



# Habitat suitability of five commonly planted non-native trees in Chile: Implications for an invasion process

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## ABSTRACT

Non-native tree (NNT) species have been deliberately introduced into new areas. Historically, NNTs were not considered as invasive species, given the benefits they provide, but that has changed during the last decades. The use of non-native trees, whichever purpose they have, should be assessed according to the location and susceptibility of the area to invasion. Forestry trees, such as *Pinus* and *Eucalyptus* have been introduced worldwide, being the most planted taxa. Here, we present a complete assessment of the actual invasive stage and potential distribution of most relevant non-native tree species established in the south-Central region of Chile (*Pinus radiata*, *Eucalyptus globulus*, *Eucalyptus nitens*, *Pinus contorta* and *Pseudotsuga menziesii*) based on its presences and absences, their global and regional niches, Species Distribution Models (SDM), climatic and anthropogenic variables. None of the studied species maintain the environmental space of their native range. Some of them (*P. radiata*, *E. globulus* and *E. nitens*) have been established under new environmental conditions, thus expanding their niches. Others, such as *P. contorta* and *P. menziesii* present a high proportion of stable populations, but there is an even higher proportion of area available for their expansion. Beyond their actual status, all the studied species are capable of expanding their populations into new areas of the studied region. Conservation efforts must be efficiently planned, to reduce these species impacts wherever necessary, but also to avoid their further dispersal into new non-invaded areas.

## 1. Introduction

Historically, deliberate introductions of tree and shrub species have occurred for horticulture, forestry, food, and agroforestry (Richardson and Rejmanek, 2011). These planned introductions, unlike those unintentionally introduced, are commonly supported by human actions to ensure a successful establishment and propagation of the species (Reichard, and White, 2001). Thus, indirectly enhancing their naturalization. For trees, commercial and other large-scale afforestation are now recognized as one of the most relevant sources of tree invasions (Brundu et al., 2020).

Plantation forests (intensively managed, monospecific, regular spacing and established for productive purposes) cover about 131 million ha (3% of global forest area) (Brundu et al., 2020). The highest proportion of these plantation forests are located in South America, where they represent 99% of the total planted-forest area. Globally, 44% of plantation forests are comprised by non-native trees (NNTs), but in

South America, forest plantations consist almost entirely of NNTs (FAO, 2020). These NNT species are considered of high cultural, commercial and/or aesthetic importance in those regions where introduction occurs, but at the same time they might produce negative impacts (Castro-Díez et al., 2019), thus creating conflict of interest, which most of the time stagnate management efforts (Richardson et al., 2014). This is the case of some of the most relevant NNT used for commercial purposes worldwide, such as the Fabaceae (*Acacia*, particularly) and Pinaceae (mainly *Pinus*) Families, which are commonly listed as invasive trees globally.

Almost twenty years ago, (Haysom and Murphy, 2003) warned that a considerable portion of species introduced with forestry purposes (total of 458 species) were already invading (61%) or naturalized (9%) somewhere else. These numbers are increasing rapidly (Krumm and Vitkova, 2016; Rejmanek and Richardson, 2013). During the last couple of decades, Pine species have received great attention (Richardson and Higgins, 1998; Bustamante and Simonetti, 2005; Nuñez and Medley,

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2011; Richardson and Rejmanek, 2011; Mcgregor et al., 2012; Gundale et al., 2014; Nuñez et al., 2017). Richardson (2006) indicated that 111 pine species had been introduced into new areas. Thirty of them have been catalogued as naturalized and 21 are considered invasive species. Although conifer invasions are being registered throughout the world (Despain 2001; Engelmark et al. 2001; Selvi et al. 2016; Essl 2005; Carrillo-Gavilán and Vilà, 2010; Nuñez et al., 2017), most attention has been given to the southern hemisphere (Froude, 2011; Ledgard, 2008; Paritsis and Aizen, 2008; Pauchard et al., 2015, 2014; Richardson et al., 2008, 2006; Richardson and Petit, 2006; Sarasola et al., 2006; Simberloff et al., 2010). Pine species were established in New Zealand, Australia, and South Africa about fifty years earlier than in Chile or Argentina (Pauchard et al., 2014). Now, evidence of invasion in those countries are considerable, shedding lights on what could occur in Chile or Argentina if nothing is done to manage or control its regeneration. Acacias have been widely studied as well, even with exclusive publication issues about its invasion history, ecology, or management (Richardson et al., 2011). Hui et al. (2014) stated that 384 species of Acacias have been introduced to new habitats, 71 of them are already naturalized in those habitats, and 23 are considered invasive. Eucalypts, on the other hand have received less attention, but this has changed in the past few years (Deus et al., 2019; Ziller et al., 2019). Hui et al. (2014) report 373 *Eucalyptus* species as introduced in new areas, 82 as naturalized and 7 of them are catalogued as invasive species. The most planted one is *E. globulus*, which is, according to Rejmanek and Richardson (2013) the most widely invasive eucalypt species, occurring in 7 of 15 geographical regions.

Globally, despite all literature available, massive tree planting campaigns to overcome climate change, among others, are commonly enhancing the use of NNTs (Brundu et al., 2020). Contrary as thought, this might not be very helpful. New evidence shows that trees might not help offset carbon emissions as much as expected and planting NNTs in inappropriate sites can increase negative impacts such as biodiversity conservation and ecosystem functioning (Bond, 2016; Bond et al., 2019; Brundu et al., 2020; Popkin, 2019; Temperton et al., 2019; Bellingham et al., 2022). Thus, tools for local prioritization of invasion management are pivotal for the forestry industry, but there are important difficulties to overcome when resources are scarce, the number of species is elevated, or the invasion affects large areas, among others (Caplat et al., 2014; Lambin et al., 2020; van Wilgen and Richardson, 2014). To deal with this, several management strategies with different approaches at local, regional, or national levels have been developed (Hobbs and Humphries 1995, Rouget et al. 2002, Robertson et al., 2003, Roura-Pascual et al. 2009, Mgidí et al. 2007, Forsyth et al. 2012). Species Distribution Models (SDM); (Pearson and Dawson 2003; Phillips et al. 2006; Soberón and Nakamura 2009) have been used to predict environmental (climatic) suitability for the species as a function of their presence/absence as well as environmental variables (Peterson and Holt, 2003). Niche models have been largely applied in several disciplines (Phillips et al., 2006), including invasion ecology (Broennimann et al., 2007; Gallien et al., 2010; Peterson et al., 2003; Thuiller et al., 2005b). A global model, considering the totality of presences known for the species worldwide (Gallien et al., 2012) is one way to get a proxy of the fundamental niche (Vetaas, 2002), a fact not possible to know with regional models (nor the niche observed in native ranges) which are an expression of the realized niche. Potential expansion of species predicted by climate requirements, can be constrained by biotic interactions, such as competition or facilitation are the ones that shape the invasion success at smaller scales (Srivastava et al., 2019). Despite that, distribution models can be useful where no other knowledge is available, therefore, they could support decision making for management strategies.

Chile represents an interesting opportunity to understand the complexities of NNT tree invasions used in commercial forestry. In fact, most non-native plants arrived in Chile from Europe before the 20th Century, mainly linked to agriculture and more traditional uses such as small-scale wood production (Camus et al., 2014). However, during the 20th

Century a wave of new introductions occurred for forestry purposes (Camus et al., 2014). Invasion processes have been reported for many of those species including *Pinus radiata*, *Pinus contorta*, *Acacia dealbata*, *Acacia melanoxylon* and *Eucalyptus* spp. (Bustamante and Simonetti, 2005; Fuentes et al., 2014; Fuentes-Ramírez et al., 2010; Langdon et al., 2010). Subventions are still available today and programs to enhance the use of exotic species are common, even when invasion reports are available. Now, the country is facing strong criticism for the environmental impacts of the large-scale afforestation and the forestry industry (Heilmayr et al., 2020, 2016) and has adopted a series of environmental certification procedures such as FSC and CERTFOR which recognize the importance of controlling NNT when they invade outside the plantation (Brundu et al., 2020). Thus, for Chile, having information on where NNT can invade and become problematic is therefore critical to reduce the impacts of large-scale forestry. Unfortunately, there is not much information available for NNT species, contrasting significantly with the information available in other regions of the world, particularly for *Pinus*, *Acacia*, and *Eucalyptus* species.

In this study, we aimed to assess if most commonly introduced non-native trees used in forestry are capable of establishing and reproducing without human support (if their climatic niche has been conserved), the current invasive status in South-Central Chile and the potential extent of an invasion process. We hypothesize that all studied NNT species should be able to successfully establish in those areas where they have been introduced for commercial purposes, given that they were selected by people to optimal growth under climatic conditions which met with their climatic niche requirements. Given that time of introduction has been relatively short and a large generation time, we maintain that these trees are not at a biogeographical equilibrium with the environment, which means that there is still more area to colonize in Chile. Our approach may shed light into how relatively simple ecological modelling can be used to prioritize areas for management of invasive species and reduce the risk of new invasions in areas of particular conservation value.

## 2. Methods

### 2.1. The species

Five NNT species were selected for this study, following two criteria: a) they are extensively planted within the study area and/or b) they are known for their invasive potential in Chile or elsewhere. Three species were selected, as mentioned earlier, because of their relevance in the forestry industry: *Pinus radiata*, *Eucalyptus globulus* and *Eucalyptus nitens*. Other two, *Pseudotsuga menziesii* and *Pinus contorta* were selected because of their invasive status in other parts of the world (Langdon et al., 2010; Nuñez et al., 2017; Pauchard et al., 2008). Basic information on their origin, ecology and presence in Chile are presented in Table 1.

### 2.2. Study area

The study was conducted in South-Central Chile, between the Maule (34°0'0"S) and the Aysén (47°0'0"S) Regions (310.000 km<sup>2</sup> approximately) (Fig. 1), including the largest forestry plantations surface in Chile (2.312.696 ha, accounting for 94,6% of all forestry plantations surface) (INFOR, 2018). This geographic range, encompasses a wide climatic differentiation, ranging from a warm temperate climate with a dry season at the north, a rainy temperate climate in the central part, and a rainy cold temperate climate without dry season at the southern extreme of Chile (Riosco and Tesser, consulted in April 2022). In terms of vegetation, Luebert and Pliscoff (2006) describe five vegetational formations in the study area: Sclerophyllous Forests, Deciduous Forests, Broad-leaved Forests, Evergreen Forests, and the Steppe. Also, more than 10 million ha of native forests are present in the study area, concentrated both in Los Lagos and Aysén Regions, with around 50% of total native forests of Chile (CONAF, 2020).

**Table 1**

General information on the origin, ecology, and presence history in Chile for the 5 studied non-native tree species. \* Area registered only for the Aysén Region.

	Origin	Juvenile period	Seed dispersion	Invasive elsewhere	Year of introduction	Planted area (ha)	Areas invaded
<i>Pinus radiata</i>	California (USA) and Mexico	5	Wind	Yes	1885	1,285,635	grasslands, shrublands, disturbed forests, coastal dunes
<i>Pinus contorta</i>	North America	5	Wind	Yes	1970?	5,117 *	Grasslands, native steppe, open forests
<i>Pseudotsuga menziesii</i>	North America	12	Wind	Yes	1963	16,480	Grasslands, Forest Edges and gaps, shrublands
<i>Eucalyptus globulus</i>	Australia	5	Wind	Yes	1879	538,429	Disturbed areas
<i>Eucalyptus nitens</i>	Australia	4	Wind	No data	1967	273,039	No information

## 2.3. Data input

### 2.3.1. Species occurrences at global scale

Data on the presence of the five species at a global scale, were recorded from different sources during 2016: Australia Virtual Herbarium (AVH, 2022), Global Biodiversity Information Facility (GBIF, 2016a, b, c, d, e), Integrated Digitized Biocollections (2016) (Complete record sets consulted available on supplementary materials), and the Intermountain Region Herbarium Network (2016) (Occurrence data from specific collections in supplementary materials).

All collected data were carefully filtered according to three criteria: (a) The data contained associated georeferenced information (e.g., datum), (b) they were recorded after 1950 to minimize erroneous georeferenced information, and (c) there is an associated voucher or were labelled under the name of the botanist who determined the sample. Duplicated records were also eliminated, and a subset of the occurrence data was created, based on the Euclidean distance between points, in order to consider just one point per cell during the modelling process. All points within 9 km of distance were removed from the data, resulting in a resolution of 2.5 arc minutes (about 4.5 km). By doing this, we intend to reduce the bias that may be produced by recording a higher number of occurrences in places of greater human activity or a higher number of introductions (establishment of commercial plantations) (Ahmad et al., 2019). These analyses were carried out using R software (version 3.3.1) (R Development Core Team, 2008). For the native range, occurrence data were selected from the global data set, based on literature (Hermann and Lavender, 1990; Lotan and Critchfield, 1990; McDonald and Laacke, 1990; Boland et al., 2006). At the native range, a polygon was then created using the minimum bounding geometry tool with the convex hull geometry type. This polygon was then used as a mask to extract all the environmental layers from the native range.

### 2.3.2. Occurrences at local scale

For the study area (South-Central Chile), occurrence data were obtained during field surveys, distinguishing planted from naturalized individuals, and excluding all urban areas, gardens, or ornamental individuals in rural areas (Ramírez-Albores et al., 2016). Again, by doing so, we expect to reduce the bias that may be produced by recording a higher number of occurrences in places of greater human activity or a higher number of introductions. Three hundred sampling points were randomly distributed through the study area using ArcGis (v. 10.2), and then, the final number was reduced according to its accessibility (no more than 1 km between each point and a primary, secondary, or tertiary road), resulting in a sample of 81 sampling points to visit. Field surveys were carried out between October and December 2017. At each sampling point, we recorded the presence of species within our visual ranges (50 m radius approx.) and georeferenced the site where the species was recorded. If on our way to a sampling point, we spotted an individual of any of the studied species, then we registered its occurrence in that point as well. This gave us a total (sampling point plus side of the roads) of 551 occurrence points (Fig. 2). At each visited point, we registered the presence of species; in the case that species trees were not registered, they were considered absences. Also, both planted and

naturalized origin were registered. The planted/naturalized status was used only for one of our analyses, which will be explained ahead. Finally, analyses were performed based on data detailed on Table 2.

### 2.3.3. Environmental layers

Bioclimatic variables were obtained from the Worldclim database (<https://www.worldclim.org/public>) repository online) with a spatial resolution of 2.5 arc minutes (Hijmans et al., 2005). Since variable collinearity may lead to over-fitting, we checked for cross-correlation between all possible pairs of variables using the Pearson correlation test using ENMTools software, version 1.44 (Warren et al., 2008). Only one variable from highly correlated pairs of variables ( $r > 0.70$ ) were included in the model, allowing us to minimize redundancy (Warren et al., 2008). Seven variables were selected based on the correlation analyses and their relevance for tree ecology: Annual mean temperature (BIO1), Maximum temperature of the warmest month (BIO5), Minimum temperature of the coldest month (BIO6), Annual precipitation (BIO12), precipitation of the wettest month (BIO13), precipitation of the driest month (BIO14), and precipitation seasonality (BIO15). To complement climatic data, we followed Gallardo et al. (2015) recommendations and included the Global Human Footprint layer (Wildlife Conservation Society (WCS) and enter for International Earth Science Information Network (CIESIN), 2005) as a variable for human influence on the species establishment and survival. This layer corresponds to the Human Influence Index (HII), which represents anthropogenic impacts on the environment. The HII is a global dataset of 1-kilometer grid cells, created from nine global data layers covering human population pressure (population density), human land use and infrastructure (built-up areas, night-time lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers) (Wildlife Conservation Society (WCS) and enter for International Earth Science Information Network (CIESIN), 2005).

## 2.4. Niche conservatism

To test if the environmental space of these species has been conserved in the introduced range, we conducted a native vs. introduced range analysis. We followed the methods implemented in previous work (Langdon et al., 2019), and the approach presented by (Broennimann et al., 2012) to test if the native niche of each species is conserved in the invaded niche (South-Central Chile). Two sets of occurrence points were prepared for each species, one for the native range and other for South-central Chile (introduced range). The environmental space was divided into  $100 \times 100$  cells, and all occurrence points were converted into density values, using a kernel function to smooth the distribution of the densities. Then 10,000 random points (i.e., pseudo-absences) were generated, to estimate the density of available environments in the environmental space. Based on the values of occurrence and available environments densities, an occupancy index was estimated. This occupancy index was plotted on the environmental space, for both the native and the introduced range. Niche overlap (shared areas between two niches) between introduced and native niche was assessed using three approaches:

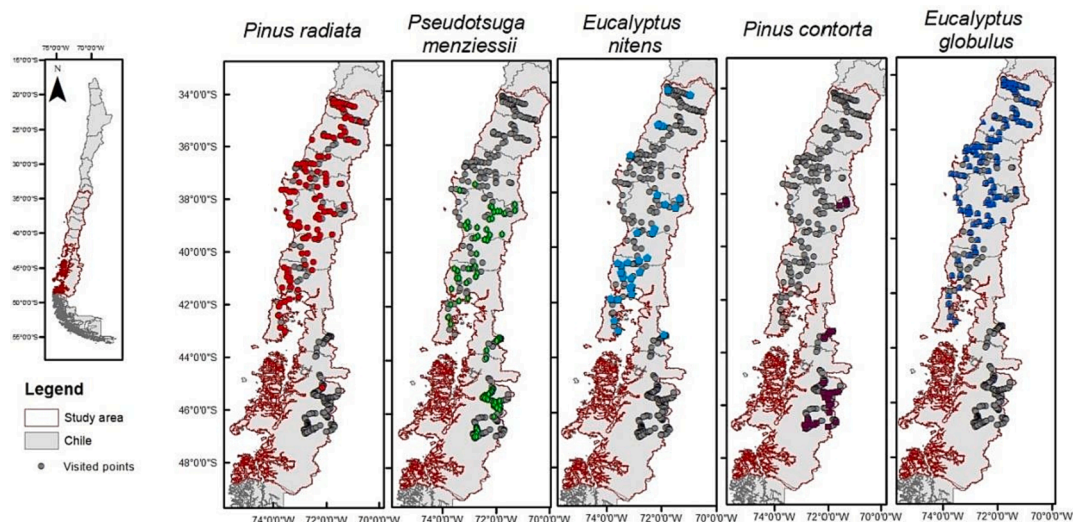




Fig. 1. Map of the study area in South-Central Chile between the Maule (34°0'0"S) and the Aysén (47°0'0"S) Regions where field work was carried out and Species Distribution Models were constructed (introduced range). Limits of the study area are indicated by red lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

- (i) Schoener's D overlap Index, ranging from 0 (no overlap) to 1 (complete overlap),
- (ii) niche equivalency, which determines whether niches of two entities in two geographical ranges are equivalent or whether the niche overlap is constant when randomly reallocating the occurrences of both entities among the two ranges). A significant

- value means a rejection of the hypothesis that the two niches are identical (Broennimann et al., 2012; Warren et al., 2008).
- (iii) niche similarity, which asks whether the Environmental Niche Models generated from two populations are identical or merely more similar than expected by chance (Warren et al., 2010). A statistically significant comparison in both directions (of native to



**Fig. 2.** Presence and absence records for each studied species within the study area (delineated in red) (introduced range). Coloured marks represent the presence of each species (*P. radiata* = 98 red circles, *P. menziesii* = 59 green diamonds, *E. nitens* = 28 blue hexagons, *P. contorta* = 26 purple squares, *E. globulus* = 94 dark blue triangles) and grey points represent all visited points where the species was absent of a total of 551 visited points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 2**

Records for each species used for the analyses. Native and global records were gathered from online databases. Regional data, at the introduced range, was collected during field work. Planted and naturalized occurrences do not sum the total, given that sometimes they were registered together in the same site.

Species	Distribution range		Introduced		
	Native	Global	Total	Naturalized	Absences
			(Naturalized + planted)		
<i>Pinus radiata</i>	48	1010	98	44	453
<i>Pinus contorta</i>	1119	1571	26	17	525
<i>Eucalyptus globulus</i>	105	886	94	27	457
<i>Eucalyptus nitens</i>	45	74	28	11	523
<i>Pseudotsuga menziesii</i>	1491	3041	59	5	492

invaded and of invaded to native) allows us to consider that both niches are more similar than expected by chance.

Complementary, according to (Petitpierre et al., 2012), overlapping the introduced and native niche in the environmental space, allowed us to identify three areas: a) stability niche area (S), b) unfilled niche area (U), and c) the expansion area (E). (Petitpierre et al., 2012) framework was limited to analogous climates between the native and invaded range, but following Webber et al. (2012), we decided to consider all available climates in both regions, including non-analogous climates. All niche analyses were carried out using R software (version 3.3.1) (R Development Core Team, 2008), with the BIOMOD, ade4, adehabitat, sp, gam, MASS, mvtnorm, gbm, dismo packages.

2.5. Species distribution models (SDM)

We used SDM to predict suitable areas for each one of the species studied in South-central Chile, both predicted from the global and the introduced range (Chile). We used Maxent (Phillips et al., 2006), a machine learning software that assesses the distribution probability of a species, by estimating the distribution probability of maximal entropy. This software has been proven to perform better than other software

commonly used with only presences data sets (Elith et al., 2006; Graham et al., 2008; Ortega-Huerta and Peterson, 2008). Model accuracy was tested using a cross-validation method. Occurrence data for each region was divided into two parts: 75 % for training and 25% for testing the model. Then, model performance was tested using the AUC (area under the ROC curve), ranging from 0.5 for a model that performs no better than chance, to 1, a model with a perfect ability to predict the species presence (Evans et al., 2009; Phillips et al., 2006). For SDMs regularization, we smoothed the models to avoid over-parameterization (Elith et al., 2011; Phillips et al., 2006). A threshold was established, defined by the 10% percentile of probability of occurrence (Townsend Peterson et al., 2011). All values, below that threshold, were discarded under the assumption that these figures represented unsuitable climatic zones. Each model was the average of 50 replicates. According to Thuiller et al. (2005a), model fitting is classified as bad when AUC < 0.8, acceptable when AUC ranges between 0.8 and 0.9, as good when AUC ranges between 0.9 as 0.95, and as excellent when ranges between 0.95 and 1.

The global SDM was constructed using all global occurrences and a global background to determine a proxy of the fundamental niche of the species. The regional SDM only considered occurrences in South-central Chile (the introduced range) with the study area background as a proxy of the realized niche of the species in the invaded range. Given that the differentiation between planted and naturalized individual is not available for occurrences gathered online, we decided to join our regional data for some of the analyses. It is known, and it will be considered during results interpretation, that the result could be affected by this decision, overestimating the potential distribution of the species to areas where it could not survive without human assistance.

For three of the species (*P. radiata*, *E. globulus* and *E. nitens*) we had enough regional occurrences of naturalized individuals to also model their potential distribution without considering planted individuals. So, in this case, we considered planted and naturalized occurrences as two datasets. This would give us an idea of the extent the species could reach without the human support given by forestry interventions.

2.6. Invasive stages

The global/ introduced range contrast was used then to infer the stage of invasion in the geographic space following Gallien et al. (2012) approach. To do that, probability occurrences predicted from both SDMs were extracted for each of the real occurrence points registered in the

invaded range. This information was depicted in a two dimensional plane, and we disposed the probability values obtained from the global (X axe) and the regional (Y axes) niche models (Gallien et al., 2012). This plane represents four hypothetical stages, defined by a threshold of 0.5: (i) quasi-equilibrium, the zone where both global and regional niche models include probabilities higher than 0.5; (ii) local adaptation, the zones where regional model predicts  $P(O) > 0.5$  and global niche model predicts  $P(O) < 0.5$ ; (iii) sink populations, the zone in which either global or regional niche models predict  $P(O) < 0.5$  and (iv) colonization stage, the zone in which global niche model predicts  $P(O) > 0.5$  and regional niche model predicts  $P(O) < 0.5$  (Gallien et al., 2012). These invasive stages were in turn projected in the geographic space which ranged from 35° to 49° latitude.

As an alternative way to assess whether each species is in a biogeographic equilibrium, we compared the environmental space of the presences versus the environmental space of the absences registered in South-Central Chile using the niche similarity index (Warren et al., 2008). If both spaces are more similar than expected by chance, then the species is not in equilibrium and more areas remain available to be invaded; if the climate environments are different, then the current presence of the species is in biogeographical equilibrium and then sites with absences are unsuitable for exotic plant establishment (Montecino et al., 2014).

### 3. Results

#### 3.1. Niche conservatism

Analyses showed that none of the five NNT species conserves their native niche in the invaded range (niche equivalency p-value of 0.0189 in all cases). This is confirmed by the Schoener's D overlap Index and the similarity test for all cases. Also, none of them presents a full overlap

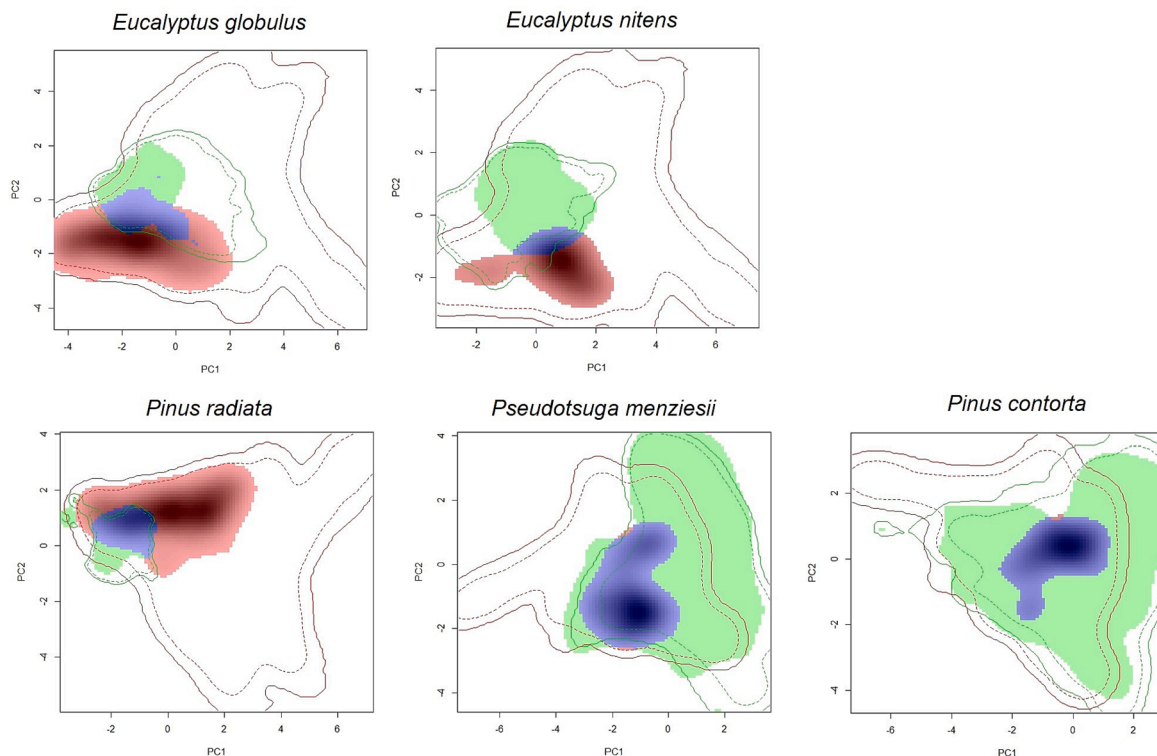
between the native and invaded niche (Fig. 3). Two of the five species, *P. menziesii* and *P. contorta*, show a high stability area, but also a high unfilling area, and a potential expansion of their niches by only 0.4% (Table 3). *Pinus radiata* and *E. globulus*, on the other hand, show a high expansion area, with a low stability area and an unfilled area of 16.9% and 55.5%, respectively. *Eucalyptus nitens* shows the higher expansion area (82.9%), with the lowest stability area (17.1%) and the highest unfilled area (89.8%).

#### 3.2. Species distributions models (SDM)

SDM fitting varied for the different species (Table S1). Global SDMs were the most accurate ones, with good (*P. contorta* and *P. menziesii*) or excellent fitting (*E. globulus*, *E. nitens*, and *P. radiata*) according to Thuiller et al. (2005a) classification. Regional SDM and Naturalized SDM (with naturalized occurrences only) presented acceptable fittings ranging between 0.8 and 0.9, except for *P. contorta* which presents good fitting in both cases.

##### 3.2.1. Variable contribution

SDMs were constructed based on different variable contributions for each species, for both the global and introduced range. In the global range, climatic variables arise as the main factor behind their distribution (Table S2). On the introduced range, on the other side, the Global Human Footprint (GHF) layer takes a more relevant role on the distribution of the species, making the highest contribution for *E. nitens*, *P. radiata*, and *E. globulus* (36.9, 35.5, and 30.9 % respectively) (Table S2). For the naturalized SDM, GHF layer was still the most relevant layer for *E. globulus* and *P. radiata*, contributing 40.6% and 32.6%, respectively.



**Fig. 3.** PCA-env results showing the climatic niche of the 5 species assessed along the two first axes of the PCA in their native (in green) and invaded (in red) ranges, and the overlapping area of both niches (in blue). Solid and dashed lines show 100% and 50% of the climatic envelope of each region. According to the Petitpierre et al. (2012) framework, the green area corresponds to the unfilled niche (U; environmental space occupied only in the native region), the red area to the expanded niche (E; occupied environmental space available only in the invaded region) and the blue area to the stability area (S; environmental space occupied both in the native and the invaded region). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Table 3**

Niche overlap assessment results for each one of the species based on the Schoener's D Overlap Index, the Similarity test (of Chile to the native range (2->1) and of the native range to Chile (1->2)), and the Niche Equivalency test. The last three columns show the [Petitpierre et al. \(2012\)](#) approach results with the Expansion (E; occupied environmental space available only in the invaded region), Stability (S; environmental space occupied both in the native and the invaded region), and Unfilling (U; environmental space occupied only in the native region) Areas for each species assessed.

Species	D	Similarity		Equivalency test p-value	Expansion (E)	Stability (S)	Unfilling (U)
		2->1	1->2				
<i>Eucalyptus globulus</i>	0.136	0.634	0.0198*	0.0198*	0.814	0.186	0.551
<i>Eucalyptus nitens</i>	0.118	0.812	0.0198*	0.0198*	0.829	0.171	0.898
<i>Pinus contorta</i>	0.346	0.178	0.099	0.0198*	0.004	0.996	0.816
<i>Pinus radiata</i>	0.14	0.238	0.0198*	0.0198*	0.794	0.206	0.169
<i>Pseudotsuga menziesii</i>	0.368	0.099	0.475	0.0198*	0.004	0.996	0.889

\*Represent statistically significant results.

3.2.2. Geographic extent

When a modelled niche was projected onto the map, we obtained a visual representation on the potential spatial extent of the species (Fig. 4). Each species shows a different potential distribution. *P. menziesii* shows the larger extent predicted by the Global SDM (304,838 km<sup>2</sup>), followed by *P. contorta*, *P. radiata*, *E. nitens* and finally *E. globulus* (134,274 km<sup>2</sup>). The Regional SDM predicts the higher potential surface of occupancy for *P. radiata* (109,250 km<sup>2</sup>), followed by *E. globulus*, *P. menziesii*, *E. nitens*, and *P. contorta* (63,269 km<sup>2</sup>) (Table 4).

To complement our results, SDM of only naturalized occurrences showed that the three modelled species (*E. globulus*, *P. radiata*, and *P. contorta*) can establish without human support along their whole regional distribution (Figure S1). Predicted areas follow the same trend as the Regional SDM, with *P. radiata* (115,030 km<sup>2</sup>) potential area being larger than the one predicted for *E. globulus* (112,088 km<sup>2</sup>) and *P. contorta* (59,254 km<sup>2</sup>).

3.3. Equilibrium of the invasion process

Our result of the similarity test carried for the environmental space of the presences and absences showed there are no differences between both environmental spaces. Equilibrium then, has not been reached by any of the studied species (Table 5). SDM comparison made following [Gallien et al. \(2012\)](#) approach showed the same trend, with all species going through different stages of the invasion process (Table 6) (Figure S2). *Pinus contorta* seems to have the highest stable population proportion (69.2%), followed by *P. menziesii* (50.9%) and *P. radiata* (48%). *Eucalyptus globulus*, on the other side, presents a high proportion

**Table 4**

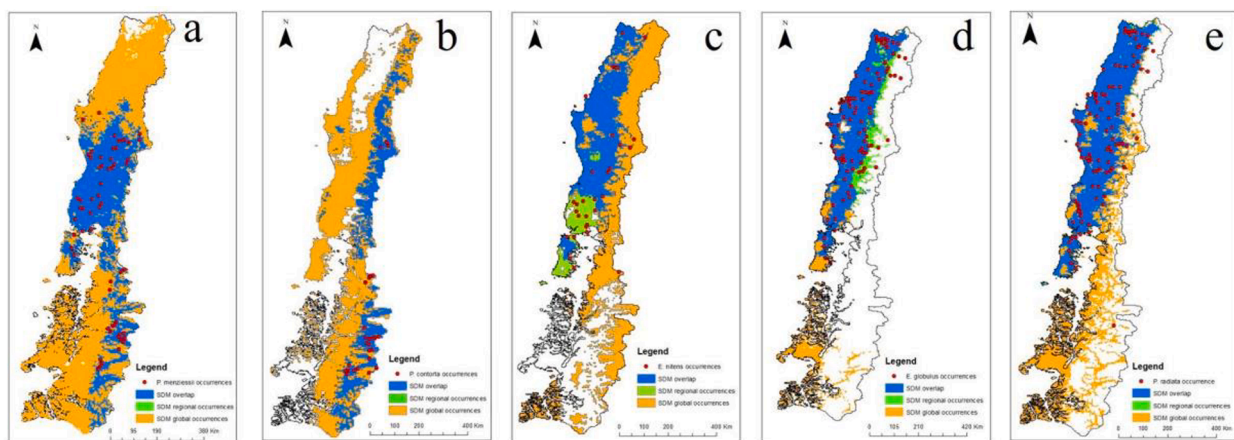
Estimated potential area of expansion for each one of the studied species in South-Central Chile according to the three Species Distribution Models (SDM) constructed for each one of them: with all Global occurrences, only regional occurrences (in the introduced range) and Naturalized occurrences (considering only naturalized occurrences in the introduced range).

SDM	Potential expansion area (km <sup>2</sup> )				
	<i>E. globulus</i>	<i>E. nitens</i>	<i>P. radiata</i>	<i>P. contorta</i>	<i>P. menziesii</i>
Global	134,274	209,173	217,151	232,120	304,838
Regional	102,293	98,175	109,250	63,269	105,339
Naturalized	112,088		115,030	59,254	

**Table 5**

Proportion of the environmental space of the presences which overlaps with the environment of their absences.

	<i>P. radiata</i>	<i>P. contorta</i>	<i>P. menziesii</i>	<i>E. globulus</i>	<i>E. nitens</i>
Schoener's D	0.653	0.353	0.523	0.722	0.694
Overlap Index					
Equivalency (p-value)	1	1	1	1	0.00198
Niche Overlap (%)	61	60	52	56	62



**Fig. 4.** Spatial distribution Models (SDM) for a) *Pseudotsuga menziesii*, b) *Pinus contorta*, c) *Eucalyptus nitens*, d) *Eucalyptus globulus*, and e) *Pinus radiata*. There are two SDM representations: Global SDM, based on global occurrences with a global background, and Regional SDM, based on regional occurrences (introduced region) with a regional background. Areas predicted only by the global niche are shown in orange, areas predicted only by the regional niche in green and areas predicted by both global and regional models (overlap area) in blue. White areas represent areas outside of both niches. Red dots correspond to occurrence points in the introduced range. SDMs were mapped using the 10% percentile rule for the probability of occurrence threshold. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 6**  
Proportion of populations (%) at each stage for each one of the species present in South-Central Chile.

Stage	<i>P. radiata</i>	<i>P. contorta</i>	<i>P. menziesii</i>	<i>E. globulus</i>	<i>E. nitens</i>
Quasi-equilibrium	48	69.2	50.9	14.2	27.6
Local adaptation	10.2	0	5.3	47.8	27.6
Colonization	27.5	15.4	31.6	5.4	3.4
Sink	13.3	15.4	12.3	32.6	41.4

of its populations going through an adapting stage (47.8%) and surprisingly, *E. nitens* presents 41% of its populations representing sink populations.

#### 4. Discussion

Our results show that all five NNT species have the potential to successfully establish and grow in South-Central Chile, thus confirming our hypothesis. It is not surprising, given that they have been introduced for commercial purposes and their establishment has been supported with technical and scientific information to secure success by climatically matching their regions of origin (Beuzeville, 1943; Elgueta et al., 1971; Prado D. et al., 1986; Toumey and Korstian, 1946). All these species have then overcome the first and second barriers of a potential invasion process, the human mediated introduction and the abiotic factors of the new environment (Richardson et al., 2000). Only two of the species, *P. contorta* and *P. menziesii*, have been planted under the same environmental space of their native niche. They share a high proportion of their climatic niche between South-Central Chile and their native areas (99.6% stability area), but there is still climatic niche available for them to occupy (81.6 and 88.9% of unfilling area, respectively). *Eucalyptus nitens*, *P. radiata* and *E. globulus* on the other side, occupy a completely different climatic space than their native ones, showing only a 17%, 18.6% and 20.6% of stability area, respectively (Table 3). In turn, they show high expansion areas (82.9%, 81.4, and 79.4%, respectively) which means that they have been planted under climatic conditions which could not meet their basic ecological requirements (as in their native range). The same issue has been discussed before for Pinaceae species (Nuñez and Medley, 2011; Pauchard et al., 2015; Zenni et al., 2014). According to Nuñez et al. (2017), foresters have tended to introduce provenances that are already adapted to the environmental conditions of the new environment. This is mostly accomplished by introducing specimens from other introduced areas instead of directly importing material from the native range.

These results are consistent with the analysis of the environmental space of presences and absences. Most of the niche studies carried out only focus on the species' presence (Valavi et al., 2021; D'Amen and Azzurro, 2020; Battini et al. 2019; Ahmad et al. 2019; Barbet-Massin et al. 2018; Taucare-Ríos et al. 2016; Gallardo and Aldridge, 2013; Václavík and Meentemeyer 2009), without considering their absence in the new territory. Including absences when analysing niche dynamics is quite relevant, given it allows better interpretation of the results and can make a difference in terms of management planning. Our results showed that there are no differences between the environmental space of species presences and their absences, allowing us to affirm that in those areas, where the species are not yet established, basic requirements should be met. Although, there are several mechanisms that could be acting behind these absences, and thus restricting the species establishment. Interaction with biotic factors, such as competition, herbivory, habitat availability or damaging agents as insects or diseases, could limit the establishment of invasive species, but on the other hand, it could simply be propagules have not yet arrived to the area. In that case, management planification should consider preventing the entrance of the species to those areas (for example, *E. nitens* to Patagonia or *P. menziesii* expanding its present distribution range to northern areas). Same trends

were found in previous work with the species *Acacia dealbata* in Chile (Langdon et al. 2019).

Global SDMs presented the best fitting for the data (Table S1), allowing us to see a proxy of the fundamental niche of each species in the introduced range. At the global scale, climatic variables are the main factor determining the presence of the species at the given locations, just as mentioned by (Gallardo et al., 2015), who stated that global occurrences of a wide variety of invaders are limited by climatic variables, but Human Footprint Index would still explain an important proportion of species distributions. Nuñez and Medley (2011) determined the same trend for pine species at the global scale, but when we downscaled our results to the introduced area or just considered the naturalized occurrences, human influence takes a higher importance. SDMs in the introduced range (for planted and naturalized occurrences) showed climatic variables as the main driver only for *P. contorta* and *P. menziesii*. For the widely planted *Pinus radiata*, *E. globulus* and *E. nitens*, potential distributions are based mainly on the GFH (Global Human footprint) variables, which could explain the large proportion of their Expansion areas (E).

According to Gallardo et al. (2015), human mediated activities arise as the main non-climatic drivers of invasion, being trade, transport, travel, and tourism the most reported ones (McNeely, 2001; Pyšek et al., 2010). In forestry, the introduction and establishment of the tree species are not the only drivers for potential invasion, there are other activities related to the industry which could enhance the process (Moore, 2005). Transport of products and/or machinery could increase seed and propagules dispersal, through soil remotion or adhesion to tires (Quiroz et al., 2009), disturbances, machinery or the use of contaminated materials related to road constructions could also promote dispersal and establishment of invasive species (Christen and Matlack, 2009; Foxcroft et al., 2010; Mortensen et al., 2009); and harvest, which given the elimination of vegetation cover and soil disturbance creates the optimal conditions for the establishment of plant invaders (Rejmanek et al., 2004; Rejmanek and Richardson, 1996).

According to our results, the large potential distribution of these species, reflects the need for a management strategy to prevent their expansion and negative impacts across multiple landscapes. Based on their global occurrences, and therefore the global SDM, *P. menziesii* and *P. contorta* present the larger potential distribution (Table 4). This is worrisome, given that both species have already been recognized as invasive in South-Central Chile with very well reported negative impacts on biodiversity and fire regimes (Franzese et al., 2020, 2017; Langdon et al., 2010; Pauchard et al., 2008; Peña et al., 2008; J Urrutia et al., 2013a,b). *Pseudotsuga menziesii* has been reported as an initial stage of the invasion process, regenerating under parent stands or in open areas of native forests, but it has the potential to negatively impact native species (Pauchard et al., 2008). *Pinus contorta*, on the other side is known for being one of the most invasive pine species, enhanced by its small seeds, the short juvenile period and regular mast seeding events (Gundale et al., 2014; Langdon et al., 2010; Ledgard, 2001; Pauchard et al., 2016; Peña et al., 2008; Rejmanek and Richardson, 1996). In Chile, *P. contorta* invasion has been widely studied (Urrutia et al., 2013; Cobar-Carranza et al. 2014; Bravo-Monasterio et al. 2016; Franzese et al. 2017; Taylor et al. 2017; Davis et al. 2019). There is just a small difference between the potential expansion area of *P. contorta* or *P. menziesii* and the area estimated for *P. radiata*, *E. globulus* and *E. nitens*, although they have not been recognized as widely expanded invasive species in Chile, yet. To date, research on *P. radiata* invasion in Chile, has determined that the species can regenerate on the edges or disturbed areas of the Maulino native forests (Bustamante and Simonetti, 2005; Gómez et al., 2011) posing a threat for this endangered ecosystem, although maintaining a closed canopy on surrounding native forests could prevent *P. radiata* wildlings to establish (Gómez et al., 2019). *Eucalyptus* species have been poorly studied in Chile, but there is evidence that *E. globulus* is the most invasive eucalypt species (Rejmanek and Richardson, 2013). Climate, plantation size and age, fire occurrence, cover type and



disturbances, among others, have been related to Eucalypt wilding establishment (Águas et al., 2017; Catry et al., 2015; Deus et al., 2019; Fernandes et al., 2016; Larcombe et al., 2013; Ziller et al., 2019).

*Pinus contorta*, *P. menziesii* and *P. radiata* present the highest proportion of stable populations (69.2, 50.9 and 48% respectively), predicted by both the global and regional SDMs. *Eucalyptus globulus* adapting populations (47.8%) are, on the other side, predicted by the Regional SDM, but not by the global SDM. This means that most of its commercial plantations are established under new conditions, different from those of its native range. Surprisingly, *E. nitens* populations are mostly established under sink conditions (not predicted by the Global or Regional SDM), which means that they could represent a lower risk of invasion given that these conditions would not fulfil their minimum requirements.

The last report on Chilean Forest Resources (INFOR, 2018), shows that commercial plantations reach 2,303,880 ha, being *P. radiata* (1,285,635 ha), *E. globulus* (558,510 ha), and *Eucalyptus nitens* (273,039 ha) the species with the highest planted area. The same report indicates that according to annual plantation surface, *P. radiata* is still the most planted species, followed by both eucalypts. Most of these plantations locate in the Biobío Region (27.4%), followed by the Araucanía (21.2%), and Maule (16.7%) Regions (INFOR, 2018). When sustainably managed, commercial plantations of non-native trees present large economic and societal benefits with low risk of invasion or negative impacts (Brundu et al., 2020), but that is the challenge. Known negative ecological impacts of NNTs are increasing rapidly, mainly due to their ability to act as ecosystem engineers, altering the structure and functioning of the ecosystem (Brundu et al., 2020). Economic impacts have also been assessed lately, and negative impacts on human well-being have only been considered for a few years, mainly through the study of effects on ecosystem services (Viñã and Hulme, 2017). Therefore, achieving sustainable management of extensively planted non-native tree species, involves economic, social, and environmental aspects. SDMs responsibly developed and interpreted can give insights into the ecology of the species, where spread is more prone to occur. But that is not enough, economic assessments to make potential management scenarios cost-effective, and community (stakeholders) engagement are crucial to develop successful long term management plans (García-Díaz et al., 2022, 2021; Keller et al., 2009; Linders et al., 2021), especially when large surfaces are already covered with the species and a larger area is available for their expansion. Our results can be an input for the ongoing “National Biodiversity Strategy 2017–2030”, which explicitly includes “Management of Exotic Invasive Species.” Horizon screening for potential new introductions, Risk assessments and prioritisation lists are being developed to manage the threat that invasive species pose to Chilean Biodiversity.

SDMs, despite being a useful tool for informing decision processes, do not consider demographic or physiological factors which finally determine the presence of a certain species at a given location (Briscoe et al., 2019). Therefore, we are aware that these results could be over-estimating the potential distribution of the species. Next steps consider using implementing better sampling techniques (Perret and Sax, 2022) and process explicit models (Briscoe et al., 2019), which incorporate biotic and abiotic factors driving species populations and determining their realized niche. Unfortunately, this approach would involve more variables which are not always easy to assess, because of the species or system studied or the lack of resources to do so. That is why initiatives as the CONTAIN Project, which aims to develop a tool for planning long term management of invasive species using an approach that considers demographic, dispersal, and environmental variables to simulate different management scenarios are much more appropriate (Lambin et al., 2020). Moreover, new studies incorporating the potential change in their distribution given climate change should be assessed. Considering climate change trends would allow for better predicting how species distributions and potential impacts would change, and therefore developing effective preventive, management, control and restoration

strategies (Etherington et al., 2022; Finch et al., 2021; Srivastava et al., 2019).

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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BL and RB Conceptualization; BL Data curation; BL and RB Formal analysis; BL, AP, and RB Funding acquisition; BL Investigation; BL and RB Methodology; BL Project administration; BL Resources; BL and RB Software; BL, RB, and AP Validation; BL Visualization; BL Roles/Writing – original draft; BL, RB, and AP Writing – review & editing.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120726>.

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