statistical analysis was performed in R (R Core Team, 2014).

RESULTS

Species richness and diversity

Relative species richness declined with increasing *P. contorta* cover at all sites, but *P. contorta* cover explained more than twice the variance in species richness at the introduced sites than at the native site (Table 1; Fig. 1(a)). In the combined model, the rate of decline in relative species richness with increasing *P. contorta* cover did not differ between the USA (native range) and introduced range sites ($F_{3,65} = 1.33$, $P = 0.272$). There was a significant negative relationship between Shannon diversity and *P. contorta* cover at CL2 ($t = -2.4$, d.f. = 17, $P = 0.028$) but no relationship at other sites.

Table 1 Results from models from each site of species richness, grass cover, forb cover, shrub cover, total plant cover and litter depth as a function of *Pinus contorta* cover. – indicates that that life-form was not present at the given site or the model was not significant at the alpha equals 0.05 level. R^2 is adjusted R^2. Results from cushion plants were not shown because there was no significant relationship with *Pinus contorta* cover at any site ($P > 0.05$). See Fig. S1 and Table S1 for full site descriptions (AR, CL1, CL2, USA).

	AR	CL1	CL2	USA
Relative species richness				
Cover	−0.492	−0.484	−0.394	−0.219
SE	0.119	0.11	0.118	0.094
t-value	−4.145	−4.4	−3.325	−2.317
P-value	0.002	<0.001	0.004	0.032
R^2	0.57	0.49	0.359	0.18
Litter depth				
Cover	0.012	0.021	0.011	0.029
SE	0.007	0.004	0.004	0.007
t-value	1.823	5.696	2.840	4.385
P-value	0.096	<0.001	0.011	<0.001
R^2	–	0.623	0.282	0.477
Grass cover				
Cover	−0.042	−0.176	−0.201	−0.061
SE	0.013	0.069	0.063	0.105
t-value	−3.159	−2.555	−3.185	−0.577
P-value	0.009	0.02	0.005	0.571
R^2	0.428	0.225	0.337	–
Forb cover				
Cover	−0.003	−0.019	−0.014	−0.185
SE	0.01	0.005	0.007	0.078
t-value	−0.316	−3.993	−1.997	−2.376
P-value	0.758	0.001	0.062	0.028
R^2	–	0.440	–	0.189
Shrub cover				
Cover	−0.421	–	0.071	−0.297
SE	0.09	–	0.137	0.104
t-value	−4.668	–	−0.514	−2.859
P-value	<0.001	–	0.614	0.01
R^2	0.634	–	–	0.264
Total cover				
Cover	−0.435	−0.236	−0.177	−0.543
SE	0.095	0.075	0.126	0.169
t-value	−4.571	−3.158	−1.406	−3.208
P-value	<0.001	0.006	0.178	0.005
R^2	0.624	0.321	–	0.317

Plant composition

Pinus contorta cover was significantly related to differences in species composition between plots within sites in both introduced and native ranges (Table 2). However, *P. contorta* cover explained twice as much of the similarity in species

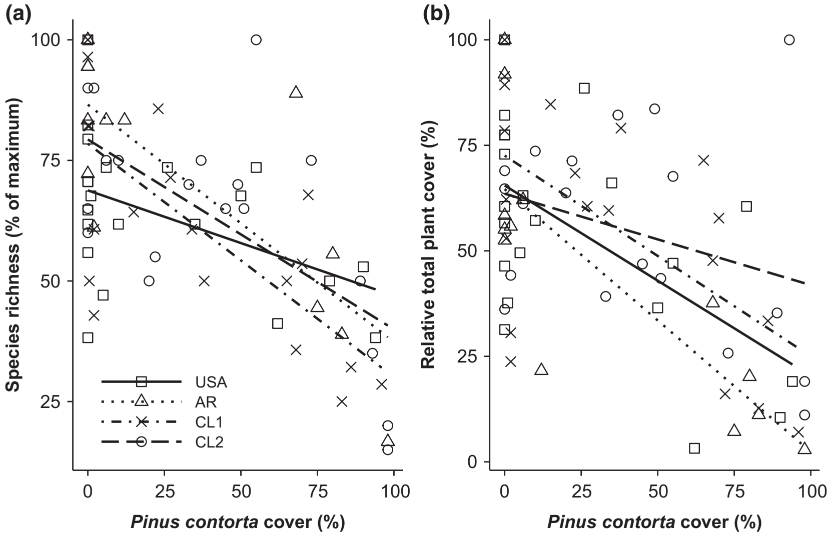

Figure 1 Relative species richness (a) and relative total plant cover (b) plotted against *Pinus contorta* cover (%) for each site with the fitted line from the combined models containing all data from all sites. Statistically, the slopes of the lines do not differ between the native site (USA) and any introduced site (AR, CL1, CL2) for both relative species richness and relative total plant cover ($P > 0.05$). Solid line and squares represent USA, dotted line and triangles represent AR, dot dashed line and x's represent CL1, and long dashed line and circles represent CL2. See Fig. S1 and Table S1 for full site descriptions (AR, CL1, CL2, USA).

Table 2 Results from the PERMANOVA (permutational multivariate analysis of variance) for each site that models Bray–Curtis distance between plot species composition as a function of *Pinus contorta* cover. AR (shrubland), CL1 (grassland) and CL2 (open forest) are introduced range sites, and USA (shrubland) is the native range site. See Fig. S1 and Table S1 for full site descriptions.

	P. contorta cover	
Site	R^2	*P*-value
AR	0.31	0.001
CL1	0.21	0.003
CL2	0.12	0.023
USA	0.11	0.023

composition between steppe plots in the introduced range (AR and CL1) than in the native range (USA; Table 2).

When examining relationships between *P. contorta* cover and individual species cover, we found that at all introduced sites most of the significant relationships ($P < 0.05$) were negative (Fig. 2; Table S3). In contrast, in the native range the only species (*Poa palustris*) that had a significant relationship with *P. contorta* cover had higher abundance in more highly invaded plots (Fig. 2; Table S3). At AR, *P. contorta* cover had a significant negative relationship with the cover of three native species (14% of the species present in at least three sampled plots), including the most frequently occurring shrub species (*Mulinum spinosum*). At CL1, *P. contorta* cover had a significant negative relationship with cover of fourteen species (37% of the species present in at least three sampled plots), including the most common grass species *Festuca pallescens* (Fig. S2). Only the native *Viola reichei* had a significant positive relationship with *P. contorta* cover at CL1 (Fig. 2; Table S3). At CL2, *P. contorta* cover had a significant negative relationship with two species (7% of species present in at least three plots), including the most common grass species (*Festuca scabriuscula*; Fig. S2).

Changes in plant cover by life-form and origin

Pinus contorta cover was negatively correlated with total plant cover at all sites except CL2 (Fig. 3; Table 1). In the combined model, the relationship between *P. contorta* cover and relative total cover did not differ between the native site (USA) and introduced sites ($F_{3,65} = 1.27$, $P = 0.293$; Fig. 1). Analysis of the sites separately showed *P. contorta* cover was negatively correlated with, grass cover at AR, CL1, and CL2 (Table 1), forb cover at CL1 and USA (Table 1), and shrub cover at USA and AR (Table 1).

Exotic species cover other than *P. contorta* was low (<2%), although some exotic species were frequently present in sampled plots (e.g. *Rumex acetosella* in introduced range sites; Table S2). Seven exotic species were found at AR and CL1, three at CL2, and six at USA. Exotic plant cover decreased with increasing *P. contorta* cover at CL1 ($F_{1,18} = 8.43$, $P = 0.010$). Exotic cover at all other sites and exotic richness at all sites were not correlated with *P. contorta* cover ($P > 0.05$ for all comparisons).

Relationship between *P. contorta* cover and litter depth

Pinus contorta cover was positively correlated with litter depth at CL1, CL2 and USA but not at AR (Table 1; Fig. 4). The relationship between litter depth and *P. contorta* cover did not differ between USA and CL1 ($t = -1.02$, d.f. = 65, $P = 0.312$), but litter depth increased more slowly with invasion at CL2 than at USA ($t = -2.33$, d.f. = 65, $P = 0.023$; Fig. 4). Litter included pine needles, but also dead material from native grasses and shrubs.

Mechanism of impact

Pinus contorta cover alone explained more of the variance in relative species richness and plant cover than did litter depth

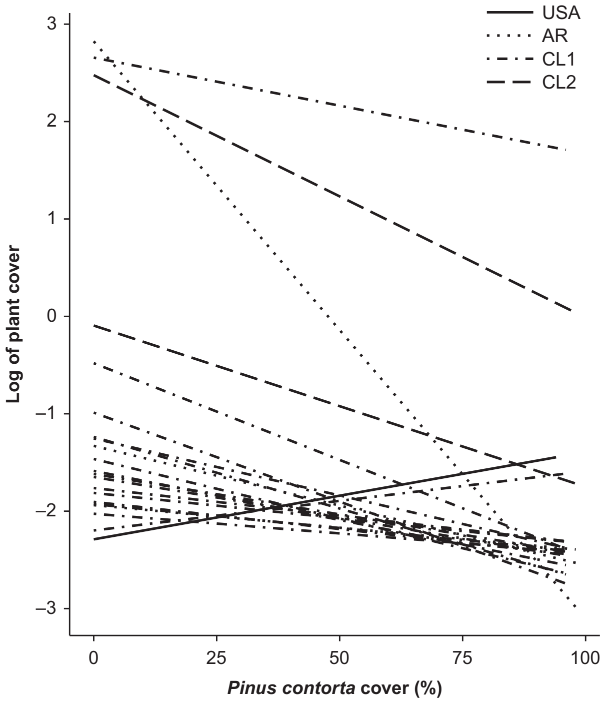

Figure 2 Fitted lines from linear models of the natural log of cover for all individual species as a function of *Pinus contorta* cover. Each line represents one species, and lines are only shown for species that had a significant relationship with *Pinus contorta* cover ($P < 0.05$). All species, their slopes, model *P*-values and sample sizes are reported in Table S3. Solid lines represent species found in the United States, dotted lines represent species found in AR, dot dashed lines represent species found in CL1, and long dashed lines represent species found at CL2. See Fig. S1 and Table S1 for full site descriptions (AR, CL1, CL2, USA).

alone (Fig. 5). The only case where litter depth explained more variance than *P. contorta* cover was for forb cover at CL2 (*Araucaria araucana* forest). In all cases, a significant amount of variance was explained jointly by *P. contorta* cover and litter depth (Fig. 5).

DISCUSSION

Pinus contorta cover was negatively correlated with plant species richness and cover at every study site (except plant cover at CL2), suggesting that pine invasion impacts on species richness and cover are similar in native and introduced ranges. However, species composition and individual species cover were more affected by *P. contorta* invasion in the introduced than native range. Additionally, invasions reach high levels of *P. contorta* cover more quickly in the introduced range than in the native range due to higher growth rates (Taylor *et al.*, 2016). Therefore, although the relationships between *P. contorta* cover and plant species richness and cover were similar between sites, the declines in these properties may occur faster in the introduced than native range.

The negative correlation between *P. contorta* cover and species richness agrees with previous studies in New Zealand (Ledgard & Paul, 2008) and Chile (Urrutia *et al.*, 2013; Franzese, J. & Pauchard, A., pers. comm.). Thus, there is mounting evidence that pine invasions into adjacent habitats will lead to declines in native plant species richness. *Pinus contorta* cover explained more of the decline in richness at the introduced steppe sites dominated by grass and shrubs where trees are likely a novel life-form (AR; CL1) than at the introduced forested site (CL2) or in the native range (USA). Species in the steppe are likely less tolerant of shade and litter accumulation than those in the *A. araucana* forest. We saw a consistent decline in richness with increases in *P. contorta* cover, unlike the hump-shaped response observed with *Pinus nigra* invasions in New Zealand (Dickie *et al.*, 2011). Neither ours nor the New Zealand study identified a threshold at which species richness changed rapidly, suggesting that pine's influence on species richness scales with invader abundance and tipping points are unlikely. Although species richness declined with increasing *P. contorta* cover, at most sites we did not see a significant decrease in Shannon diversity. This finding contradicts other studies, with a broader range of species, that found lower diversity in invaded plots than in non-invaded plots (Hejda *et al.*, 2009; Vilà *et al.*, 2011).

Contrary to expectations, the rate of species loss associated with increasing *P. contorta* cover was the same in the native and introduced ranges. Other studies examining species richness associated with invasive species in their introduced and native ranges found a neutral or positive relationship between the invader and species richness in the native range (Inderjit *et al.*, 2011; Kaur *et al.*, 2012; Shah *et al.*, 2014). Our results may differ because we assessed species richness associated with an active *P. contorta* invasion in the native range, whereas in other studies, the target species was invading in the introduced but not native range. Similar decreases in species richness in native plant communities following *P. contorta* invasion, and native woody encroachment in general, have also been observed (Haugo & Halpern, 2007; Ratajczak *et al.*, 2012). Therefore, results from this study and previous work suggest that conifer invasion of treeless areas is likely to decrease species richness, even in the native range.

Relative total plant cover decreased significantly with increasing *P. contorta* cover at the same rate in all sites. At all the grassland or shrubland sites, the dominant life-form (grass in CL1 and shrubs in AR and USA) declined significantly with higher *P. contorta* cover. Additionally, at all introduced sites, cover of dominant species had negative relationships with *P. contorta* cover. Changes in the dominant life-forms and species, as a result of invasion, will likely alter litter quantity and quality, which could result in cascading effects on belowground communities (Bardgett & Wardle, 2010; Dickie *et al.*, 2011). The switch from grasslands or shrublands to areas with high tree cover and little shrub or grass cover in AR, CL1 and USA, may also affect animal communities that depend on grass and shrubs for habitat (Pawson *et al.*, 2010). The only site with native forest (CL2)

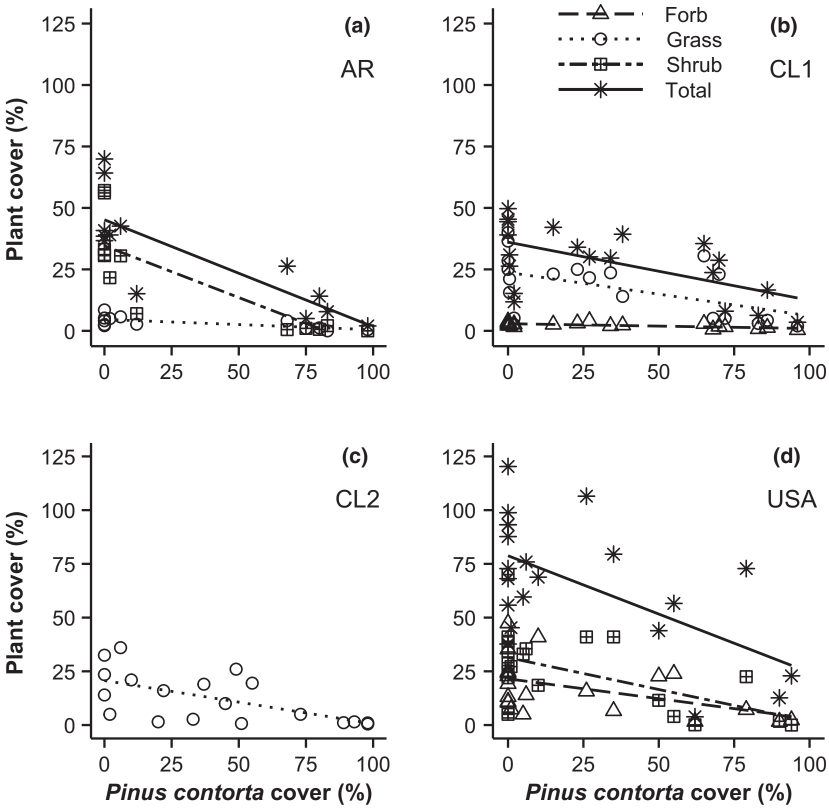

Figure 3 Relationship between *Pinus contorta* cover and plant cover by life-form and total plant cover at introduced (AR (a), CL1 (b), CL2 (c)) and native (USA (d)) sites. Only lines for relationships between *Pinus contorta* cover and life-forms that were significant at the $P = 0.05$ level (Table 1) are shown. Dashed lines and triangles represent forb cover, dotted lines and circles represent grass cover, dot dashed lines and squares represent shrub cover, and solid lines and asterisks represent total plant cover. See Fig. S1 and Table S1 for full site descriptions (AR, CL1, CL2, USA).

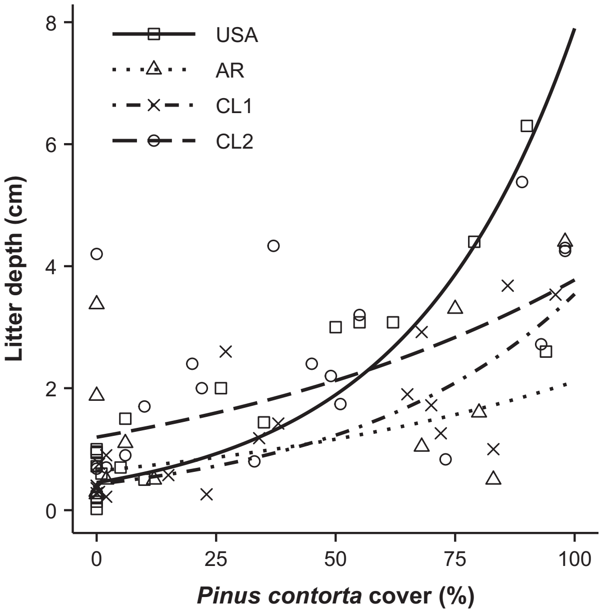

Figure 4 Litter depth and cover of *Pinus contorta* at the three introduced (AR, CL1, CL2) and one native (USA) sites, with the fitted lines from the linear model of the natural log of litter depth (back transformed to original scale). Solid line and squares represent USA, dotted line and triangles represent AR, dot dashed line and x's represent CL1, and long dashed line and circles represent CL2. See Fig. S1 and Table S1 for full site descriptions (AR, CL1, CL2, USA).

showed no significant decline in total plant cover with increasing *P. contorta* cover, potentially because many native species growing in this forested site are shade tolerant. Another study also found less impact of *P. contorta* invasion on plant communities in an *A. araucana* forest than in a Patagonian steppe site (Franzese, J. & Pauchard, A., pers. comm.). A trend of greater invader impact on species richness in shrublands than forests has been observed in Mediterranean-type ecosystems as well (Gaertner *et al.*, 2009). Our results support the concept that impacts on plant communities depend on the traits of both the invader and the native communities (Levine *et al.*, 2003; Maron & Marler, 2008; Kumschick *et al.*, 2015).

Impacts on species composition and individual species differed between the native and introduced range, suggesting that species richness alone is not the best metric to understand plant community change following non-native plant invasions (Parker *et al.*, 1999). The most pronounced differences in plant species composition across the invasion gradient in our study were observed in the introduced range (Table 2). Cover of 19 individual species declined as *P. contorta* cover increased in the introduced range, while in the native range no individual species had a significant negative relationship with *P. contorta* cover (Fig. 2; Table S3). This difference between native and introduced ranges is exemplified by the grass genus *Festuca,* which was the most abundant grass genus at all sites, but only declined in abundance with increasing *P. contorta* cover in the introduced range

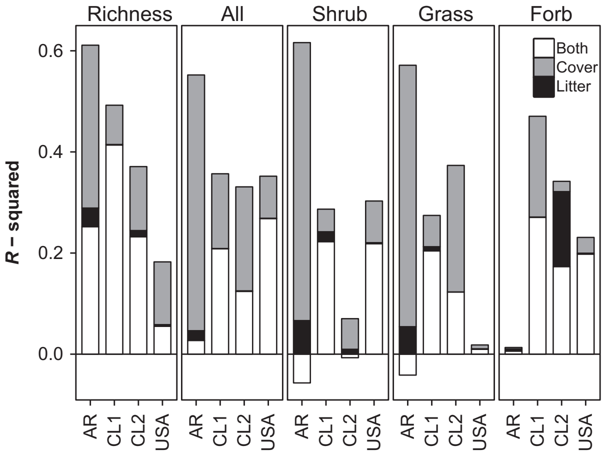

Figure 5 Results from the commonality analysis showing the percentage of the variance explained (R-squared, also known as the coefficient of determination) by either *Pinus contorta* cover or litter depth, or shared explanatory power due to collinearity, in the full model for each site. The responses include relative species richness (richness), all plant cover (All), shrub cover, grass cover and forb cover for each site. See Fig. S1 and Table S1 for full site descriptions (AR, CL1, CL2, USA).

(Fig. S2). Although species with high or intermediate abundance were more likely to decline with *P. contorta* invasion in the introduced than native range, there were locally rare species at the USA site that were sensitive to invasion (Table S2). Overall, differences in the impacts on species composition and individual species cover between native and introduced ranges suggest that Rocky Mountain grassland and shrubland communities, which have a long history of co-evolution with pines, may be less fundamentally altered by pine invasions. While invaded areas will likely experience a decline in species richness, species composition is expected to remain similar between invaded and uninvaded areas, at least for the first 50 years of invasion.

We saw little colonization by forest understorey species in *P. contorta* invaded plots in the native range. This observation differs from a study in Oregon, USA, in which native conifer invasion into subalpine meadows was associated with colonization of forest understorey species within two decades of tree establishment (Haugo & Halpern, 2007). Perhaps such spread of forest understorey species at our USA site requires more than 50 years. Given that the Pinaceae is a novel family in Patagonia, it is unclear whether understorey species from native *Nothofagus* forest will colonize pine-dominated forest, especially in the steppe (AR and CL1) where dispersal distances to the nearest forest may be long.

Several studies have found increased exotic species richness correlated with the presence of an invasive species in the introduced range (Kaur *et al.*, 2012; Shah *et al.*, 2014). We saw no support for this type of 'invasional meltdown' (Simberloff & Von Holle, 1999; Dickie *et al.*, 2014). However, a study in New Zealand found only exotic species persisting in the understorey of a *P. contorta* invasion 30 years after introduction (Ledgard & Paul, 2008). Another study in New Zealand found that legacy impacts from pine invasions on soil processes promoted exotic grasses and forbs (Dickie *et al.*, 2014). Therefore, the potential for *P. contorta* to promote invasion by herbaceous exotic species is not consistent between sites.

Often native communities are altered as a result of the different litter quantity or quality from exotic plants (Skurski *et al.*, 2014). The sharpest increase in litter depth with increasing *P. contorta* cover was seen in the native range (USA; Fig. 4), potentially because invasions in the United States are at least 15 years older than invasions in the introduced range, so there has been more time for litter to accumulate. Alternatively, the deeper litter could be due to differences in decomposition rates related to the colder conditions in Montana (USA) than the Southern Hemisphere sites (Table S1). The changes in litter depth and quality may result in changes to soil processes or biotic communities (Dehlin *et al.*, 2008; Dickie *et al.*, 2014; de Oliveira *et al.*, 2014). Increased litter abundance may also create a more continuous wildfire fuel bed in the steppe ecosystems where traditionally bareground patches have limited fire size (Baker, 2009; Paritsis *et al.*, 2013).

Although litter accumulation is likely a mechanism driving impact, the results of our commonality analysis show that *P. contorta* cover alone explains more of the variance in species richness and plant cover than does litter depth alone. Therefore, increased shade is a strong mechanism causing changes in the plant community; although as litter accumulates over time, as these young pine trees age, litter depth and influence on biogeochemical processes could become more important in explaining native plant response. At the forested site (CL2), a decline in forb cover was more related to litter depth than *P. contorta* cover, potentially because forb species at this site may be adapted to low light situations, whereas pine litter chemistry likely differs from native species litter. In fact, *Pinus ponderosa* litter limited germination of several native Patagonian grass species (Raffaele & Schlichter, 2000). At all sites, a large amount of variability in species richness and plant cover was jointly explained by *P. contorta* cover and litter depth. The overlap in explanatory power between litter depth and canopy cover is likely because litter is a measure of leaf area index which also represents shade. Therefore, these results highlight the need for manipulative experiments to separate the mechanisms of invader impacts.

Our results, along with those of previous studies, suggest that pine invasions will likely have significant impacts on plant communities in native and introduced ranges. We found that high *P. contorta* cover led to a decline in species richness whether it occurred in its native or introduced range. Impacts on native communities scaled with *P. contorta* abundance and no thresholds were found beyond which rapid declines in species richness or cover occurred. Contrary to previous biogeographic studies of plant invasion impacts, trends in species richness and plant cover were similar in the introduced and native ranges. Thus, biogeographic novelty alone does not govern all aspects of invader impact. Presence of a novel life-form and specific species traits may determine invader impact on recipient plant communities. Nonetheless, fundamental components of the plant communities, such as species composition, were more altered by pine invasions in the introduced than native range. Therefore, for some characteristics, native invaders may have less capacity than exotic invaders to cause significant impacts. These results highlight the need to examine multiple metrics of plant communities in order to fully understand invader impacts. In addition, to elucidate the importance of specific mechanisms of pine invasion impact on native ecosystems, management of pine invasions could be integrated with experimentation by designing treatments and follow-up monitoring.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Photographs of *Pinus contorta* invasion at all study sites.

Table S1 Site descriptions.

Table S3 Results from the significant models of individual species cover as a function of *Pinus contorta* cover.

Figure S2 Relationship between *Festuca* spp. and *Pinus contorta* at all sites.

Table S2 List of all species recorded in each site.

BIOSKETCH

The research team is generally focused on understanding the processes driving the spatial distribution, dynamics, spread and impacts of non-native plant species, with a recent focus on pine invasions across the globe. K.T.T., B.D.M. and L.J.R. are part of the Weed and Invasive Plant Ecology and Management Group at Montana State University (http://weedeco.msu.montana.edu).

Author contributions: K.T.T., B.D.M., A.P. and M.N. conceived of the ideas. B.D.M. funded the study. K.T.T. and B.D.M. collected the data. K.T.T. analysed the data with input from B.D.M. and L.J.R. K.T.T. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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