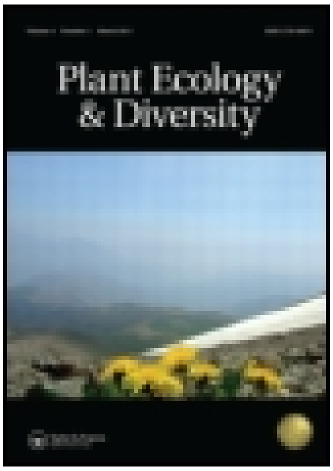

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Climatic and socio-economic factors determine the level of invasion by alien plants in Chile

Nicol Fuentes[ab], Alfredo Saldaña[c], Ingolf Kühn[def] & Stefan Klotz[df]

[a] Laboratorio de Invasiones Biológicas, Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, Chile

[b] Instituto de Ecología y Biodiversidad, Santiago, Chile

[c] Departamento de Botánica, Universidad de Concepción, Concepción, Chile

[d] Department of Community Ecology, UFZ, Helmholtz Centre for Environmental Research, Halle, Germany

[e] Institute of Biology/Geobotany and Botanical Garden, Martin-Luther University Halle-Wittenberg, Halle, Germany

[f] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

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Climatic and socio-economic factors determine the level of invasion by alien plants in Chile

Nicol Fuentes[a,b], Alfredo Saldaña[c]*, Ingolf Kühn[d,e,f] and Stefan Klotz[d,f]

[a]*Laboratorio de Invasiones Biológicas, Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, Chile;* [b]*Instituto de Ecología y Biodiversidad, Santiago, Chile;* [c]*Departamento de Botánica, Universidad de Concepción, Concepción, Chile;* [d]*Department of Community Ecology, UFZ, Helmholtz Centre for Environmental Research, Halle, Germany;* [e]*Institute of Biology/Geobotany and Botanical Garden, Martin-Luther University Halle-Wittenberg, Halle, Germany;* [f]*German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany*

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Background: Economic activities are substantial factors in alien plant establishment and invasions. Climate also plays an important role in the distribution of alien species.
Aims: We evaluate the relationship between alien species density and both climatic and socio-economic factors at the scale of provinces located in a latitudinal-bioclimatic gradient in Chile.
Methods: We used generalised linear models with backward selection to evaluate the relative importance of each parameter (human population, gross domestic product, length of traffic routes, crop cover, abandoned crop cover, artificial plantations, protected areas, annual rainfall and temperature) on species density. We compared the average species density among climate types.
Results: Alien density was higher for provinces located in the most populated areas with Mediterranean and temperate oceanic climates (south-central Chile) and decreased for less populated provinces in the north and the southernmost parts (desert and sub-Antarctic wetlands). Human population, length of traffic routes and annual rainfall significantly explained the variation in alien species density in Chile.
***Conclusions*:** Although human population still increases, the results can be used especially in high priority conservation areas where traffic routes and human settlements can be objectively reduced or managed, to reduce the potential increase in the number of alien species.

Keywords: alien plants; Chile; latitudinal gradient; climate; socio-economic parameters

Introduction

Economic development plays an important role in the intensity and spatial distribution of alien plant occurrences (Thuiller et al. 2006; Lin et al. 2007; Pyšek et al. 2010). Increments in economic developments result in an increase in human activities (i.e., trade, travel, transport, land use and land use change, such as deforestation), which yield increased propagule pressure from alien plants and results in their subsequent establishment (Lonsdale and Lane 1994; Taylor and Irwin 2004). Thus, propagule pressure is directly related to alien plant invasion and can be used to determine the level of biological invasion in a region. Detailed data on propagule pressure are hard to obtain, and is the data are often assessed by using surrogates (e.g., human population, traffic routes and macroeconomic parameters) (Vilà and Pujadas 2001; Westphal et al. 2008; Essl et al. 2011). For instance, human population density and per capita gross domestic product (GDP) have been positively correlated with alien plants (Dalmazzone 2000; Taylor and Irwin 2004; Liu et al. 2005; Pyšek et al. 2010). However, the relationship between socio-economic parameters and alien plants must be interpreted with caution since these parameters are not direct causal determinants of the invasion process, but instead reflect the intensity of human activities, which results in more alien plants being transported, increasing the risk of their invasion.

Nonetheless, alien plant distributions are not only affected by human activities (Thuiller et al. 2006; Pyšek et al. 2010; Dainese et al. 2014). Climatic factors also affect their distributions. Alien plants can only succeed in new areas where climatic conditions allow them to survive, establish and spread (Panetta and Mitchell 1991; Scott and Panetta 1993), but the effect of climatic factors can be overridden by the impact of human activities (Pyšek et al. 2007; Pyšek et al. 2010). Hence, the combination of these factors is particularly interesting to study in areas with marked climatic heterogeneity, such as southern South America, where also there are few studies about plant invasions but an increasing need to recognise threats and develop programmes to better control invasive species (Gardener et al. 2012; Fuentes et al. 2013).

Chile, a biodiversity hotspot of the world (Myers et al. 2000), is experiencing immense economic growth, which results in increasing propagule pressure by alien plants (Fuentes et al. 2010; Pauchard et al. 2011). This pressure, associated with current climatic and environmental variation, and increasing human activities in Chile, may represent an ideal opportunity for alien plant establishment and

*Corresponding author. Email: asaldana@udec.cl

spread (Arroyo et al. 2000; Fuentes et al. 2008; Pauchard et al. 2011). For instance, Arroyo et al. (2000) documented a positive relationship between alien plant richness and land use at a regional scale. However, this study did not include alien plants that can impact natural ecosystems and did not take into account the wide climatic and environmental variations within the country. Therefore, a better understanding of the factors, which enable alien plants to colonise new environments, involving human-generated habitat disturbances and climatic factors is needed. Identifying the factors that influence the distribution of alien species on a spatial scale that is related to the intensity of economic activities (i.e., province scale) is desirable to relate the invasion process along a climatic gradient to land use and potentially aid in orienting conceiving programmes for their management or control.

In this article, we examined the relationship between alien plant species density and both climatic and socio-economic factors. Specifically, this article aimed to answer the following questions: (1) Which factors (i.e., human population, GDP, land use types, annual rainfall and temperature) determine the level of biological invasions, defined as the number of alien plants in Chilean provinces? (2) What is the relative importance of climatic factors, compared with socio-economic factors?

Materials and methods

Study area

Given that Chile has been strongly isolated from other areas of South America (Armesto et al. 1998) and is considered a continental island with a wide ecological gradient (Arroyo et al. 1999), the country represents an ideal location to evaluate the introduction and invasion by alien plants as a result of the five centuries of interchange between the Old World and the New World (Fuentes et al. 2010). Chile extends over 40 degrees of latitude (4300 km), and administratively, the country is divided into 50 provinces (which range from 582 to 67,813 km^2 in extent), sequentially ordered from north to south. This arrangement is closely correlated with increasing precipitation and decreasing temperature with increasing latitude (Di Castri and Hajek 1976; Luebert and Pliscoff 2006), establishing a smooth gradient in climatic conditions and a sequence of biomes, from hyperdesert in the north, a central Mediterranean climate region in the centre and temperate rain forest and cold sub-Antarctic wetlands in the south (Figure 1(a)).

Data source

The number of alien plant species in each province was obtained from the Chilean alien plants database (see details in Fuentes et al. 2013). The Chilean alien plant database includes spatial distribution records (geo-referenced) of all alien plants that are considered naturalised in terrestrial habitats (*sensu* Richardson et al. 2000). The spatial distributions were obtained from the records compiled within the assessing large-scale environmental risk for biodiversity with tested methods (ALARM) Project (Settele et al. 2005), which are also based on the CONC Herbarium. Although herbarium records are heterogeneous in terms of locations and habitat descriptions and are also limited by different criteria and sampling efforts (Delisle et al. 2003; Lavoie et al. 2005; Fuentes et al. 2008), they do provide valuable information for retrospective and predictive studies of plant invasions and represent an accessible data source for exploring large-scale patterns of alien plant distributions (Deutschewitz et al. 2003; Seabloom et al. 2006).

Using the Chilean alien plants database, we developed a geographic information system layer and compiled all naturalised species present in each Chilean province. Additionally, two-thirds of all alien plants in the database are invasive elsewhere (Fuentes et al. 2013). We used alien plant species density per province (total number of alien plant species divided by the $\log_{10}$ area of each province), to avoid biases due to the differing sizes of the provinces (Lonsdale 1999). We included provinces with at least one alien species that had more than 50 specimens registered in that province. Species with fewer specimens were excluded from the analyses because it was difficult to infer their geographical/temporal distribution, due to the strong sampling biases in herbarium records in Chile (Fuentes et al. 2013). Considering a minimum of 50 specimens, we ensured that at least the species did not disappear after some time, because this amount of records can reflect that a given species has had enough time to be naturalised (Aikio et al. 2010). Moreover, 50 specimens per species has been found useful in assessing the trend of expansion of invasive species over a long period of time, estimating the initial and the end of the invasion (Aikio et al. 2010). The socio-economic and climatic factors included human population density, GDP per area, length of traffic routes, percentage of crop cover, percentage abandoned crop cover, percentage of artificial plantations (*Pinus* spp., *Eucalyptus* spp. and *Atriplex* spp.), percentage of protected areas (parks, reserves and monuments), annual rainfall and temperature (maximum, minimum and mean annual) (Table 1). The climatic variables were obtained from the WorldClim database (www.worldclim.org). We averaged seven to nine values per each climatic parameter from randomly selected points in each province from a raster cell resolution of 25 × 25 km, to include the environmental heterogeneity at this spatial level (average surface per province = 15,000 ± 2300 km^2).

Statistical analysis

All variables were standardised to zero mean and unit variance to achieve comparable influence. The standardised values were used to test for multicollinearity, using a correlation matrix (Sokal and Rohlf 1995). We arbitrarily considered $r^2 = 0.8$ as a threshold of collinearity between two predictors. Among closely correlated predictors, we

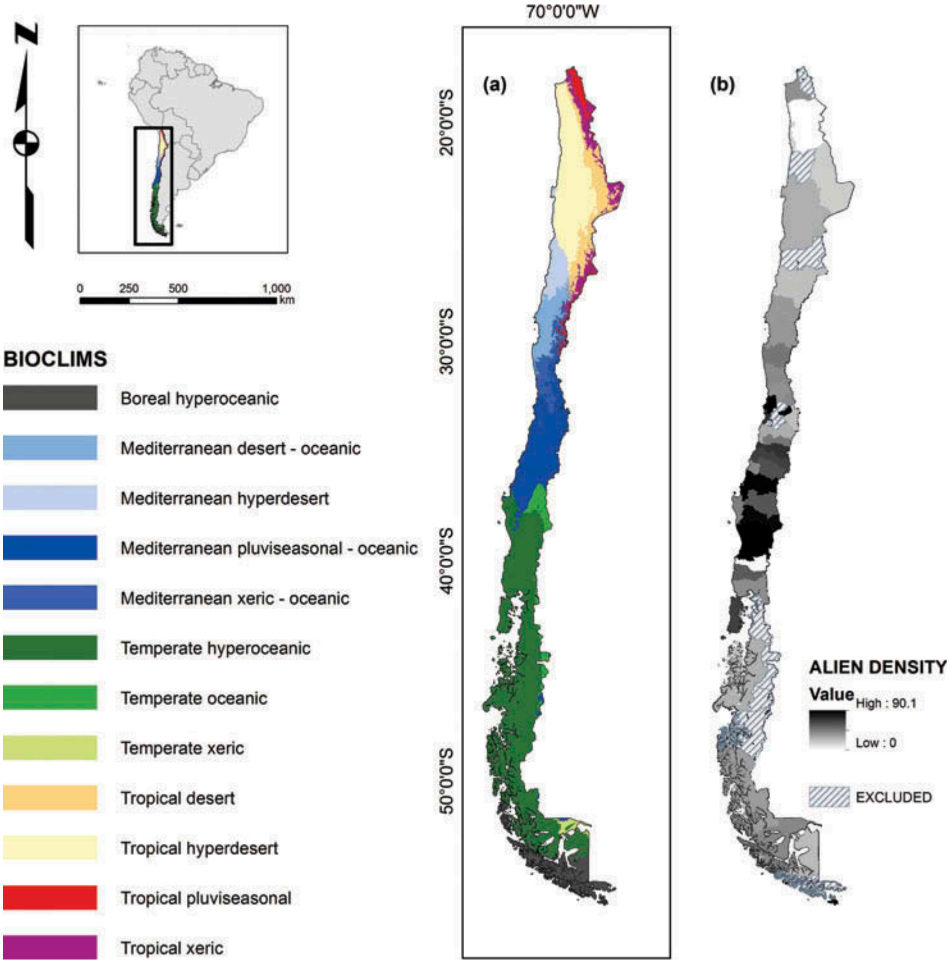

Figure 1. Climates zones and alien plant species density by province of continental Chile. (a) Geographic location and climate zones of continental Chile (Source: Luebert and Pliscoff 2006, 2009). (b) Graphic representation of alien plant species density by province (38 provinces), from high (black) through intermediate (grey) to low (white). Twelve provinces were excluded from the analysis (solid line) (see Methods section for details) (North area: Parinacota, Tocopilla and Chañaral. Central area: Chacabuco, Melipilla, Talagante and Maipo. South area: Palena, Coyhaique, General Carrera, Capitan Prat and Antartica).

Table 1. Sources of the land use, climatic and socio-economic parameters to analyse their relationship with alien plant species density at the province scale in Chile.

Parameter	Units	Source of data
Human population density	Inhabitants/km^2	Instituto Nacional de Estadísticas, INE (2009)
Gross domestic product	CLP$	INE (2009)
Length of traffic routes	km	Ministerio de Obras Publicas (MOP)
Crop cover	ha	INE (2009)
Abandoned crop cover	ha	INE (2009)
Forest plantations (*Pinus* spp., *Eucalyptus* spp. and *Atriplex* spp.)	ha	INE (2009)
Protected areas (parks, reserves and monuments)	ha	INE (2009)
Annual rainfall	mm	Jones et al. (2008)
Temperature (maximum, minimum and mean annual)	°C	Jones et al. (2008)

chose the one with more direct ecological impact on alien plant species distributions. The highest correlation among predictors in the final model was $r^2 = -0.72$, between percentage protected areas (parks, reserves and monuments) and maximum temperature (see Supplemental Data). We used generalised linear models (GLM) with backward selection based on Akaike's Information Criterion to evaluate the importance of each predictor on alien plant species density. We used a spatial Durbin–Watson test for residual autocorrelation (Seber and Wild 1989; Sol et al. 2008). Spatial correlation was estimated using Moran's *I* correlograms and significance was

Table 2. Partial coefficients of GLM between alien plant species density and land use, climatic and socio-economic parameters in Chile.

Parameters	Partial coefficients
Human population density	0.54***
Length of traffic routes	0.18**
Crop cover	0.07
Abandoned crop cover	0.04
Artificial plantations	0.10
Annual rainfall	0.34***
Temperature (minimum and maximum)	0.08
R^2	0.74
R^2 adj	0.71
Durbin–Watson (test for spatial autocorrelation)	0.30

Notes: Thirty-eight provinces were included in the analysis since 12 provinces had 50 or less alien plant specimens recorded.
**, $P < 0.01$; ***, $P < 0.001$.

assessed by using 1000 permutations (Bjørnstad 2004; Kühn 2007). A total of 38 provinces were included in the analyses, since 12 provinces had only alien species with 50 or less specimens collected (Figure 1(b)). The excluded provinces were those located in the extreme north (Parinacota, Tocopilla and Chañaral) and the extreme south (Palena, Coyhaique, General Carrera, Capitan Prat and Antartica) of Chile, with the exception of four provinces located in the central part (Chacabuco, Melipilla, Talagante and Maipo) (Figure 1(b)). We did not find significant spatial autocorrelation among the residuals of our analysis of the 38 provinces, neither using the spatial Watson–Durbin test (Table 2) nor Moran's *I* correlograms (see Supplemental Data). We carried out a one-way analysis of variance to test for significant differences in mean alien species densities among climate types. This analysis was run with seven climate types because it was necessary to merge some of the similar climates to increase the number of provinces per climate (e.g., tropical desert with tropical hyperdesert; Figure 1(a)).

Results

We found a positive correlation between human population density and GDP per area ($r^2 = 0.94$) and between minimum and maximum temperatures and mean annual temperatures ($r^2 = 0.91$ and 0.95, respectively). Thus, we selected human population density instead of GDP and minimum and maximum temperatures instead of mean annual temperatures for further analysis (see Supplemental Data correlation matrix).

Mean alien plant species density showed significant differences among climate types ($F_{6,31} = 2.994$, $P < 0.05$). Hence, alien species density was higher for provinces located in the south-central part (i.e., the most populated area of the country with Mediterranean climates) and decreased for less populated provinces in the northern and southern parts (i.e., desert and boreal hyperoceanic climates [cold sub-Antarctic wetlands], respectively) (Figure 1(b)). We found significant positive relationships between alien plant species density and human population density, length of traffic routes and annual rainfall, explaining almost 75% of the variation (Table 2).

Discussion

This study identified the correlates of the distribution of alien plants, namely human population density, length of traffic routes and annual rainfall, hence evaluating these patterns with better resolution (i.e., province scale) than the few previous studies in Chile. Thus, it helps to better understand the invasion process throughout the environmental gradients across this country. Our results showed that the level of alien plant species richness could be predicted to a reasonably high degree. This result corroborates claims that both parameter types (climatic and socio-economic factors) must be simultaneously assessed to elucidate their influence on the level of alien plant distribution.

Annual rainfall was significantly related to alien plant species densities, which is not unexpected, since climatic conditions constitute an important factor in influencing the distribution of plant species richness along latitudinal gradients (Gaston 2000). Additionally, the physical factors that favour high numbers of native species also directly increase niche opportunity for alien species (Shea and Chesson 2002). In this case, annual rainfall was related to the potential geographical range where alien plants can establish populations within Chile, influencing habitat quality and population dynamics. Interestingly, the level of alien plant occurrence did not increase with temperature but with precipitation. This suggests that in Chile, alien species are not limited by temperature but limited by available water (Currie 1991; Francis and Currie 2003). On the other hand, alien plant species density was not only related to climatic conditions, supporting the hypothesis that their distribution is a consequence of the combined effects of various factors, including human activities. It is most likely that these factors operate at different spatial scales, with socio-economic factors acting at local scales (since they reflect perturbation and local land management) (Essl et al. 2011), and climatic factors working at larger spatial scales (Shea and Chesson 2002).

Human occupation and various related activities contribute to increasing alien plants (Arroyo et al. 2000; Mckinney 2002; Pyšek et al. 2010; Sharma et al. 2010; Marini et al. 2012). Urban centres represent hubs of alien species by being storage sites for seeds (intentionally or accidentally introduced) that originate from trade (external and internal) and by being meeting points of traffic routes that not only facilitate the spread of, but are also habitats for alien plants (Trombulak and Frissell 2000; Christen and Matlack 2009). The combined effects of both of these factors make cities and traffic routes sources as well as receptors and corridors for the spread of alien plants. This may explain the low density of alien plants in provinces with less human population and traffic routes (north and south parts). Additionally, recent studies in Chile have confirmed the important role of roadsides for the dispersal of alien plants into protected areas (Pauchard and Alaback 2004) and have also linked the exchanges of alien plants between Chile and Argentina (Fuentes et al. 2010).

Contrary to our expectations, we found no significant effects of forest plantations and crop cover on the density of alien plant species, though both were related to the arrival and increment of alien plants collected since the early nineteenth century (Fuentes et al. 2008). In Chile, many plants have been introduced for crops, ornamental and medicinal purposes over the last century (Matthei 1995). As a result, many alien plants introduced as contaminants with imported seeds eventually have become naturalised and invasive (Matthei 1995; Arroyo et al. 2000; Pauchard et al. 2011). However, in heavily managed crops and forest plantations, many alien plants are unable to survive the intense competition, management selection of species and the effect of agrochemicals (Thiele et al. 2009). This could explain the low number of alien plants in provinces located in central Chile (Chacabuco, Melipilla, Talagante and Maipo), which have intensive and heavily managed crops (Matthei 1995). Taking this into account, traffic routes and cities probably constitute less competitive habitats than croplands and forest plantations do and have a greater effect on alien plant invasions.

Conclusions

Human population, length of traffic routes and annual rainfall were significantly related to alien plant species density at the province scale in Chile. However, we also recognise that variation in alien plant densities may be attributed to differences in residence time (or time since introduction) and propagule pressure of species pre-adapted for Mediterranean/temperate climate areas (Figueroa et al. 2004; Castro et al. 2005). Further research on the factors that determine the level of invasion in Chile should also include these parameters. Propagule pressure has been high in Mediterranean/temperate climates in Chile since the Spanish colonisation (Aronson et al. 1998; Fuentes et al. 2008), in contrast to northern and southern Chile; areas that exhibit disproportionately low introduction efforts of species pre-adapted to those more extreme climates (Fuentes et al. 2013). Thus, traffic routes, human population, climatic factors and several facets of propagule pressure all co-vary and influence alien plant species density. We recognise that the human populations, along with the disturbances they cause, are undoubtedly far from decreasing. Knowing that these factors (together with climate variation) influence alien plant species density and show considerable lag times (Essl et al. 2011) can aid in improving designing management and control programmes and calls for rapid action, especially in areas of high conservation priority, where traffic routes and human settlements can be objectively reduced to avoid alien plant invasions (Gardener et al. 2012; Squeo et al. 2012). In this context, Latin American countries show the need to develop spatially explicit inventories, research on the invasion process and weed risk assessments that can help to prioritise and streamline actions (Gardener et al. 2012). On the other hand, in areas of high human population and disturbances, returning the ecosystems to a more pristine condition may be not possible in terms of time, effort and resources, since eradication of alien plants has limited application and control is expensive (Wittenberg and Cock 2005). In order to maximise resources, conservation value and ecosystem services, we should to consider novel approaches to management those types of ecosystems containing new combination of species that arise through human action, environmental changes and introduction of species (i.e., novel ecosystems) (Hobbs et al. 2006; Gardener et al. 2012). Since novel ecosystem will increase, it will be necessary for a deeper understanding on how to manage them, in ways that will promote ecosystem services and conservation value. In this context, to identify the factors that influence the distribution of alien species on a small spatial scale in a climatic gradient, can help to determine which of these factors are more associated with those zones where the landscape maintain their historical configuration, mix new and old biotic components, or form entirely novel systems (Hobbs et al. 2009).

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Supplemental data

Supplemental data for this article can be accessed here.

Notes on contributors

Nicol Fuentes is a postdoctoral researcher who is interested in ecology of alien plant species and invasion processes.

Alfredo Saldaña is a full professor whose research interests focus on plant species distribution and plant ecophysiology.

Ingolf Kühn is a researcher who is interested in plant invasions and their relevance for the diversity of plant species.

Stefan Klotz is the head of the Department of Community Ecology at the Helmholtz Centre for Environmental Research – UFZ, Germany. He is mainly interested in biogeography and ecology of alien and native plant species.

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