RESEARCH PAPER

Drivers of plant invasion vary globally: evidence from pine invasions within six ecoregions

Kimberley T. Taylor[1]*, Bruce D. Maxwell[1], Aníbal Pauchard[2,3],
Martin A. Nuñez[4], Duane A. Peltzer[5], André Terwei[2,3] and Lisa J. Rew[1]

[1]*Land Resources and Environmental Sciences Department, Montana State University, Bozeman, MT 59717, USA,* [2]*Facultad de Ciencias Forestales, Universidad de Concepción, Casilla 160-C, Concepción, Chile,* [3]*Institute of Ecology and Biodiversity, Chile,* [4]*Grupo de Ecología de Invasiones, INIBIOMA, CONICET, Universidad Nacional del Comahue, Quintral 1250, San Carlos de Bariloche CP 8400, Argentina,* [5]*Landcare Research, PO Box 69040, Lincoln 7640, New Zealand*

*Correspondence: Kimberley T. Taylor, Land Resources and Environmental Sciences Department, Montana State University, Bozeman, MT 59717, USA.
E-mail: Kimberleytaylor7@gmail.com

ABSTRACT

Aim To determine biotic and abiotic controls on pine invasion globally within six ecoregions that include both introduced and native ranges.

Locations Río Negro province, Argentina; Aysén and Araucanía regions, Chile; South Island (two ecoregions), New Zealand; Greater Yellowstone ecosystem, USA.

Methods We quantified tree abundance and size across invasion fronts of the widespread invasive tree species *Pinus contorta* at each of the nine sites, encompassing both the native and introduced range. We also determined the relative importance of propagule pressure, abiotic characteristics and biotic factors for invasion success. Finally, key plant population metrics such as individual tree growth rates and reproductive effort were compared between native and introduced ranges.

Results *Pinus contorta* density decreased with increasing distance from source population in all cases, but the importance and shape of this relationship differed among sites due, primarily to biotic factors. For example, areas dominated by native southern beech forest (*Fuscospora cliffortioides* or *Nothofagus* spp.) were not invaded, and this biotic resistance was not overcome by high propagule pressure. In contrast, shrublands were more highly invaded than grasslands, contradicting previous generalizations about pine invasions. *Pinus contorta* growth was faster, age to maturity was earlier and reproductive effort was higher in the introduced ranges compared with the native range, suggesting a demographic shift towards more rapid population growth in introduced regions. Climatic differences between the ranges may explain, at least in part, the observed pattern.

Main conclusions We demonstrate that although biological invasions are driven by propagule pressure across different ecoregions, these processes interact strongly with biotic factors. Intriguingly, our results suggest that propagule pressure may become less important than biotic interactions as invasions proceed. Multi-region studies including both the native and introduced ranges provide unparalleled opportunities for understanding how these interactions change among regions as invasions proceed.

Keywords
Biogeography, biological invasions, biotic resistance, New Zealand, non-native tree invasion, Patagonia, *Pinus contorta*, propagule pressure, tree population dynamics.

INTRODUCTION

Biological invasions generally, and non-native tree species in particular, are rapidly increasing components of global change that can have profound impacts on ecosystems (Richardson *et al.*, 2014). Pines (genus *Pinus*) have been widely introduced across the Southern Hemisphere, where several species have become highly invasive (Richardson *et al.*, 1994; Simberloff

et al., 2010) and have strongly altered native biodiversity (Ledgard & Paul, 2008; Pawson *et al.*, 2010; Urrutia *et al.*, 2013), belowground communities (Dehlin *et al.*, 2008; Dickie *et al.*, 2011, 2014) and hydrological processes (Simberloff *et al.*, 2010). The widespread introduction of pines to diverse regions of the Southern Hemisphere is an ideal 'natural experiment' for determining which processes drive pine invasions and whether these processes are globally consistent or context dependent (Gundale *et al.*, 2014b). Some species also invade open habitats in their native range (Simberloff *et al.*, 2012), thus enabling direct comparisons of invasions in both the native and introduced ranges and generating insights into the processes and mechanisms underlying invasions that are not possible using more biogeographically constrained approaches (Pauchard *et al.*, 2004; Hierro *et al.*, 2005; Leishman *et al.*, 2014). Multi-region studies are also essential to determine if results found at individual sites depend on local land-use history, biotic and abiotic conditions and disturbance or are more generalizable (Kueffer *et al.*, 2013; Moodley *et al.*, 2014).

Comparing invasion patterns across regions provides insights into the environmental and ecological processes and filters that operate at different stages of invasion (Dietz & Edwards, 2006; Theoharides & Dukes, 2007; Catford *et al.*, 2009). Early in invasion, propagule pressure (i.e. the supply and frequency of introduction of plant propagules) is widely thought to drive invasion success (Lockwood *et al.*, 2005; Theoharides & Dukes, 2007; Catford *et al.*, 2009; Simberloff, 2009). The role of propagule pressure later in invasion is less certain; evidence both for continued (Rouget & Richardson, 2003; Lockwood *et al.*, 2005; Simberloff, 2009) or diminished importance relative to abiotic factors and biotic resistance (Theoharides & Dukes, 2007; Catford *et al.*, 2009) suggests that interactions among these drivers are likely. Therefore, studies that determine how propagule pressure, biological and environmental factors interact to determine invasion success are needed (Rouget & Richardson, 2003).

Pine invasions are an ideal system for determining the relative importance of habitat, disturbance and propagule pressure during the spread phase of invasion. Deliberately established plantations have created similar source populations for invasions across the Southern Hemisphere (Gundale *et al.*, 2014b). Although pine species used in forestry are often more invasive than non-forestry species (Essl *et al.*, 2010), invasion away from plantations does not always occur (Zenni & Nuñez, 2013). A given pine species is more likely to be broadly invasive if it has relatively small seeds, rapid onset of reproduction and more frequent large seed crops (Richardson *et al.*, 1994). Studies of specific pine species invasions can also resolve the role of changing invasion drivers at the intraspecific level (Dietz & Edwards, 2006) because of the known introduction history.

Pinus contorta, Dougl. (lodgepole pine), native to western North America, is one of the most invasive pine species introduced to the Southern Hemisphere (Richardson *et al.*, 1994). *Pinus contorta* has recently encroached into grasslands, shrublands and subalpine meadows in its native range (e.g. Jakubos & Romme, 1993; Widenmaier & Strong, 2010). Here-

after, we refer to this encroachment as invasion (Jakubos & Romme, 1993; Boulant *et al.*, 2009). *Pinus contorta* is a 'model species' for comparing hypotheses of invasion success because it has a known introduction history, it can be aged providing an invasion history and it has been planted under different biotic and abiotic conditions (Gundale *et al.*, 2014b). There have been several studies describing patterns of, and limitations to, *P. contorta* invasion in Chile (Peña *et al.*, 2008; Langdon *et al.*, 2010), Argentina (Simberloff *et al.*, 2002; Sarasola *et al.*, 2006; Nuñez *et al.*, 2008, 2009) and New Zealand (Allen & Lee, 1989; Ledgard, 2001, 2006); however, no study has compared invasion patterns among ecoregions and the relative importance of propagule pressure, native vegetation, topography and climate in determining invasion patterns across ecoregions. These factors are consistently important in determining the distribution of invasive species (e.g. Rouget & Richardson, 2003; Catford *et al.*, 2009). Additionally, understanding if invasive species behave or grow differently in their introduced range than in their native range is a central question in invasion biology (e.g. Willis *et al.*, 1999; Parker *et al.*, 2013).

We evaluated differences in the patterns and processes that drive *P. contorta* invasion across nine sites in six ecoregions in Argentina, Chile, New Zealand and its native range in the western USA. Specifically, we predicted that: (1) propagule pressure would be more important in explaining *P. contorta* invasion patterns than biotic or abiotic factors across all ecoregions; (2) *P. contorta* invasion success, measured by invasion density, would be higher in the introduced than the native range; and (3) that ecoregions with the highest invasion densities would also have the highest *P. contorta* growth rates and fecundity.

METHODS

Study species

Pinus contorta is a shade-intolerant fast-growing tree species that first reproduces at 3 to 15 years of age and has small seeds capable of long-distance dispersal by wind (Richardson *et al.*, 1994; Despain, 2001; Ledgard, 2001). *Pinus contorta* is native to North America, where it has a wide distribution ranging from South Dakota (103° W) to the Pacific coast (134° W) and from Baja California, Mexico (31° N) to the Yukon Territory, Canada (64° N) (Lotan & Critchfield, 1990).

Study sites

Sampling occurred at nine sites in six ecoregions (based on Olson *et al.*, 2001) in Argentina, Chile, New Zealand (all introduced) and the USA (native; Table 1; Appendix S1 in Supporting Information). The first site in Bariloche, Argentina (AR1a) was a shrub steppe community (*Mulinum spinosum*, *Acaena* spp.) with patches of the small tree *Nothofagus antarctica*. Fires have burned through this area in the past 15 years. Site AR1b, 3 km away, was dominated by the same shrub community but had a younger source population (Table 1). Coyhaique Alto, Chile (CL1) was a grass steppe community (*Festuca* spp.) with several

Table 1 Descriptions of all study regions (AR1, CL1, CL2, NZ1, NZ2, USA1) and sites within regions. Introduced range regions included AR1 in Argentina, CL1 and CL2 in Chile and NZ1 and NZ2 in New Zealand. The native range region USA1 was in Montana and Wyoming, USA. For more site details see Appendix S1.

Site	Long.	Lat.	Ecoregion	Density plots	Source type	Source age (years)	Ann. temp. (°C)	Ann. precip. (mm)
AR1a	−71.2	−41.2	Patagonian shrub steppe	786	Plantation	34	8.2	846
AR1b	−71.2	−41.2		153	Planted shelter	25	8.2	846
CL1	−71.7	−45.5	Patagonian grass steppe*	434	Plantation	23	5.8	715
CL2	−71.5	−38.4	Valdivian temperate forests	54	Forestry trial plots	43	6.7	1586
NZ1	170.2	−44.1	Canterbury–Otago tussock grasslands	402	Plantation	45	9.3	658
NZ2a	171.7	−43.2	South Island montane grasslands	247	Plantation	53	7.3	2241
NZ2b	171.7	−43.2		84	Planted shelter	46	8.3	1652
USA1a	−111.1	45.1	South central Rockies forest–shrub steppe	1024	Native Forest	> 100	1.4	643
USA1b	−111.0	44.7		827	Native Forest	25	1.6	587

Abbreviations: long., longitude; lat., latitude; ann., annual; temp., temperature; precip., precipitation.
*We differentiate here between grass steppe and shrub steppe cf. Olson *et al.* (2001).

large patches of *N. antarctica* and small areas of *Pinus ponderosa* plantation and *Nothofagus pumilio* forest (Langdon *et al.*, 2010). The second Chilean site was located in Reserva Nacional Malalcahuello (CL2) and was dominated by *Araucaria araucana* woodland, had areas of *N. antarctica* and an understorey comprising mainly *Chusquea culeou* (Peña *et al.*, 2008; Urrutia *et al.*, 2013). The sites in New Zealand were all in the Canterbury Region on the South Island. NZ1 was dominated by a mixture of native and non-native grasses and forbs (*Agrostis capillaris*, *Hieracium* spp., *Festuca novae-zelandiae*). The more diverse Craigieburn Forest Park site (NZ2a) had a similar mixture of grasses and forbs, but also contained the tall shrub *Leptospermum scoparium*, shorter shrubs and *Fuscospora cliffortioides* forest. NZ2b was a grass-dominated community similar to NZ1. NZ2a and NZ2b were located 10 km apart and differed in the age and size of their source populations (Table 1). The sites in the USA were located in the Greater Yellowstone ecosystem, Montana and Wyoming, and included unburned (USA1a) and burned (in 1988; USA1b) sagebrush steppe (*Artemisia tridentata*, *Festuca idahoensis*). The oldest invading trees at USA1 were older than 100 years; however, most of the encroachment has occurred in the last 50 years. We tried to minimize differences between sites (grazing, management), but inevitably some differences in land-use history may have contributed to variation in our data.

Field sampling within each ecoregion

Within each study site, random points along the *P. contorta* source population were selected as starting points for 10-m wide transects. Transects were located perpendicularly away from the source until they: (1) entered another *P. contorta* stand, (2) reached 2 km from the source, or (3) were impassable due to topographic barriers. At NZ1 the invasion spread farther from the source requiring longer (3.5 km) transects. Tree density in 100-m² plots was collected continuously along each transect

except in NZ1 and CL2 where density was collected in randomly selected plots ($n = 1$–5 every 100 m). Along all transects, height, basal diameter, age and current year cone production for all *P. contorta* individuals were measured within complete sample plots ($n = 1$–5 every 100 m). No serotinous cones were observed in the introduced range, but were occasionally seen in the native range.

Statistical analysis

All statistical analyses were conducted using R version 3.1.1 (R Core Team, 2014).

Importance of propagule pressure, biotic factors, and abiotic factors within ecoregions

To determine the relative importance of drivers for invasion success, we created negative binomial mixed models of *P. contorta* density for each ecoregion (AR1, CL1, CL2, NZ1, NZ2, USA1); this accounts for both overdispersion (Ver Hoef & Boveng, 2007) and spatial autocorrelation (Fournier *et al.*, 2012; Skaug *et al.*, 2013). AR1, NZ2 and USA1 had two sites within the ecoregion (e.g. AR1a and AR1b) so site was included in models for those ecoregions. Fixed effects in all models included: distance from source edge (nearest *P. contorta* plantation or forest), slope, cosine of aspect, sine of aspect, elevation, vegetation type [grass, *Araucaria araucana*, *Fuscospora cliffortioides*, *Nothofagus* spp., *Pinus ponderosa* plantation, short shrub (< 1 m), tall shrub (> 1 m)] and the interaction between vegetation type and distance from source (Table S2 in Appendix S1). Where the interaction was not significant ($P > 0.05$) it was removed from the model. In AR1, fire (if burned in the last 15 years) was also included as a fixed effect. Correlograms suggested that the maximum distance of density correlation was around 50 m and that including 50-m clusters as a random effect in the model significantly reduced the spatial autocorrelation. A post-hoc

Markov chain (MCMC) run for 10,000 simulations was used to estimate model coefficients. Likelihood ratio tests were also used to test fixed effects.

The relative importance of propagule pressure (at the local scale, represented by distance from the source edge), biotic (vegetation type) and abiotic (slope, sine and cosine of aspect, elevation, fire) factors (*sensu* Catford *et al.*, 2009) in explaining the density of *P. contorta* in each region was determined by assessing the improvement in model fit (Akaike information criterion corrected for small sample size, AICc) over the null model (random cluster effect and, where necessary, site) due to each predictor group (propagule pressure, biotic, abiotic). Only the native region (USA) had a large temperature and precipitation range within the region, so a second mixed effect negative binomial model for the US data only was created to assess the role of climate with the fixed effects of vegetation type, distance to forest edge, mean annual temperature and mean annual precipitation. The random effects included site and cluster. We recognize that each of these factors do not represent all components of propagule pressure, biotic factors and abiotic factors that affect invasions. For example, soil nutrients, texture and biota likely differed between plots and could also affect invasion density. However, given the broad scale of our study, we selected factors that are directly comparable amongst contrasting sites, are well known to determine plant growth or performance and have been used in other studies examining species distributions (e.g. Brummer *et al.*, 2013). Although additional abiotic (e.g. soil variables) and biotic (e.g. soil biota) factors can also contribute to variation in invasion success, these were beyond the scope of our study, and would contribute to unexplained sources of variation in our models.

Comparing densities between sites

A mixed negative binomial model of tree density was constructed using data from all sites. The fixed effects were site, distance from source, vegetation type, the interaction between vegetation type and distance from source and the interaction between site and distance from source. The random effect was cluster. In this global model, site was significant, so to further determine what factors explained the site effect, we also constructed models with climate variables and plantation age. We explored the potential for climate to explain differences between sites using 19 bioclimatic variables (Hijmans *et al.*, 2005). Many bioclimatic variables were collinear so we first created models with the fixed effects of one bioclimatic variable, vegetation type, and distance from source. Site and cluster were included as random effects. In the final model we used the most explanatory climate variable, based on the AICc from these models. This process was then repeated for data from just the introduced range. With data from the introduced range we also explored the possibility that differences in plantation age contributed to different invasion patterns between sites by including source age (young, < 30 years; old, > 30 years) and its interaction with distance from plantation (instead of climate, due to collinearity) in a separate model. Finally, to estimate invasion potential in each

site regardless of source age, we compared invasion densities next to the source edge at all sites by modelling the density of the plots within 200 m of the source with a mixed negative binomial model with site and vegetation type as fixed effects and cluster as a random effect.

Differences in growth and reproduction between ecoregions

Data for tree size and reproduction from all ecoregions were combined. Only trees aged ≤ 20 years (a total of 4784) were used for this analysis since several sites did not contain trees older than 20 years. A mixed linear model of log-transformed basal diameter was run with tree age, ecoregion, vegetation type, distance from source and the interaction between age and ecoregion as fixed effects and plot as a random effect (Bates *et al.*, 2014). *P*-values were calculated with Satterthwaite's approximations (Kuznetsova *et al.*, 2014). The number of cones per tree was modelled as a response to the fixed effects of tree age, ecoregion, vegetation type, distance from source and the interaction between age and ecoregion, as well as the random effect of plot, with a Poisson model fit with quasi-likelihood (Venables & Ripley, 2002). Some sites had low *P. contorta* densities so ecoregion (AR1, CL1, CL2, NZ1, NZ2, USA1) rather than site was used in these models.

RESULTS

Importance of propagule pressure, biotic factors and abiotic factors within ecoregions

Across all regions there was a negative relationship between tree density and distance from source (see Table S3 in Appendix S2 for detailed model results). In the introduced range, variation in *P. contorta* density was best accounted for by distance from source at CL1, CL2 and NZ1, whereas vegetation type was the most explanatory variable at AR1 and NZ2, and also important at CL1 (Table 2). Areas dominated by southern beech (*Nothofagus* spp. and *Fuscospora cliffortioides*) in all ecoregions, and by tall shrubs at NZ2, had low *P. contorta* densities (Fig. 1; Table S3). The relationship between distance from source and density differed between vegetation types at AR1 and CL1 (Table S3), because density was consistently near zero for vegetation dominated by *N. antarctica* but not other vegetation types. Abiotic factors were never the strongest predictor of *P. contorta* density (Table 2), although some topographic factors were significant at some sites (Table S3). Recently burned areas had lower *P. contorta* densities at AR1 (Table S3). The sites AR1a and NZ2a had higher densities than AR1b and NZ2b, respectively (Tables 1 & S3).

In the native range (USA1), distance from source was the most important explanatory variable (Table 2). Higher *P. contorta* densities were associated with areas with short shrubs compared with grass-dominated areas close to the forest edge (significant vegetation by distance to source interaction) and there was a negative relationship between elevation and *P. contorta* density (Fig. 1, Table S3). Higher *P. contorta* densities

Table 2 The improvement in the Akaike information criterion corrected for small sample size (AICc) of each model over the null model (random cluster effect, and where necessary, site) within each ecoregion (the more negative, the more improvement over the null model). Definitions of the region codes and further region descriptions can be found in Table 1 and Appendix S1. See Appendix S2 for more detailed results.

| | Improvement in AICc | | | |
Region	P	A	B	PAB
AR1	−14.8	−8.3	−98.7	−137.7
CL1	−48.8	4.9	−37.9	−107.5
CL2	−11.5	−2.6	2.7	−14.8
NZ1	−12.8	−8.4	2.1	−12.8
NZ2	1.8	−12.6	−48.3	−78.0
USA1	−14.5	−2.7	−0.2	−37.9

P stands for the model containing the propagule pressure (distance from source) covariate, B for the model containing the biotic covariate (vegetation type), A for the model containing abiotic covariates (elevation, slope, aspect (sine and cosine), and fire), and PAB for the model containing all covariates.
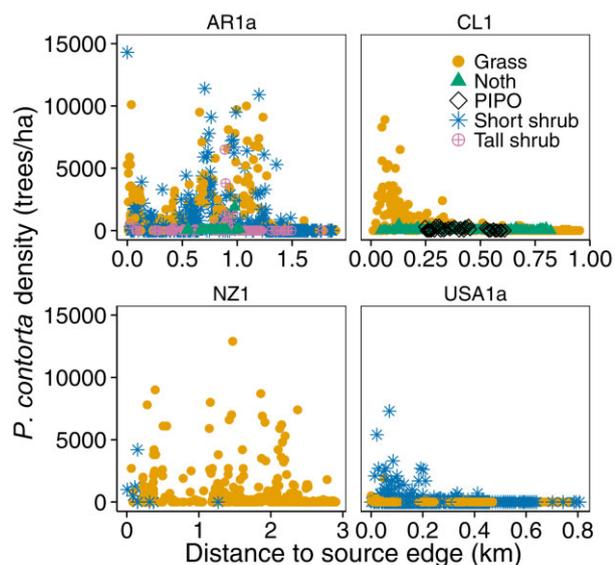

Figure 1 Relationship between tree density (*Pinus contorta* trees ha⁻¹) and distance from source populations (km) for four sites (AR1a, CL1, NZ1, USA1a) representing different ecoregions (Table 1, Appendix S1). *Pinus contorta* is native to sites in the USA but not to other ecoregions. Vegetation (biotic) differences within individual sites are shown using contrasting symbols for data points representing plot vegetation type. 'Noth' represents native *Nothofagus* spp. trees and 'PIPO' represents *Pinus ponderosa* plantation.

Figure 2 Fitted relationships between *P. contorta* density (trees ha⁻¹) and distance from source population (km) for grass-dominated areas from the global model which contained distance from source, vegetation type, site, distance from source by vegetation interaction and distance from source by site interaction as explanatory variables (Table S5 in Appendix S3). Introduced range sites included AR1a and AR1b in Argentina, CL1 and CL2 in Chile and NZ1, NZ2a and NZ2b in New Zealand. Native range sites included USA1a and USA1b in Montana and Wyoming, USA (Table 1, Appendix S1).

$P < 0.0001$; and $\chi^2 = 11.0$, d.f. = 1, $P = 0.0009$, respectively; Fig. S2 in Appendix S4).

Comparing densities between sites

Density, in the global model, was explained by distance from source ($\chi^2 = 61.5$, d.f. = 1, $P < 0.001$), vegetation type ($\chi^2 = 136.9$, d.f. = 3, $P < 0.001$), site ($\chi^2 = 2906.6$, d.f. = 8, $P < 0.001$), distance from source by vegetation interaction ($\chi^2 = 7.6$, d.f. = 3, $P = 0.054$; Fig. 1) and distance from source by site interaction ($\chi^2 = 272.1$, d.f. = 8, $P < 0.001$; Fig. 2, Table S5 in Appendix S3). Average *P. contorta* density decreased with increasing distance from the source. Forested areas and areas dominated by tall shrubs had lower *P. contorta* densities than grasslands, while areas dominated by short shrubs had higher densities than grasslands. NZ1, NZ2a and AR1a had a smaller decline in density with distance from source than the native unburned site (USA1a; Table S5). The two native sites had lower mean *P. contorta* densities in the first 200 m of invasion than all introduced sites ($P < 0.001$ for all pairwise comparisons). Invasion density was positively correlated with mean temperature of the coldest quarter when using data from all sites ($\chi^2 = 356.7$, d.f. = 1, $P < 0.001$; Table S6 in Appendix S4) and, in just the

were observed in USA1a (unburned) than USA1b (burned in 1988; Table S3). The climate model for USA1 showed that both mean annual temperature and precipitation were positively associated with *P. contorta* density ($\chi^2 = 23.3$, d.f. = 1,
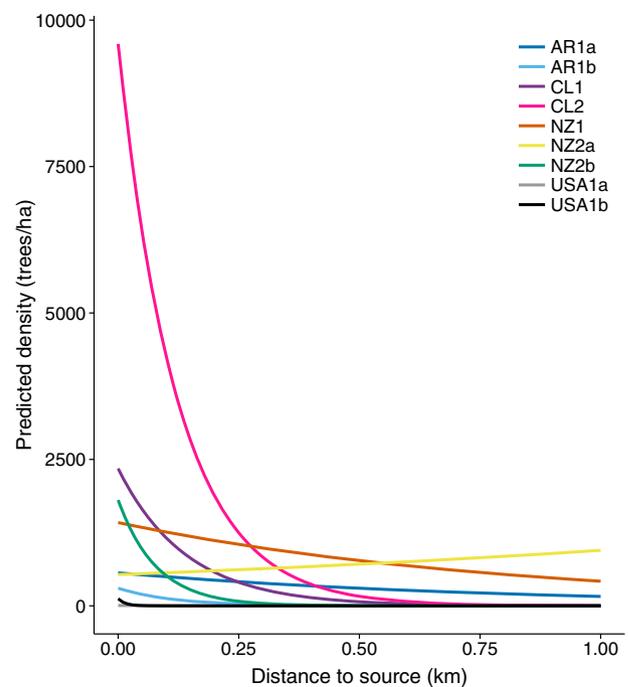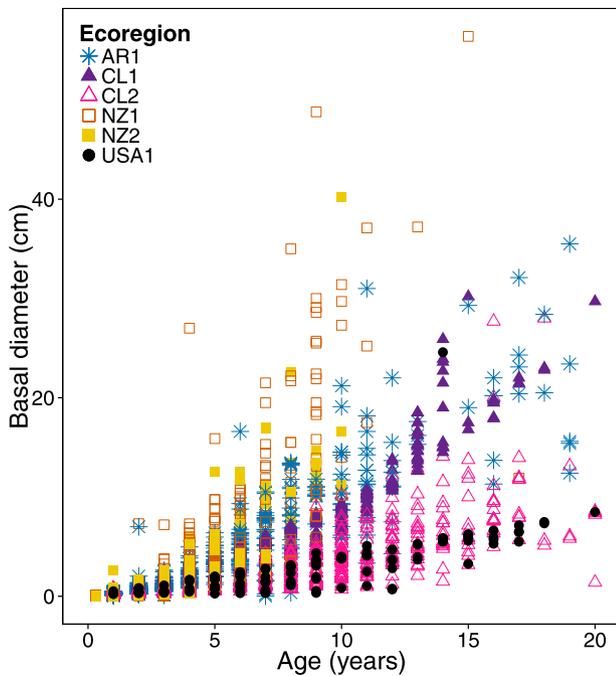
Figure 3 Relationships between *Pinus contorta* tree size (basal diameter, cm) and age (years) among ecoregions. Data shown are coloured/shaded by ecoregion and shaped by country (but filled or hollow based on ecoregion). Descriptions of the ecoregions can be found in Table 1 and Appendix S1.
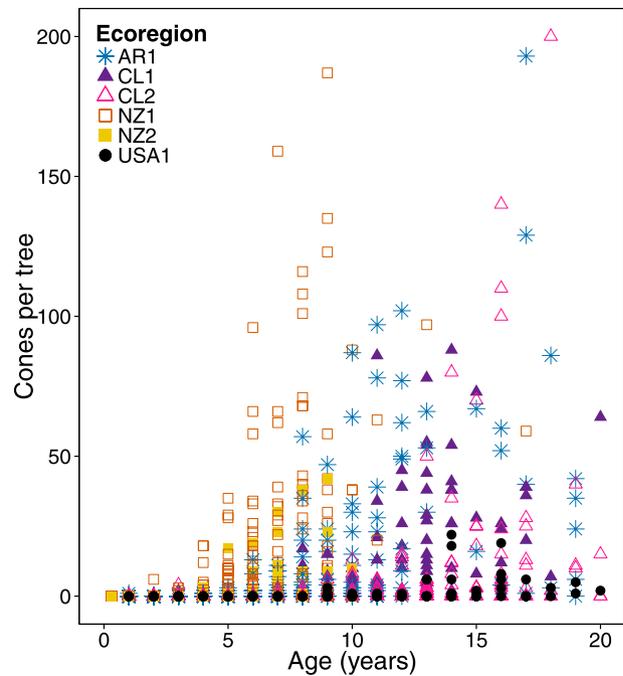

Figure 4 Relationships between *P. contorta* reproductive effort or fecundity (number of cones produced in a sampling year per tree) and tree age (years) among ecoregions. Data shown are coloured/shaded by ecoregion and shaped by country (but filled or hollow based on ecoregion). Descriptions of the ecoregions can be found in Table 1 and Appendix S1.

introduced range, density was positively correlated with mean temperature of the wettest quarter ($\chi^2 = 4.25$, d.f. = 1, $P = 0.039$). Introduced sites with source plantations younger than 30 years had a significantly steeper decline in density with increasing distance from plantations than sites with older source plantations ($\chi^2 = 39.5$, d.f. = 1, $P < 0.001$).

Differences in growth and reproduction between ecoregions

Pinus contorta grew fastest and produced more cones at the youngest ages at the New Zealand sites; CL2 and USA1 had the slowest growth rates and the lowest cone production, and AR1 and CL1 were intermediate. Ecoregion, tree age and their interaction best predicted variation in *P. contorta* basal diameter ($\chi^2 = 251.6$, d.f. = 5, $P < 0.001$; $\chi^2 = 12{,}591.1$, d.f. = 1, $P < 0.001$; $\chi^2 = 1491.2$, d.f. = 5, $P < 0.001$, respectively). Vegetation type was also a significant predictor of basal diameter ($\chi^2 = 16.7$, d.f. = 5, $P = 0.005$) with higher growth rates in *P. ponderosa* plantations ($t = 3.23$, d.f. = 747, $P = 0.001$) and short shrublands ($t = 2.28$, d.f. = 266, $P = 0.023$) compared with grasslands. The relationship between basal diameter and tree age differed between the native ecoregion and all introduced ecoregions ($P < 0.001$ for all pairwise comparisons; Fig. 3).

Ecoregion, tree age and their interaction were also all highly significant predictors of the number of cones per tree ($\chi^2 = 107.9$, d.f. = 5, $P < 0.001$; $\chi^2 = 13{,}385.4$, d.f. = 1, $P < 0.001$;

$\chi^2 = 164.5$, d.f. = 5, $P < 0.001$, respectively). Trees in all introduced ecoregions produced, on average, more cones at a younger age than trees in the native ecoregion ($P < 0.05$ for all pairwise comparisons; Fig. 4).

DISCUSSION

We provide empirical evidence that the relative importance of widely accepted drivers of invasion (propagule pressure, biotic factors and abiotic factors) varied strongly amongst six ecoregions for a widespread invasive tree species. This variation in factors driving invasion was due to plantation age, local vegetation and climate, but also a consistent shift in demographic properties of the invasive tree towards faster growth, greater reproductive effort and higher rates of establishment in the introduced than in the native range. Biological resistance at the introduced sites altered invasion patterns and became more important than propagule pressure as the invasion proceeded. These findings provide a better understanding of variation in major drivers of biological invasions across biogeographic regions, as outlined below.

Propagule pressure

Propagule pressure is thought to be the major driver of biological invasions (Lockwood *et al.*, 2005; Simberloff, 2009). Consistent with this view, we observed negative relationships between

P. contorta density and distance from source (Fig. 2) as did previous studies at individual sites (Ledgard, 2001; Sarasola *et al.*, 2006; Peña *et al.*, 2008; Langdon *et al.*, 2010). However, we additionally found that the relative importance of propagule pressure differed among regions. In the introduced range the sharpest decrease in density with increasing distance from the source population occurred at sites with recent invasions (AR1b, CL1), whereas older invasions (AR1a, NZ1, NZ2a) maintained high densities farther from the source (Fig. 1). One explanation for this is that habitat characteristics or biotic factors may become increasingly important relative to propagule pressure as invasion proceeds (Dietz & Edwards, 2006). This idea is supported by our finding that vegetation type was more important than propagule pressure for older invasions at AR1a and NZ2. Similarly, Donaldson *et al.* (2014) also report that source population was most important in explaining invasion abundance early in the tree invasion process, but that the invader's reproduction rate was more important for later stages. In the native range, distance to source was the most important variable despite the older source age, potentially due to the harsh abiotic conditions (Theoharides & Dukes, 2007). However, we could not disentangle fully the effects of propagule pressure from the source population or plantation from those of propagules supplied by previously invading trees (Fig. S3 in Appendix S5). Overall, our results show that biotic effects outweighed propagule pressure at some stages of invasion, and therefore strongly suggest that understanding the long-term biotic interactions that occur during biological invasions are important, even though these interactions are not typically considered by, for example, climate matching models (e.g. Nuñez & Medley, 2011).

Biotic factors

There was little invasion by *P. contorta* into areas dominated by either tall shrubs or southern beech across our study sites, suggesting that biological regulation of tree invasion may be a common feature and should occur in other introduced ranges. More generally, it has been suggested that forests and shrublands are less likely than grasslands to be invaded by pines (Richardson *et al.*, 1994). Consistent with this idea, a previous study also found a negative relationship between *P. contorta* invasion success and presence of the native tree *Nothofagus antarctica* (Peña *et al.*, 2008). In contrast, native *Araucaria araucana* forests were easily invaded (our study and Peña *et al.*, 2008), suggesting that biological regulation of tree invasions can be context dependent, in this case probably related to overall canopy cover in the different forest types (Peña *et al.*, 2008) or due to associated biological interactions not considered here, such as the availability and efficacy of mutualistic species (e.g. Dickie *et al.*, 2010; Hayward *et al.*, 2015). Our global model incorporating data across all sites demonstrates that short shrublands had higher tree invasion densities than grasslands. Although we did not investigate the potential mechanisms involved, such as resource competition between grasses and *P. contorta* seedlings (Ledgard, 2001, 2006), our results suggest that areas with higher

soil moisture and greater plant cover were consistently more resistant to invasion by *P. contorta*. Such biological mediation of invasion success is likely to be widespread. For example, in Chile (near CL1), native grass steppe communities were more easily invaded than European forage grass communities (Langdon *et al.*, 2010). Boulant *et al.* (2009) found that the effect of shrub cover on pine invasion rate depended on grazing intensity. Therefore, our results coupled with previous studies demonstrate that generalizations about whether forests, shrublands or grasslands may be more easily invaded are not warranted, but rather that biological factors per se (e.g. vegetation type, herbivory, presence of mutualists or pathogens) determine differences in invasion success; thus invasion rate and extent is context dependent (e.g. Wood *et al.*, 2015).

High propagule pressure is thought to overwhelm the effect of biotic resistance to invasions (Von Holle & Simberloff, 2005). However, we observed little *P. contorta* invasion from plantations into adjacent areas dominated by tall shrubs or southern beech despite relatively long-term (decadal) high propagule pressure (Fig. 1). For example, in Chile (site CL1), there was little invasion of *P. contorta* into adjacent savanna-like vegetation dominated by the native tree *N. antarctica* despite available bare ground and low canopy cover, factors typically thought to promote establishment and invasion by conifers (Lotan & Critchfield, 1990; Ledgard, 2001). This highlights the difference between propagule pressure and establishment success. There are a range of likely biotic mechanisms mediating between propagule pressure and establishment success, such as missing mutualists (Nuñez *et al.*, 2009), herbivory or granivory by animals (Buckley *et al.*, 2005; Nuñez *et al.*, 2008; Boulant *et al.*, 2009) or accumulated pathogens and disease (Diez *et al.*, 2010). This highlights the importance of considering site-specific interactions between individual drivers (propagule pressure, biotic factors, abiotic factors) when explaining invasion patterns (Catford *et al.*, 2009).

Differences in density and growth between sites could also be a result of biotic interactions. Although climate differs between the native and introduced ranges (Table 1), the importance of winter temperature in the global density model may represent differences between the USA and other sites generally, including climate factors but also other differences not included in the model. For example, there could be native pathogens or herbivores that are more abundant in the USA than in introduced ranges. Seed predation could cause reduced establishment in the native range, where it is higher than in all other sites (K.T.T., unpublished). Soil feedbacks on *P. contorta* have been found to be more negative in native soil than soil from the introduced range (Gundale *et al.*, 2014a), which could also contribute to the observed differences in growth. Finally, ectomycorrhizae could contribute to differences in growth rates, as evidenced by the higher growth rate of *P. contorta* invading *P. ponderosa* plantations than the grass steppe (where pine-specific ectomycorrhizae are likely less abundant) and higher growth rates at NZ2 where *P. contorta* associates with 14 ectomycorrhizal species (Dickie *et al.*, 2010), compared to CL1 where it often associates with just one ectomycorrhizal species (Hayward *et al.*, 2015).

Abiotic factors

We did not find strong or consistent effects of topographic variables on *P. contorta* density; however, climate had a more important role. The ability of *P. contorta* to grow on most slopes, aspects and elevations probably reflects its broad fundamental niche (Rehfeldt *et al.*, 1999). Where topographic factors were important, elevation was most likely to show a relationship with density; however, the direction of the relationship was not consistent among locations. In the USA the relationship between elevation and density may be largely explained by the positive correlation between mean annual temperature and *P. contorta* invasion density. Within the warmer low-elevation areas, those that received higher precipitation had higher densities. Similarly, in the introduced range the most important climate variable in explaining invasion density was temperature during the wettest quarter of the year. This suggests that *P. contorta* establishes and survives better in areas with high precipitation during the warmer months. The importance of abiotic factors in explaining invasion density may have been higher if we had been able to include other abiotic factors, such as detailed soil data.

At AR1 and USA1 there were lower levels of invasion in recently burned areas than in unburned areas. While at USA1 the difference in fire history is confounded with site, the vegetation and abiotic settings of the sites are extremely similar, so fire is likely to be partially responsible for the differences found in invasion density. Thus, fire through low-density invasion fronts may reduce invasion rates where native plants are adapted to regenerate following fire (Widenmaier & Strong, 2010), contrary to concerns that a positive feedback could form between pine invasions and fire (Simberloff *et al.*, 2010). Our results suggest that prescribed fire in low-density invasions could be explored as a management option. In contrast, fire through higher-density invasions or plantations in the introduced range may have different outcomes because dense invasions alter fuel structure (Cóbar-Carranza *et al.*, 2014) and therefore may alter fire behaviour and the post-fire plant community.

Global differences in density, size and reproduction

Pinus contorta invasion density was consistently higher in the introduced range than the native range. Several other plant species also have higher densities in their introduced than native ranges; however, for some species densities do not vary across ranges (Parker *et al.*, 2013). Therefore it is important to recognize that *P. contorta* does behave differently when invading open areas in its native and introduced ranges, which could reflect differences in the underlying processes causing invasion between the native and introduced ranges. Although *P. contorta* can form extremely dense stands in forested areas in its native range, particularly after fire, our results suggest that these densities are not reached in situations where *P. contorta* encroaches from forest edges into shrubland steppe in its native range, even after fire. It is possible that invasion from plantations (introduced range) may proceed differently from invasion from forest edges (native range), where the surrounding vegetation has evolved in proximity to pines. Plantations often are highly disturbed during the planting process, and post-planting management (such as removing lower limbs) may alter wind dynamics and seed dispersal. Additional differences between the native and introduced range that could affect the invasion process include different seed predators, herbivores and pathogens, as well as climatic differences that may result in a longer photosynthetic period in the warmer introduced ranges.

Pinus contorta trees grew faster and reproduced more prolifically and at a younger age in the introduced than the native range. Other plant species have also increased growth or seed production in their introduced range, although the underlying mechanisms are unresolved (Willis *et al.*, 1999; Parker *et al.*, 2013). The observed difference in *P. contorta* cone production could result in significantly higher propagule pressure in the introduced range than the native range, and this could explain the difference in invasion densities between ranges. Given the relatively long generation time of *P. contorta* and the young age of the plantations in most areas it is more likely that the differences in density, growth and reproduction are phenotypic responses to differences in climate or pathogens and herbivores rather than the result of rapid evolution in the introduced range (Buswell *et al.*, 2011). Our results suggest that higher temperatures are correlated with higher invasion densities, especially when sufficient moisture is present. In its native range in British Columbia, Canada, *P. contorta* occurs in climates that are colder and more continental than those in which optimal growth occurs (Rehfeldt *et al.*, 1999). The warmer, more maritime, climates found at the Southern Hemisphere study sites may thus be more optimal for growth of *P. contorta*. More detailed investigation of the mechanisms involved (e.g. climatic effects) and differences in fundamental traits (e.g. variability in seed number and quality among individuals; Coutts *et al.*, 2012) is thus warranted. Overall, our data suggest that a coordinated demographic shift towards faster growth and earlier, greater, reproductive effort in the introduced range has occurred; however, the underlying mechanisms involved and the persistence of these demographic shifts remains to be determined.

Management implications

The best management approach for tree invasions depends on both habitat heterogeneity and tree demography (Caplat *et al.*, 2014). We found that invasion success was driven by propagule pressure but that certain habitats, such as closed-canopy forests or tall shrublands, resisted pine invasions regardless of propagule pressure. Therefore, low-density *P. contorta* invasions in these habitats should be a low priority for management. Low-lying areas with dense herbaceous cover may also provide resistance to pine invasion (Ledgard, 2006), especially if herbivory is common (Buckley *et al.*, 2005). Additionally, we found that *P. contorta* demography varied between sites, suggesting that invasion spread rates will probably differ between sites even within a management jurisdiction. Therefore, monitoring invasions and the response to management will help prioritize which populations to manage (Rew *et al.*, 2007; Wilson *et al.*, 2014).

REFERENCES

Allen, R.B. & Lee, W.G. (1989) Seedling establishment microsites of exotic conifers in *Chionochloa rigida* tussock grassland, Otago, New Zealand. *New Zealand Journal of Botany*, **27**, 491–498.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: linear mixed-effects models using Eigen and S4. Available at: http://CRAN.R-project.org/package=lme4.

Boulant, N., Garnier, A., Curt, T. & Lepart, J. (2009) Disentangling the effects of land use, shrub cover and climate on the invasion speed of native and introduced pines in grasslands. *Diversity and Distributions*, **15**, 1047–1059.

Brummer, T.J., Maxwell, B.D., Higgs, M.D. & Rew, L.J. (2013) Implementing and interpreting local-scale invasive species distribution models. *Diversity and Distributions*, **19**, 919–932.

Buckley, Y.M., Brockerhoff, E., Langer, L., Ledgard, N., North, H. & Rees, M. (2005) Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology*, **42**, 1020–1030.

Buswell, J.M., Moles, A.T. & Hartley, S. (2011) Is rapid evolution common in introduced plant species? *Journal of Ecology*, **99**, 214–224.

Caplat, P., Hui, C., Maxwell, B.D. & Peltzer, D.A. (2014) Cross-scale management strategies for optimal control of trees invading from source plantations. *Biological Invasions*, **16**, 677–690.

Catford, J.A., Jansson, R. & Nilsson, C. (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, **15**, 22–40.

Cóbar-Carranza, A.J., García, R.A., Pauchard, A. & Peña, E. (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.

Coutts, S.R., Caplat, P., Cousins, K., Ledgard, N. & Buckley, Y.M. (2012) Reproductive ecology of *Pinus nigra* in an invasive population: individual- and population-level variation in seed production and timing of seed release. *Annals of Forest Science*, **69**, 467–476.

Dehlin, H., Peltzer, D.A., Allison, V.J., Yeates, G.W., Nilsson, M.-C. & Wardle, D.A. (2008) Tree seedling performance and below-ground properties in stands of invasive and native tree species. *New Zealand Journal of Ecology*, **32**, 67–79.

Despain, D.G. (2001) Dispersal ecology of lodgepole pine (*Pinus contorta* Dougl.) in its native environment as related to Swedish forestry. *Forest Ecology and Management*, **141**, 59–68.

Dickie, I.A., Bolstridge, N., Cooper, J.A. & Peltzer, D.A. (2010) Co-invasion by *Pinus* and its mycorrhizal fungi. *New Phytologist*, **187**, 475–484.

Dickie, I.A., Burrows, L.E., Yeates, G.W., St. John, M.G., Hunt, J.E., Peltzer, D.A., Scott, J.T., Orwin, K.H., Stevenson, B., Rillig, M.C., Aislabie, J., Barbour, M.M. & Kirschbaum, M.U.F. (2011) Ecosystem service and biodiversity tradeoffs in two woody successions. *Journal of Applied Ecology*, **48**, 926–934.

Dickie, I.A., St John, M.G., Yeates, G.W., Morse, C.W., Bonner, K.I., Orwin, K. & Peltzer, D.A. (2014) Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. *AoB PLANTS*, **6**, plu056.

Dietz, H. & Edwards, P.J. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87**, 1359–1367.

Diez, J.M., Dickie, I., Edwards, G., Hulme, P.E., Sullivan, J.J. & Duncan, R.P. (2010) Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, **13**, 803–809.

Donaldson, J.E., Hui, C., Richardson, D.M., Robertson, M.P., Webber, B.L. & Wilson, J.R.U. (2014) Invasion trajectory of alien trees: the role of introduction pathway and planting history. *Global Change Biology*, **20**, 1527–1537.

Essl, F., Moser, D., Dullinger, S., Mang, T. & Hulme, P.E. (2010) Selection for commercial forestry determines global patterns of alien conifer invasions. *Diversity and Distributions*, **16**, 911–921.

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

Gundale, M., Kardol, P., Nilsson, M.C., Nilsson, U., Lucas, R.W. & Wardle, D.A. (2014a) Interactions with soil biota shift from negative to positive when a tree species is moved outside its native range. *New Phytologist*, **2**, 415–421.

Gundale, M.J., Pauchard, A., Langdon, B., Peltzer, D.A., Maxwell, B.D. & Nuñez, M.A. (2014b) Can model species be used to advance the field of invasion ecology? *Biological Invasions*, **16**, 591–607.

Hayward, J., Horton, T.R., Pauchard, A. & Nuñez, M.A. (2015) A single ectomycorrhizal fungal species can enable a *Pinus* invasion. *Ecology*, **96**, 1438–1444.

Hierro, J.L., Maron, J.L. & Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93**, 5–15.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Jakubos, B. & Romme, W.H. (1993) Invasion of sub-alpine meadows by lodgepole pine in Yellowstone National Park, Wyoming, USA. *Arctic and Alpine Research*, **25**, 382–390.

Kueffer, C., Pyšek, P. & Richardson, D.M. (2013) Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. *New Phytologist*, **200**, 615–633.

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2014) lmerTest: tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-11. Available at: http://CRAN.R-project.org/.

Langdon, B., Pauchard, A. & Aguayo, M. (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. & Paul, T.S.H. (2008) Vegetation successions over 30 years of high country grassland invasion by *Pinus contorta*. *New Zealand Plant Protection*, **61**, 98–104.

Leishman, M.R., Cooke, J. & Richardson, D.M. (2014) Evidence for shifts to faster growth strategies in the new ranges of invasive alien plants. *Journal of Ecology*, **102**, 1451–1461.

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.

Lotan, J.E. & Critchfield, W.B. (1990) *Pinus contorta* Dougl. ex. Loud. Lodgepole pine. *Silvics of North America. Volume 1 Conifers*. (ed. by R.M. Burns and B.H. Honkala), pp. 302–315. USDA Forest Service Agriculture Handbook 654. US Department of Agriculture, Forest Service, Washington, DC.

Moodley, D., Geerts, S., Rebelo, T., Richardson, D.M. & Wilson, J.R.U. (2014) Site-specific conditions influence plant naturalization: the case of alien Proteaceae in South Africa. *Acta Oecologica*, **59**, 62–71.

Nuñez, M.A. & Medley, K.A. (2011) Pine invasions: climate predicts invasion success; something else predicts failure. *Diversity and Distributions*, **17**, 703–713.

Nuñez, M.A., Simberloff, D. & Relva, M.A. (2008) Seed predation as a barrier to alien conifer invasions. *Biological Invasions*, **10**, 1389–1398.

Nuñez, M.A., Horton, T.R. & Simberloff, D. (2009) Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology*, **90**, 2352–2359.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the worlds: a new map of life on Earth. *Bioscience*, **51**, 933–938.

Parker, J.D., Torchin, M.E., Hufbauer, R.A. *et al.* (2013) Do invasive species perform better in their new ranges? *Ecology*, **94**, 985–994.

Pauchard, A., Cavieres, L.A. & Bustamante, R.O. (2004) Comparing alien plant invasions among regions with similar climates: where to from here? *Diversity and Distributions*, **10**, 371–375.

Pawson, S.M., McCarthy, J.K., Ledgard, N.J. & Didham, R.K. (2010) Density-dependent impacts of exotic conifer invasion on grassland invertebrate assemblages. *Journal of Applied Ecology*, **47**, 1053–1062.

Peña, E., Hidalgo, M., Langdon, B. & Pauchard, A. (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. Available at: http://www.R-project.org.

Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L. & Hamilton, D.A. (1999) Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs*, **69**, 375–407.

Rew, L.J., Lehnhoff, E.A. & Maxwell, B.D. (2007) Non-indigenous species management using a population prioritization framework. *Canadian Journal of Plant Science/ Revue Canadienne de Phytotechnie*, **87**, 1029–1036.

Richardson, D.M., Williams, P.A. & Hobbs, R.J. (1994) Pine invasion in the Southern Hemisphere: determinants of spread and invasability. *Journal of Biogeography*, **21**, 511–527.

Richardson, D.M., Hui, C., Nuñez, M.A. & Pauchard, A. (2014) Tree invasions: patterns, processes, challenges and opportunities. *Biological Invasions*, **16**, 473–481.

Rouget, M. & Richardson, D.M. (2003) Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *The American Naturalist*, **162**, 713–724.

Sarasola, M.M., Rusch, V.E., Schlichter, T.M. & Ghersa, C.M. (2006) Tree conifers invasion in steppe areas and *Austrocedus chilensis* forests in NW Patagonia. *Ecologia Austral*, **16**, 143–156.

Simberloff, D. (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 81–102.

Simberloff, D., Relva, M.A. & Nuñez, M. (2002) Gringos en el Bosque: introduced tree invasion in a *Nothofagus/ Austrocedrus* forest. *Biological Invasions*, **4**, 35–53.

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

Simberloff, D., Souza, L., Nuñez, M.A., Barrios-Garcia, M.N. & Bunn, W. (2012) The natives are restless, but not often and mostly when disturbed. *Ecology*, **93**, 598–607.

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A. & Bolker, B. (2013) *Generalized linear mixed models using AD Model Builder*. R package version 0.7.7.

Theoharides, K.A. & Dukes, J.S. (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, **176**, 256–273.

Urrutia, J., Pauchard, A. & García, R.A. (2013) Differences in plant composition in an *Araucaria araucana* (Molina) K.Koch and *Nothofagus antarctica* (G. Forst.) Oerst. forest in a *Pinus contorta* Douglas ex Loudon invasion gradient. *Gayana Botánica*, **70**, 92–100.

Venables, W.N. & Ripley, B.D. (2002) *Modern applied statistics with S*, 4th edn. Springer, New York.

Ver Hoef, J.M. & Boveng, P.L. (2007) Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology*, **88**, 2766–2772.

Von Holle, B. & Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, **86**, 3212–3218.

Widenmaier, K.J. & Strong, W.L. (2010) Tree and forest encroachment into fescue grasslands on the Cypress Hills plateau, southeast Alberta, Canada. *Forest Ecology and Management*, **259**, 1870–1879.

Willis, A.J., Thomas, M.B. & Lawton, J.H. (1999) Is the increased vigour of invasive weeds explained by a trade-off between growth and herbivore resistance? *Oecologia*, **120**, 632–640.

Wilson, J.R.U., Caplat, P., Dickie, I.A., Hui, C., Maxwell, B.D., Nuñez, M.A., Pauchard, A., Rejmánek, M., Richardson, D.M., Robertson, M.P., Spear, D., Webber, B.L., van Wilgen, B.W. & Zenni, R.D. (2014) A standardized set of metrics to assess and monitor tree invasions. *Biological Invasions*, **16**, 535–551.

Wood, J.R., Dickie, I.A., Moeller, H.V., Peltzer, D.A., Bonner, K.I., Rattray, G. & Wilmshurst, J.M. (2015) Novel interactions between non-native mammals and fungi facilitate establishment of invasive pines. *The Journal of Ecology*, **103**, 121–129.

Zenni, R.D. & Nuñez, M.A. (2013) The elephant in the room: the role of failed invasions in understanding invasion biology. *Oikos*, **122**, 801–815.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Additional site information.
Appendix S2 Results from models within each ecoregion.
Appendix S3 Global model comparing density between sites.
Appendix S4 Invasion density and climate.
Appendix S5 Difference in establishment between the native and non-native ranges.

BIOSKETCH

The research team focuses on understanding the processes driving the spatial distribution, dynamics, spread and impacts of non-native plant species, with a recent emphasis 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).

Editor: Linda Beaumont