



Native bamboo increases biotic resistance to *Pinus contorta* invasion in temperate forest ecosystems

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Abstract One of the tree species with the greatest invasive potential worldwide is *Pinus contorta* Douglas ex Loundon, which is characterized by producing a great number of individuals in short periods of time, generating different impacts on the ecosystems it invades. The genus *Chusquea* is present in a diverse number of ecosystems in South America. In the temperate forests of Chile and Argentina, it forms dense thickets in the undergrowth as well as in open areas. Its rapid growth and vegetative reproduction, with large numbers of individuals, allow the species to dominate and restrict the establishment of other plant species. This study focused on analyzing the effect of the presence of individuals of *Chusquea culeou* E. Desv. on the establishment of the invasive

species *Pinus contorta*, as well as on other native herbaceous and shrub species in *Araucaria-Nothofagus* forest. With this aim, we established 204 plots within the Malalcahuello National Reserve (in the Andes of south-central Chile) along a gradient of *P. contorta* invasion, where the presence or absence of these species was recorded through different percentages of *Chusquea* cover. The results showed that the probability of presence of *P. contorta* decreases significantly in areas where *Chusquea* cover is greater than 25%. Native species also decrease their presence, but to a lesser extent compared to *P. contorta*. Our results demonstrate the inhibitory effect of *Chusquea* for the establishment of other plant species, but more markedly for invasive conifers.

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Resumen Una de las especies arbóreas con mayor potencial de invasión a nivel mundial es *Pinus con-*

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torta Douglas ex Loudon, la cual se caracteriza por producir una gran cantidad de individuos en cortos periodos de tiempo, lo que genera distintos impactos sobre los ecosistemas que invade. El género *Chusquea*, con varias especies de bambú, está presente en diversos ecosistemas de Sudamérica. En los bosques templados de Chile y Argentina forma densos matorrales en el sotobosque y zonas abiertas. Su rápido crecimiento y alta reproducción vegetativa, le permiten dominar y restringir el establecimiento de nuevas especies vegetales una vez establecido. El presente estudio se enfocó en analizar el efecto de la presencia de la especie *Chusquea culeou* E. Desv. sobre la abundancia y la probabilidad de establecimiento de la conífera invasora *P. contorta* y también de especies nativas de carácter herbáceas y arbustivas en Bosques de *Araucaria -Nothofagus*. Para ello se establecieron 204 parcelas en la Reserva Nacional Malalcahuello a lo largo de un gradiente de invasión de *P. contorta*, donde se registró la presencia/ausencia de estas especies a través de distintos porcentajes de cobertura de *Ch. culeou*. Los resultados mostraron que la abundancia y la probabilidad de establecimiento de *P. contorta* disminuye significativamente en lugares donde la cobertura de *Chusquea* es mayor al 25%. Las especies nativas también disminuyen su presencia, pero en menor magnitud en comparación al invasor *P. contorta*. Estos resultados demuestran el efecto inhibitorio de *Ch. culeou* para el establecimiento de individuos de otras especies vegetales, pero más marcadamente para la conífera invasora.

Keywords Biotic resistance · Pine invasion · *Araucaria araucana* · Bamboo

Palabras claves Resistencia biótica · Invasión de pino · *Araucaria araucana* · Bambú

Introduction

The introduction of non-native tree species into different ecosystems is mediated by anthropogenic vectors, where two main sources can be identified (Brundu et al. 2020). The first corresponds to the introduction of non-native trees for ornamental purposes, which are concentrated in urban centers, where some of the species can escape from the original cultivation, mainly by human vectors such as vehicles and urban

rivers (e.g., *Acer platanoides*, *Acacia dealbata*) (Säumel and Kowarik 2010). Secondly, the forest industry has historically functioned as a source of introduction of non-native tree species, being responsible for more than 65% of these tree species introductions. The main introduced species worldwide are of the genera *Pinus*, *Eucalyptus*, *Acacia*, *Leucaena* (Simberloff et al. 2010; Richardson et al. 2014). The success associated with the invasion of non-native trees is related to the fact that these species generally exhibit traits such as high propagule production, easy and early establishment, rapid growth, wide range of climatic tolerance and the ability to colonize disturbed ecosystems (Colautti and MacIsaac 2004; Peña et al. 2008; van Kleunen et al. 2010a, b; Van Kleunen et al. 2010a, b).

Some species of the genus *Pinus* are among the most invasive species worldwide (Lowe et al. 2000). In the southern hemisphere they are one of the most common genus of invasive tree species (Richardson 2006; Taylor et al. 2016). Within the genus *Pinus*, one of the most invasive species is *Pinus contorta* Douglas ex Loudon (Taylor et al. 2016), which invades Andean and Patagonian ecosystems in central and southern Chile (Langdon et al. 2010). The invasiveness of this species is mainly due to early seed production (5 to 10 years), small seeds that are easily transported by wind over long distances, and rapid seedling growth (Ledgard 2001; Peña et al. 2008; Langdon et al. 2010; Pauchard et al. 2016).

The invasion success of *P. contorta* also depends on the invasibility of ecosystems, where sites with high disturbance (e.g., fire-affected sites), exposed mineral soil, low temperatures and limited vegetation cover are favorable environments for its establishment and further invasion (Peña et al. 2008; Pauchard et al. 2016). Biotic resistance has historically been one of the factors that regulate the success of plant invasions, this regulation is primarily mediated by competition from resident plants (Levine et al. 2004; Beaury et al. 2020). However, other types of interactions can also regulate the success of plant invasions, such as predation, herbivory, and diseases caused by parasitic fungi, which can reduce both the establishment and recruitment of non-native plants (Nunez-Mir et al. 2017). In the case of *Pinus* species, it has been determined that the structure, composition, richness, and abundance of the resident community are key factors that reduce invasion (Richardson and Bond 1991). In

this context, it has been observed that grassland communities, open soils, and abandoned fields are more susceptible to invasion by *Pinus* species (Richardson and Bond 1991). On the other hand, mixed shrublands, shrubs, and forests tend to generate higher biotic resistance against *Pinus* species (Richardson et al. 1994). For example, studies conducted in central Chile have indicated that the probability of establishment of *Pinus radiata* individuals decreases significantly with increasing native forest coverage (Gómez et al. 2019). Meanwhile, in the Argentinean pampas, it has been determined that the presence of native rodents through granivory has controlled the invasion of the invasive trees *Robinia pseudoacacia* and *Gleditsia triacanthos* (Muschetto et al. 2015).

The arrival of *P. contorta* in Chile and its establishment is due to its use for soil protection, erosion control and dune stabilization (Peña et al. 2008). During the 1970s, the Chilean Forestry Institute (INFOR) developed a program for the introduction of non-native species, aimed at the productive sector (Peña et al. 2008). Among these experimental plots, some that were located in the Malalcahuello National Reserve (MNR), in La Araucanía region stand out, from which an invasion process has been generated within the same reserve, mainly affecting the Andean ecosystem dominated by the long-lived, native conifer *Araucaria araucana* and species of the genus *Nothofagus* (hereafter termed as *Araucaria-Nothofagus* forest). The understory of these forests are dominated by *Chusquea culeou* and *Chusquea quila* (Peña et al. 2008; Langdon et al. 2010; Urrutia et al. 2013; Cobar-Carranza et al. 2014). The main impacts of the invader *Pinus contorta* documented in the MNR are the reduction of native plant richness, which varies depending on the density of the invasion (Urrutia et al. 2013; Franzese et al. 2017), changes in soil biota, changes in fire regimes (Cobar-Carranza et al. 2014; Taylor et al. 2016; Policelli et al. 2019), changes in the functional traits of local communities (Bravo-Monasterio et al. 2016) and changes in the microclimatic conditions of invaded ecosystems (García et al. 2023).

In the *Nothofagus-Araucaria* forests of the MRN, one of the main species that make up the understory are the species of the genus *Chusquea* spp. The species of the genus *Chusquea* (Fam: Poaceae, Subfam: Bambusoides) have a great effect on the distribution, establishment and growth of seedlings, mainly of the

seed bank of native species (Holz and Veblen 2006). This species has a heterogeneous distribution within MRN forests, forming clusters of approximately 6 m in diameter that dominate the understory. Its occurrence is more frequent in forests that have been logged or previously affected by fires, whether natural or human induced (Marchesini Victoria et al. 2009).

The presence of populations of *Chusquea* spp. generates important changes in the microclimatic conditions of the ecosystem they inhabit (Caccia et al. 2015). For example, it has been found that dense stands of *Chusquea* spp. can reduce average light radiation levels, reduce soil and air temperature (~2 °C less than in sites without *Chusquea* spp.), and increase litter depth and soil moisture (Holz and Veblen 2006; Caccia et al. 2009). These conditions of low temperature, high humidity and low light availability generate direct impacts on vegetation, such as the generation of sub-optimal conditions for the establishment of native and non-native species (Caccia et al. 2015). In addition, there are other indirect impacts, such as the increase of pathogenic fungi and herbivory that increase the mortality rate of native and non-native species (Holz and Veblen 2006; Caccia et al. 2015).

It is also important to highlight the phenological processes of *Chusquea* spp., which are an important factor influencing the dynamics of regeneration and recruitment of native species in the forests of southern Chile (Sanguinetti and Kitzberger 2009). This is because species within the genus exhibit gregarious flowering, massive seed production, and rapid senescence, occurring at intervals ranging from 3 to 120 years (Marchesini Victoria et al. 2009). These phenological patterns result in significant changes within forests, such as alterations in microclimatic conditions (Holz and Veblen 2006) and reductions in granivory and herbivory (Sanguinetti and Kitzberger 2009). Additionally, this creates space and releases soil resources in the understory that can be utilized by new species (Caccia et al. 2015).

In this context, the presence of *Chusquea* sp. functions as a species that provides biotic resistance, regulating the establishment of both native plants, such as species of the *Nothofagus* genus, and non-native plants (Torres et al. 2018). The mechanisms associated with the biotic resistance exerted by this species encompass a wide range of interactions. On one hand, it increases competition for light, and its high

seed production (50 million per hectare) enhances granivory and herbivory, reducing the recruitment capacity of native species. Additionally, it modifies microclimatic conditions, increasing humidity and decreasing temperature, thereby favoring the attack of pathogenic fungi that directly affect the recruitment of both native and non-native plants (Holz and Veblen 2006; Marchesini Victoria et al. 2009). Thus, the population dynamics of *Chusquea* spp. may be playing a fundamental role in the invasion dynamics of *P. contorta* in the Malalcahuello National Reserve, since on the one hand it may be functioning as a biotic filter that prevents the establishment of *P. contorta* individuals, but on the other hand, when a process of mass mortality occurs, *P. contorta* individuals may be benefited by finding the space, biotic and abiotic conditions necessary to establish themselves and expand their invasive range within this ecosystem. These patterns have already been observed in other ecosystems invaded by *P. contorta*. For example, in New Zealand the presence of native shrubs such as *Fucosportia cliffortioides* prevent the establishment of *P. contorta* individuals, functioning as a biotic filter to control the invasion of this species (Taylor et al. 2016).

In this context, it is important to evaluate how the presence of *Ch. culeou* could play a role on the invasion process of *Pinus contorta*, mainly by reducing its establishment and growth. For this we asked whether the increase in the cover of *Ch. culeou* decreases the abundance and the probability of establishment of individuals of *P. contorta*, as well as for other herbaceous and shrub species. We hypothesized that the increase in the cover of *Ch. culeou* within the *Araucaria-Nothofagus* forests of the Malalcahuello National Reserve will significantly decrease the abundance and probability of establishment of plant species, with this effect being more intense on the non-native invasive species *P. contorta*.

Methods

Study area

The study area corresponds to the Malalcahuello National Reserve located in La Araucanía Region,

Chile (38 °S 25'; 71 °W 33'; 1420 m.a.s.l.) (Fig. 1). The area has a mean annual temperature ~9 °C and a mean annual precipitation of 3000 mm (Franzese et al. 2017). Topographically, it is an ecosystem that has been shaped by volcanic and glaciological activity that gives it unique characteristics in terms of the biodiversity (Gajardo 1994). This ecosystem is naturally dominated by open forests of *Araucaria araucana* ((Mol.) C. Koch.; Araucariaceae) and *Festuca scabriuscula* (Phil.; Poaceae) (Urrutia et al. 2013). There are also small and dense patches dominated by *Nothofagus antarctica* (G. Forst. Oerst.; Nothofagaceae) and *Chusquea culeou* (E. Desv.; Poaceae) (Franzese et al. 2017). The forest structure has undergone modification due to the invasion of *P. contorta*, leading to a significant increase in tree canopy cover attributable to the presence of this species (García et al. 2023). *Ch. culeou* is present in patches of varying sizes distributed heterogeneously throughout the landscape. The establishment of *Ch. culeou* predates the invasion and subsequent crown closure in areas with larger pine trees. Therefore, it is currently possible to find patches of this shrub in both invaded and non-invaded areas by *P. contorta* (Fig. S1).

Study specie

Pinus contorta is a native species of North America that can grow up to 35 m in height and 60 cm in diameter at breast height (DBH). It is considered a pioneer species, intolerant to shade, and exhibits rapid growth. It has a broad ecological range and tolerance, growing from sea level up to 3600 m a.s.l. It can withstand temperatures ranging from -57 to 38 °C and annual precipitation varying between 250 and 500 mm (Cóbar-Carranza et al. 2014). It was introduced in the 1970s (initial population <0.5 ha) along with other species of the genus *Pinus* (e.g., *P. sylvestris*, *P. ponderosa*) in the Malalcahuello National Reserve. Currently, it is estimated that the invasion area of *P. contorta* exceeds 100 ha, reaching densities of <6600 plants ha⁻¹, specially in the sectors with greater invasion (Peña et al. 2008; Cóbar-Carranza et al. 2014; Franzese et al. 2017).

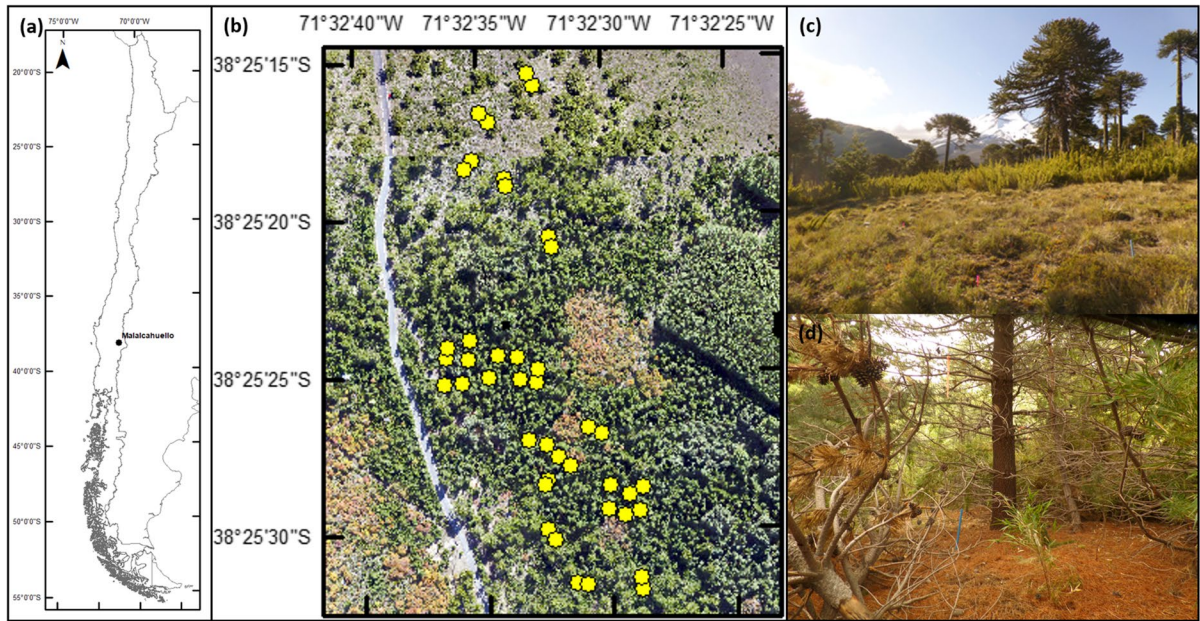


Fig. 1 **a** Location of the study site in the Malalcahuello National Reserve. **b** Distribution of sampling points along a fraction of the pine invasion gradient. At each point (yellow)

between 4 and 6 plots of 1 m² were established. **c** Un-invaded *Araucaria-Nothofagus* forest with presence of *Ch. culeou* patches. **d** Core area of *P. contorta* invasion

Sampling

To evaluate the abundance and probability of presence of species with herbaceous and shrub habit, as well as seedlings of *P. contorta* (height < 1 m), 204 plots of 1 m² were randomly established in the Malalcahuello N.R., within an invasion gradient of *P. contorta* ranging from 12.5 ton/ha⁻¹ to 150 on/ha⁻¹. Within each plot, the abundance of all vascular plant species was quantified by analyzing the percentage of cover occupied by each species in the 1 m² plot, which was subdivided into 25 quadrants. *Chusquea quila* cover was estimated by the projection of its “crown” over the 1 m² plot. Tree canopy cover was quantified by means of a hemispherical photograph under low light conditions, which was placed in the center of the 1 m² plot at 1 m above the ground. In each plot, the presence (1) and absence (0) of herbaceous and shrub (excluding *Ch. culeou*) species and individuals of *P. contorta* were recorded to evaluate the probability of establishment as a function of *Ch. culeou* cover and tree canopy cover. It is important to consider that a large percentage of the tree canopy cover in the study sites consists of *P. contorta* individuals, with

a smaller percentage comprising tree species such as *A. araucana* and *Nothofagus spp.*

Data analysis

To determine the effect of the presence of *Ch. culeou* and its tree canopy cover on the abundance of the different growth forms, a generalized linear model (GLM) was performed, fitting a poisson distribution with a *log* link function. To determine the effect of the percentage cover of *Ch. culeou* and tree canopy cover on the probability of establishment of species of herbaceous and shrub growth form and the presence of *P. contorta* individuals, a logistic regression was modeled and fitted with a binomial distribution and a *logit* link function. The *glm* function was used in both models above-mentioned. To analyze the percentage of variance of the binomial model, the Pseudo R² value was used. Finally, to determine the best model (*Ch. culeou* cover or tree canopy cover) to explain changes in abundance and establishment probability, the Akaike Information Criterion (AIC) was used, where the best model was chosen with the lowest AIC value (Akaike 1973). All data analyses were performed with R version 4.0.5 (Team 2015),

Table 1 GLM results of the effect of *Ch. culeou* and Tree canopy cover on the abundance of herbs, shrubs, and individuals of *P. contorta*

		Estimated	Std. error	P-value
Herbs	Intercept	6.266	0.038	<0.001
	Chusquea cover	0.010	0.067	<0.001
	Tree canopy cover	-0.048	0.075	<0.001
	Chusquea cover × Tree canopy cover	-0.060	0.015	<0.001
	Intercept	6.483	0.041	<0.001
Shrubs	Chusquea cover	-0.003	0.008	0.002
	Tree canopy cover	-0.003	0.007	0.001
	Chusquea cover × Tree canopy cover	-0.004	0.001	<0.001
	Intercept	0.201	0.013	<0.001
<i>P. contorta</i>	Chusquea cover	-0.009	0.005	<0.001
	Tree canopy cover	-0.051	0.002	<0.001
	Chusquea cover × Tree canopy cover	-0.003	0.003	<0.001

and all the plots were performed using the *ggplot2* R package (Wickham 2008).

Results

Species composition and abundance at the study site

A total of 41 plant species were recorded, of which 59% correspond to herbaceous species, 34% to shrubs and only 7% were trees. In relation to the biogeographic origin of the species, 93% of the species are native and only 7% correspond to non-native species (Table S1). The most frequent species were the non-native tree *P. contorta* that was present in 79.41% of the plots sampled. Followed the native conifer *A. araucana* (4.41%), and the shrubs *Chusquea culeou* (75.98%) and *Gaultheria pumila* (45.09%). Finally, the herbaceous layer was composed mainly by species *Festuca acanthophylla* (38.24%) and the exotic species *Rumex acetosella* (20.09%).

Chusquea culeou cover had a significant effect on the decrease of cumulative abundance of *P. contorta* individuals ($p < 0.001$) (Table 1; Fig. 2). This same effect was observed for species with herbaceous ($p < 0.001$) and shrub ($p < 0.001$) growth forms (Fig. 3a). In the case of tree canopy cover, the cumulative abundance of herbaceous ($p = 0.003$) and shrubs ($p = 0.002$) decreased, while a slight increase in the cumulative abundance of *P. contorta* ($p < 0.001$) was observed (Table 1, Fig. 3b). For both *P. contorta* species and the other growth forms, the interaction between *Ch. culeou*

cover and tree canopy cover was significant ($p < 0.001$) (Table 1).

Effect of *Ch. Culeou* cover and tree canopy cover on the probability of establishment of growth form

The probability of establishment of *P. contorta* individuals is significantly reduced as a function of increasing *Ch. Culeou* cover (Table 2; $p < 0.001$) (Fig. 4c), and increases as a function of tree canopy cover ($p < 0.001$) (Table 2; Fig. 4c). Regarding the percentage of variance explained, *Ch. Culeou* cover explains 19.76% of the data, while tree canopy cover explains 4.41% of the data. The Akaike information criterion (AIC) determined that the best model to explain the probability of establishment of *P. contorta* is the cover of *Ch. Culeou* (AIC = 240.63).

The probability of establishment of other herbaceous and shrub growth forms also decreases significantly as a function of *Ch. Culeou* cover (Table 2; Fig. 4a and b) and tree canopy cover (Table 2; Fig. 4a and b). As for the percentage of variance explained, the variable *Ch. Culeou* cover explains 26.04% of the data for the probability of herbaceous establishment, while tree canopy cover explains only 17.39%. In the case of shrub growth form, the variable *Ch. culeou* cover explains only 11.88% of the data, while tree canopy cover explains 22.66% of the data. The AIC determined that the best model to explain the probability of herbaceous species establishment is the one containing the cover of *Ch.*

Fig. 2 **a** Effect of *Chusquea culeou* and **b** tree canopy cover on the cumulative abundance of herbs (black), shrub (orange) and *P. contorta* (blue) individuals

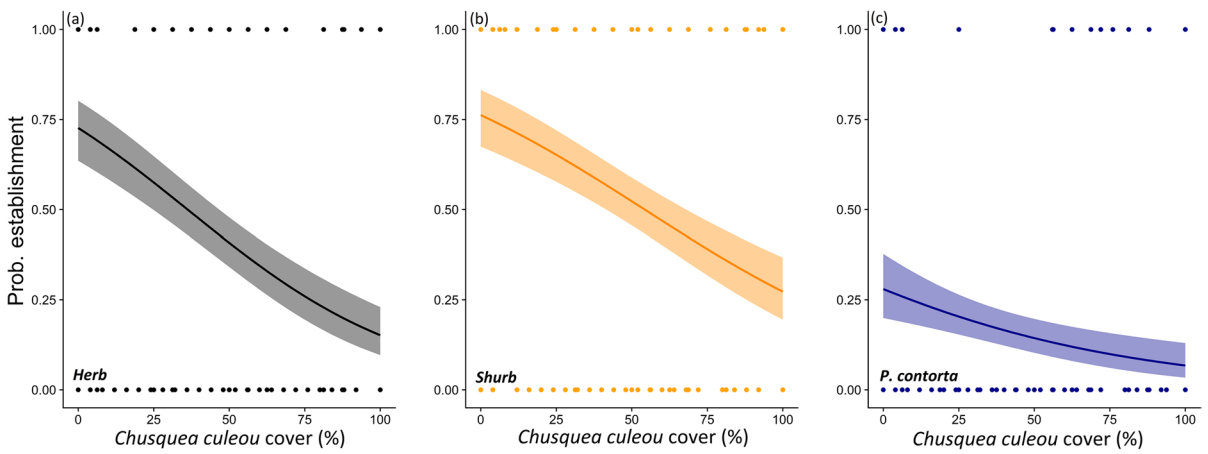
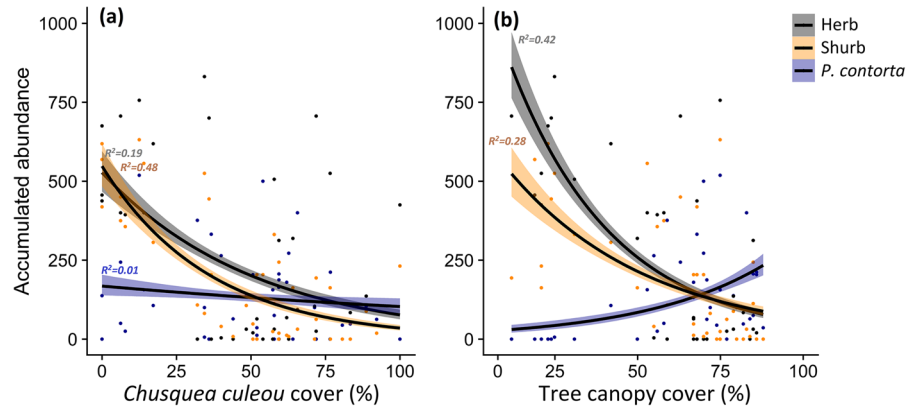


Fig. 3 Probability of establishment for **a** herbs, **b** shrubs and **c** *P. contorta* individuals, under the cover of *Chusquea culeou*. The curves indicate the values predicted by the binomial model for each of the individuals analyzed

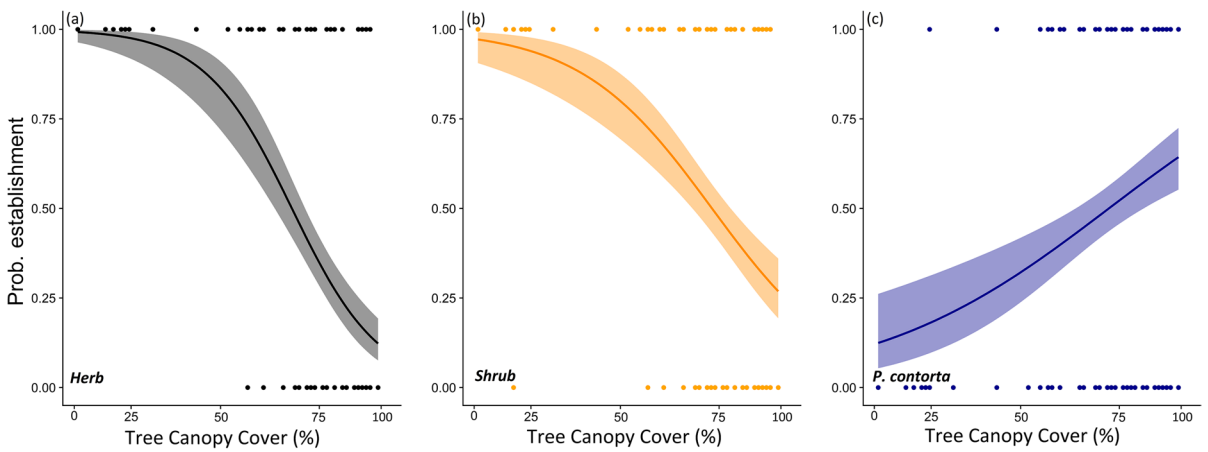


Fig. 4 Probability of establishment for **a** herb, **b** shrub and **c** *P. contorta* individuals, under tree canopy cover. The curves indicate the values predicted by the binomial model for each of the individuals analyzed

Table 2 Results of binomial models explaining the effect of *Ch. Culeou* and Tree canopy cover on the probability of establishment of herbs, shrubs and individuals of *P. contorta*

		Estimated	Std. error	<i>P</i> -value
Herbs	Intercept	7.691	1.071	<0.001
	Chusquea cover	-0.033	0.004	<0.001
	Intercept	6.150	1.010	<0.001
	Tree canopy cover	-9.183	1.353	<0.001
Shrubs	Intercept	1.163	0.221	<0.001
	Chusquea cover	-0.021	0.003	<0.001
	Intercept	4.374	0.796	<0.001
	Tree canopy cover	-5.974	1.059	<0.001
<i>P. contorta</i>	Intercept	-0.315	0.206	0.127
	Chusquea cover	-0.025	0.004	<0.001
	Intercept	0.373	0.477	0.433
	Tree canopy cover	-2.455	0.702	0.004

culeou (AIC = 265.55), while for the probability of shrub species establishment the best model was for tree canopy cover (AIC = 309.08).

Discussion

Based on these results, we can assign an important role to the native bamboo *Ch. culeou* in reducing the abundance and probability of establishment of the invasive species *P. contorta*. This also occur to a lesser extent with other herbaceous and shrub species. In terms of tree cover, it tends to increase the abundance and establishment probability of *P. contorta*. On the other hand, tree canopy cover reduces the probability of occurrence of herbaceous and shrub species, with a maximum establishment probability of up to 45% under significant tree canopy cover.

The impact of *Ch. culeou* cover on the abundance and probability of establishment of herbaceous and shrubby growth form species, as well as *P. contorta* individuals, is mainly due to two key drivers. The first is the rapid growth of *Chusquea sp* species, which tends to quickly dominate the understory of *Nothofagus-Araucaria* forests (Veblen 1982). The second driver is the phenology of this species, which is characterized by a long period of time in vegetative state (3–20 years) and then a synchronized period of

flowering and death, which varies within populations, but with an average periodicity of 15 years (Guerreiro 2014). The extent of this impact should be high, given that *Ch. culeou* dominates the understory in these temperate forests in the Andes (Holz and Veblen 2006).

This dominance of the understory in tropical and temperate forests of South America makes them an important component of the dynamics and structure of plant and animal communities (Budke et al. 2010). For example, the abundance of *Ch. culeou* may play an important role in the recruitment of different native species in the temperate forests of southern Chile (Holz and Veblen 2006; Guerreiro 2014). As for the wildlife, the understory of *Chusquea sp.* are the major source of food and shelter for most herbivores (Areta et al. 2009).

These characteristics cause species of the genus *Chusquea* to generate impacts on microclimatic conditions (Caccia et al. 2015), species diversity (Muñoz et al. 2012) and on the biotic interactions occurring under the understory (Caccia et al. 2009). In this context, it has been observed that the presence of *Chusquea sp* in forests of *N. obliqua* in the Chilean Patagonia, generates a decrease in light availability, higher soil moisture, and lower temperatures, which results in an increase in the mortality rate of juvenile individuals of *N. obliqua* (Caccia et al. 2009). Regarding the change in biotic interactions, it has been observed that the increase in the abundance of *Chusquea sp.* species generates an increase in the attack by pathogenic fungi (Abe et al. 2001), as well as an increase in herbivory and seed granivory of tree species (Sanguinetti and Kitzberger 2009).

This dominance of *Ch. culeou* in the understory and the impacts that its presence generates on the *Nothofagus-Araucaria araucana* forest may be a key factor that explains the dynamics of the invasion of *P. contorta*. The high dominance in the understory functions as a biotic filter that may be inhibiting germination and establishment of pines. In this context, our results are consistent with previous studies where it has been determined that the establishment success of *P. contorta* individuals within invaded ecosystems in southern Chile and New Zealand decreases as a function of the presence of native shrub and tree species (Taylor et al. 2016). This response is related to the fact that *P. contorta* is considered a pioneer species

that in early stages of development needs a large amount of light for its establishment (Ledgard 2001; Pauchard et al. 2016). The results obtained regarding the higher abundance of *P. contorta* individuals in areas with greater tree canopy cover are mainly due to the fact that these areas also experience a higher invasion of *P. contorta*, resulting in increased recruitment of *P. contorta* seedlings in these zones (García et al. 2023). This invasion pattern has been observed in both forested and treeless ecosystems, where the propagule pressure is higher in the vicinity of mature trees (Pauchard et al. 2016; Langdon et al. 2019).

Sporadic flowering and gregarious death events could be a key factor explaining the mechanism by which *P. contorta* individuals can invade. In addition to this effect of flowering and gregarious death, *Ch. culeou* populations play a fundamental role in the fire regime, as it is a species prone to burn forming fire ladders that facilitate crowning. These disturbances may function as a driver to facilitate the dispersal and establishment of *P. contorta* individuals across the landscape (Langdon et al. 2019). It has also been shown that in areas invaded by *P. contorta*, fire can increase the quality of the seedbed and the rate of pine establishment, mainly if they are ecosystems with older invasion (Taylor et al. 2017).

Finally, it is important to consider these results from an invasion management point of view. Our results indicated that the presence of *Ch. culeou* significantly reduces the probability of establishment of *P. contorta* individuals and to a lesser extent herbaceous and tree species. Therefore, when carrying out management strategies in invaded areas, maintaining the cover of *Ch. culeou* could prevent recruitment of *P. contorta* individuals, allowing other native species (herbaceous or arboreal) to colonize these ecosystems. In addition, maintaining *Ch. culeou* could inhibit the effect of post-control or eradication invasion legacies, which will allow for better recruitment of native species in cases of restoring invaded ecosystems.

Conclusions

Our study determined that the cover of *Ch. culeou* significantly influences the abundance and probability of establishment of species with herbaceous and arboreal growth form, and especially on the

non-native species *P. contorta*, even being more significant than the arboreal cover. These results are important for planning conservation strategies in the Malalcahuello National Reserve since the presence of a dense understory composed of species of the genus *Chusquea* could function as a biotic and even abiotic filter (changes in microclimatic conditions) that prevents the establishment and further invasion of *P. contorta*.

A deeper understanding of the phenological processes associated with historical and future *Chusquea* sp. species could be key to disentangle the invasion dynamics of *P. contorta*, as these stochastic processes of flowering and gregarious death, combined with natural and intentional disturbances, could favor the advance of the invasion in the Malalcahuello National Reserve.

It is important to be careful with these results for both management and control of *P. contorta*, because although the cover of *Ch. culeou* tends to reduce the probability of establishment of *P. contorta*, its spatial distribution within the Malalcahuello National Reserve tends to be heterogeneous within the landscape (clustered distribution in the landscape) unlike the tree canopy cover of *P. contorta* that tends to homogenize the ecosystem and be more constant in the landscape. Therefore, although the cover of *Ch. culeou* may increase biotic resistance, *P. contorta* individuals could establish in areas close to the propagule source that are free of *Ch. culeou* populations. The establishment of these pines could eventually suppress the *Ch. culeou* in the long term.

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Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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