RESEARCH ARTICLE



A classification system for predicting invasiveness using climatic niche traits and global distribution models: application to alien plant species in Chile

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Abstract

Functional traits that predict plant invasiveness are a central issue in invasion ecology. However, in many cases they are difficult to determine, especially for a large set of species. Climatic niche traits can overcome this problem due to the ease of acquiring them for a large number of species. This effort is critical given that knowledge of species invasiveness is necessary (although not sufficient) to anticipate/manage invasive species.

In this study, we examined thermal and hydric niche traits to predict plant invasiveness. We used a set of 49 alien plant species, representative of the alien flora of Chile. Niche traits were obtained using environmental information (WorldClim) and global occurrences. Invasiveness was estimated using global niche models and projection of the potential distribution in Chile. As a final step, we reviewed the literature for a subset of species, documenting their impacts on a) biodiversity, b) crop agriculture and c) livestock.

Thermal niche breadth and thermal niche position were the most important niche traits to predict potential distribution (a proxy of invasiveness). Using thermal niche breadth and niche position traits, we constructed a graphical model that classifies alien species as highly invasive (wide thermal niche breadth and low niche position) or low potential to be invasive (narrow niche breadth and high niche position). We also found no association between our invasiveness classification and the documented impact of alien species.

Keywords

Chile, climatic niche, alien plants, functional traits, hydric niche, invasiveness, potential distribution, thermal niche, invasion ecology

Introduction

Which traits make alien species invasive? This question has been central in invasion ecology (Drake 1989; van Kleunen et al. 2010). Amongst alien plants, morphological, functional or life history traits have often been used to explore which traits are the best predictors of invasiveness; i.e. the capacity of alien species to spread across new ranges (Rejmánek et al. 2005). However, this approach is controversial due to the difficulty of obtaining accurate and representative trait values for a large set of species (van Kleunen et al. 2010), as well as because, in some cases, their predictive value is variable, as the adaptive value of traits can be context-dependent (Daehler et al. 2004; Pyšek and Richardson 2007; van Kleunen et al. 2010).

An alternative approach has been the use of climatic niches of alien species to predict invasiveness (Castro-Díez et al. 2011; Thuiller et al. 2012). The climatic niche is defined as the set of climatic conditions within which a species is able to persist and maintain a stable population (Soberón 2007). Once an alien species arrives in a new range, climate is the first barrier it must surmount in order to establish and eventually spread across the new range (Higgins and Richardson 2014; Pearson and Dawson 2003).

According to niche-biotope duality (Colwell and Rangel 2009), species distribution models (SDMs) are appropriate tools to link niche requirements to geographic space, generating a probabilistic map that describes habitat suitability (Elith and Leathwick 2009). For alien species, these models can be used to extrapolate potential distribution from native ranges to other regions (transferability) (Peterson et al. 2011). Transferability of SDMs assumes that niches are conserved in alien species (Wiens et al. 2010); consequently, predictions should properly be made only to climate analogue regions (Di Febbraro et al. 2013; Richardson and Thuiller 2007). Moreover, the size of the area predicted by SDMs can be regarded as a *proxy* of invasiveness, as this area represents the potential area that the species might occupy (Castro-Díez et al. 2011; Lloret et al. 2004).

As alien species certainly colonise non-analogue climate regions due to niche shift (Tingley et al. 2014), it is possible to construct global species distribution models (GSDMs) using information of the totality of regions where the species have been registered (Pertierra et al. 2017). Under these conditions, the niche conservatism assumption is not necessary (Gallien et al. 2012).

At a biogeographical level, two climatic niche traits can be used: (i) climatic niche breadth (i.e. the range of climate variation where a species occurs) (Gregory and Gaston 2000; Quintero and Wiens 2013) and (ii) climatic niche position (i.e. the degree of matching between climatic niche requirements and the climate in the invaded

range) (Thuiller et al. 2012). Estimating these traits requires records of species occurrences and of the climate conditions associated with such occurrences; climatic niche breadth and climatic niche position have been successfully used to predict invasiveness in other studies (Jiménez-Valverde et al. 2011; Quintero and Wiens 2013; Slatyer et al. 2013). Moreover, they can be easily estimated for a large number of species, given the huge amount of freely-accessible climate information (WorldClim: https://www. worldclim.org/) and the availability of occurrence data for invasive species worldwide (GISD; http://www.iucngisd.org/gisd/search.php).

Chile is currently home to a large and rapidly increasing number of alien plants; more than 700 alien vascular plants have been recorded (Fuentes 2014; Fuentes et al. 2013). Additionally, Chile contains a notable variation in climate regions (Di Castri and Hajek 1976), so it constitutes an ideal scenario for invasion by alien plants from different biogeographic regions of the world (Fuentes 2014). In particular, Chile has a wide range of temperatures and precipitation along elevation and latitude gradients, so climatic niche traits ought to be critical for an understanding of the invasive potential of alien plants in Chile (Cuesta et al. 2019).

The term invasiveness is often correlated positively with harmful impacts on biodiversity, economy or health. This may be because, as a species spreads across a larger area, it has a greater probability of producing detrimental effects on the environment (Ortega and Pearson 2005; Ricciardi et al. 1996); however, the evidence indicates that, in some cases, this is not the situation (Ricciardi and Cohen 2007). Therefore, the assumption that invasiveness implies harmful impact needs to be tested case by case.

Making a distinction between invasiveness and impact is critical for management. The Chilean government has identified various different actions needed for the management of invasive species in Chile. One of them is to conduct basic and applied research to develop validated procedures to study invasiveness and risk analysis for hundreds of alien species living in aquatic and terrestrial ecosystems ("Estrategia Nacional de Biodiversidad" (2017–2030). The information about GSDMs of alien species and methods we have proposed in this study should contribute to these needs by calculating the "likelihood" of aliens to spread, as well as the climatic determinants of such spread (Benito et al. 2009; Settele et al. 2005).

In this study, we have examined climatic niche traits to predict invasiveness for a set of alien plants in Chile. In order to do so, we used global climate information to obtain the thermal and hydric niche breadth and position of 49 species and GSDMs to predict the sizes of their distribution areas in Chile. We summarise this information in a predictive framework that enables us to classify species as having either high or low predicted invasiveness. In addition, we have explored the association between invasiveness and impact using our results and impact information obtained from literature.

Methods

The stages followed to collect and analyse data are summarised in Fig. 1.



Figure 1. Flow chart which represent the different methodological phases followed in this study.

Phase I (Species selection)

The number of alien species selected for this study was 49; two shrubs and 47 herbs (see Suppl. material 2 for the scientific names). We focused mainly on herbs because they constitute 90.4% of alien plants in Chile (53.4% annuals and 42% perennials) and because there is considerable knowledge about their ecology and distribution (Matthei et al. 1995). We did not include more woody plants because there is little information on their invasive status or their biogeography (Fuentes 2014; Fuentes et al. 2013; Matthei et al. 1995; Quiroz et al. 2009). The 49 alien plant species used in this study belong to 19 families, with Poaceae (10 spp), Asteraceae (8 spp), Fabaceae (5 spp) and Caryophylaceae (4 spp) the most numerous, constituting 55% of the total species.

Phase 2 (Global occurrences and climate data)

The 49 alien species were obtained from published information (Castro et al. 2005; Fuentes et al. 2013); these species were selected *a priori* to include species with narrow, medium and broad recorded distributions in Chile (see Suppl. material 1). We collected occurrence data for each species from the Global Biodiversity Information Facility (http://www.gbif.org/) and 'Sp. Link' (http://splink.cria.org.br/) to obtain species occurrences at the global scale. For Chile (regional scale), occurrence data were recorded from herbaria located at the University of Concepción and the National Museum of Natural History, Santiago de Chile. For both global and regional scales, we

ensured the validity of the occurrence data by eliminating duplicates and discarding points that were located in the ocean, snow or rock. We reduced the spatial dependence of data, creating a buffer zone (0.09 degrees) around each occurrence point, thus leaving points at least 10 km apart. Despite the reduction of occurrence points, we kept a reasonable amount of data for SDM analysis (from 208 occurrences for *Datura ferox* to 6429 for *Cirsium vulgare*). For the construction of global models, we used the totality of occurrences.

The climate information required for the GSDMs was obtained from WorldClim (Hijmans et al. 2005). There are 19 variables available in WorldClim; however, to avoid change by model over-fitting, we used a Spearman correlation test (Holt et al. 2009) restricting the climate parameters to pairs of variables with correlation values ≤ 0.7 . In these cases, we selected the climate variable with the higher biological relevance (Merow et al. 2013). The selected variables were maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), mean maximum temperature of the warmest month (BIO7), mean annual precipitation (BIO12), precipitation of the driest month (BIO14) and precipitation in the warmest quarter (BIO18).

Phase III (Global species distribution models)

From the *GSDMs*, we estimated alien plant invasiveness using the size of the potential distribution area as a *proxy*. We used MaxEnt software, which implements a machine-learning method that enables potential distribution to be predicted using only presences, under the principle of maximal entropy (Phillips et al. 2006). GSDMs are used to examine species niche potentials, detecting new environments where species occur in invaded regions, but they do not occur in native ranges due to dispersal limitation, biotic interactions or simply because they no longer exist in the native range (Gallien et al. 2012).

The climate envelope of the GSDMs included the climates of the five continents (excluding Antarctica), so for each model, we increased the number of pseudo-absences to 10,000, following Merow et al. (2013) and reduced the magnitude of the regulator to 0.5 (Merow et al. 2013; Phillips and Dudík 2008). To quantify the potential distribution size (in km²), we selected the average model obtained from 25 bootstrap replicates; for each replicate, we used 70% of the occurrences for training and 30% for testing the model (Phillips et al. 2006; Thuiller et al. 2005). To validate the capacity of average models to discriminate between false positives and false negatives, we used the criteria of Thuiller et al. (2005) for AUC values, being the most common test for SDMs. If AUC = 0.5, then the model does not have discrimination capacity (Phillips and Dudík 2008). When AUC is between 0.5 and 0.7, the model has poor discrimination capacity; if AUC values are between 0.7 and 0.9, then the model has a reasonable discrimination capacity; values higher than 0.9 indicate a model with a very good discrimination ability (Pierce and Ferrier 2000) In addition, we calculated the Boyce Index for each average model. This Index is a threshold-independent accuracy estimator which uses the Spearman rank coefficient to correlate the occurrence points vs. the predicted areas for two datasets (Boyce et al. 2002). If the Index is positive for a model, then its predictions are consistent with the distribution of presences in the evaluation dataset. If the values are close to zero, then the model is no different from a random model; when values are negative, then there are counter-predictions (Hirzel et al. 2006).

Binary projections to discern suitable/unsuitable habitats that are generated by different thresholds in SDMs may differ drastically; therefore, choosing the correct threshold is not arbitrary (Liu et al. 2005; Magory Cohen et al. 2019). For instance, in some studies, the thresholds are selected by simulations (Liu et al. 2005), others use several thresholds simultaneously (Escalante et al. 2013), while others consider the importance of omission/commission errors (Norris 2014). Given that we aimed to model the alien species' full potential to invade in Chile, we selected the threshold that minimises the omission error; i.e. the minimum training presence provided by Max-Ent (0% omission rate); this threshold has been used successfully in other studies using GSDMs (Magory Cohen et al. 2019).

Phase IV (Distribution size and niche traits)

From climate information obtained from WorldClim (Hijmans et al. 2005) and species occurrences obtained from data bases, we calculated climatic niche breadth and position for the alien species, looking for the occurrences with the maximal and minimal observable climate values (Quintero and Wiens 2013). Thermal niche breadth (*TNB*) was estimated for each species by subtracting the maximum temperature in the warmest month (BIO5) from the minimum temperature of the coldest month (BIO6).

TNB Species
$$i = (\max BIO5 - \min BIO6)$$
 (1)

Hydric niche breadth (*HNB*) was estimated by subtracting the maximum precipitation in the wettest month (BIO13) from the minimum precipitation in the driest month (BIO14)

HNB Species
$$i = (\max BIO13 - \min BIO14)$$
 (2)

We defined the thermal niche position of species i (*TNP*_{*i*}) as the difference (or distance) between the mean thermal niche and the mean annual temperatures in Chile (Eq. 3). Similarly, the hydric niche position (*HNP*_{*i*}) is the difference (or distance) between the mean hydric niche and the mean annual precipitation in Chile (Eq. 4). (Phase 4, Fig. 1).

TNPi Species
$$i = \left(\frac{\max BIO5 + \min BIO6}{2}\right) - \text{Chile}\left(\frac{\max BIO5 + \min BIO6}{2}\right)$$
 (3)

HNP_i Species $i = (\max BIO13 + \min BIO14)/2)$ - Chile $(\max BIO13 + \min BIO14/2)$ (4)

Phase V (GAMLSS)

We related potential distribution size to thermal and hydric niche traits. The distribution size data followed a Weibull distribution (see Suppl. material 1: Table S1 and Suppl. material 3: Fig. S1). We fitted a general additive model for location, scale and shape (GAMLSS) (Rigby and Stasinopoulos 2005) using the GAMLSS package in R, which supports the Weibull distribution (Stasinopoulos and Rigby 2007).

Phase VI (Species classification)

We summarised our results in a bi-dimensional plane including species position in relation to the two most important climatic niche traits. Our aim was to provide a predictive tool to classify species invasiveness using only climatic niche traits. We are aware that there are factors other than climate that may determine invasion success; however, climate is the first barrier for colonisation. Following validation, this approach could provide a rapid screen to measure invasiveness for a large number of alien species (animals and plants) in a short time. We standardised the niche traits for species using the algorithm:

$$\frac{(NT_i - aNT)}{\sigma NT},$$

where NT_i represents niche traits of species i (thermal or hydric niche amplitude or position); aNT is the average niche trait estimated for the 49 species and σNT is the standard error of NT. In this way, the plane is divided into four regions. In Quadrant I, TNB values are negative and TNP values are positive; species that fall into this zone have low invasive potential. In Quadrant IV, TNB values are positive and TNP values are negative; species that fall into this zone have high invasive potential. Quadrant II and Quadrant III contain the species with intermediate invasive potentiality (for more details see the text in Fig. 4).

To determine whether there is an association between predicted invasiveness, based on climatic niche and impacts of alien species, we conducted literature reviews to assess evidence of impact during the last 30 years. The impact was measured qualitatively; that is, whether there was any documentation of impacts or not. We classified impact into three general categories: (i) on biodiversity, (ii) on crop agriculture and (iii) on livestock.

We searched for evidence of impact of alien species that fall within Quadrant I (low invasiveness) and Quadrant IV (high invasiveness) (Fig. 4). We used a X^2 test (1 d.f.) for proportions to compare the probability of impact between species with low invasiveness vs. species with high invasiveness. For this analysis, we pooled the information for the three different kinds of impact. To collect impact information, we searched Google Scholar using the terms *Scientific name* **AND** *Invasive* **AND** *Impact*.

Results

GSDMs

The performance of the GSDMs was quite good as measured by the AUC values (average = 0.977; SD = 0.014) and the Boyce Index (average = 0.970; SD = 0.06) (for detailed data, see Suppl. material 1). The potential distribution sizes in Chile ranged from 763,778 km² for *Spergula arvensis* (Caryophylaceae) to 43,473 km² for *Atriplex nummularia* (Amaranthaceae) (Fig. 2A, C). The average size was 568,420 km². In 31 species (63% of the total), the distribution size for the species was higher than average; the families that contributed most to this sub-group were Poaceae, (7 spp), Asteraceae (5 spp), Fabaceae (3 spp) and Caryphylaceae (3 spp) (for some examples, see Fig. 2C, D). The distribution sizes of 18 species were lower than the average (37% of the total) and the most numerous families for these species were Asteraceae (3 spp), Poaceae (3 spp), Amaranthaceae (3 spp) and Fabaceae (2 spp).

GAMLSS

We detected significant positive effects of *TNB* on potential distribution size (Table 1, Fig. 3A), but no significant effects were detected for hydric niche breadth or position (Table 1; Fig. 3C, D). The effects of *TNP* on potential distribution size were negative, but not statistically significant (Table 1). As the p-value for this trait was close to $\alpha = 0.05$ (p = 0.08), we decided to correlate *TNP* with the potential distribution size independently; we detected a significant negative correlation (Pearson's product-moment = -0.62; t = -5.4527, d.f. = 47, p < 0.001; Fig. 3B).

Species classification

Standardised *TNP* and standardised *TNB* were negatively correlated (Pearson; r = -0.69, p < 0.001; Fig. 4). In Quadrant I; i.e. the zone of low invasiveness, there are 19 species (38% of the total species); the most-represented families are Fabaceae (2 spp), Poaceae (3 spp) and Asteraceae (3 spp). Distribution size for 82% of these 19 species was lower than the average (grey spots in Quadrant I, Fig. 4). In Quadrant IV, the sector that corresponds to the highest predicted level of invasiveness, there are 20 species (41% of the

Table 1. GAMLSS for testing the effect of thermal and hydric niche traits on potential distribution	ution pre-
dicted from global niche models on 49 alien plant species in Chile. The pseudo-R ² of the model	was 0.45.

Factors	Estimate	Standard error	t – value	p – value
Intercept	12.659	0.640	19.786	<< 0.001
Thermal niche breadth (TNB)	0.022	0.009	2.526	0.016
Thermal niche position (TNP)	-0.043	0.024	-1.798	0.082
Hydric niche breadth (HNB)	-0.0006	0.0008	-0.798	0.429
Hydric niche position (HNP)	-0.001	0.002	-0.470	0.641



Figure 2. Global Species Distribution Models (GSDMs) projected in Chile for a sub-set of species
A Spergula arvensis (the highest distribution size) B Atriplex numularia (the lowest distribution size)
C Agrostis capillaris (representative of Poaceae) D Cirsium vulgaris (representative of Asteraceae) D Medicago sativa (representative of Fabaceae). For the rest of exotic species, see Suppl. material 2.

species); the most-represented families are Fabaceae (3 spp), Poaceae (5 spp) and Asteraceae (3 spp). The predicted distribution size for all of these species was higher than the average (black spots in Fig. 4). The rest of the 10 species were located in Quadrants II and III; i.e. intermediate level of invasiveness. For a summary of alien plants located in Quadrant 1 and 4, see Table 2.

Invasiveness and impact

We detected no association between predicted Invasiveness (based on quadrant position, Figure 4) and impact (obtained from literature) of alien species ($X^2 = 0.02$, d.f. = 1 p = 0.85; Table 3). In fact, of the total number of species documented to have some impact in Chile (n = 23; see Table 3), 58% (n = 11) of them were classified as having low invasiveness or being non-invasive and 60% (n = 12) were classified as having high invasiveness; these percentage values were not statistically significant (Z score = -0.34, p = 0.90). (For the details of species, impacts and references, see Suppl. material 2).

Species with low invasiveness (Quadrant I)	veness (Quadrant I) Species with high invasiveness (Quadrant IV)	
Ammi visnaga	Aira caryophyllea	
Atriplex nummularia	Bromus catharticus	
Atriplex suberecta	Bromus sterilis	
Carthamus lanatus	Cardamine hirsuta	
Conyza bonariensis	Cirsium vulgare	
Cynosurus echinatus	Convolvulus arvensis	
Datura ferox	Daucus carota	
Dolichos lignosus	Erodium cicutarium	
Fumaria agraria	Galium aparine	
Lupinus arboreus	Hordeum jubatum	
Mesembryanthemum crystallinum	Matricaria discoidea	
Pennisetum clandestinum	Medicago sativa	
Ruta chalepensis	Polypogon monspeliensis	
Sanguisorba minor	Rumex longifolius	
Scirpus mucronatus	Sonchus asper	
Sonchus tenerrimus	Spergula arvensis	
Spergularia media	Stellaria media	
Stellaria pallida	Veronica scutellata	
Vulpia muralis	Vicia sativa	
-	Vicia villosa	

Table 2. List of alien plant species which fall into Quadrant I (low invasiveness) and Quadrant IV (highly invasiveness), according to the classification obtained from Figure 4.

Table 3. Contingency table showing the number of alien species cross-classified by invasiveness and impact: a) low invasiveness and high invasiveness: the counts were obtained from Quadrant 1 and Quadrant 4; Figure 4; b) species recorded with some impact and species with no impact (for the list of species and the references, see Suppl. material 2).

	Impact	No impact	Total
Low invasiveness	11	8	19
High invasiveness	12	8	20
Total	23	16	39

Discussion

In our study, we examined the importance of thermal and hydric niche traits to predict alien plant invasiveness. We have also provided a simple protocol for a rapid assessment of invasiveness. We will discuss our results in light of plant physiology, the use of SDMs in terms of advantages and limitations of our study to support the control and management of alien species.

One surprising result was that hydric niche traits were not important for explaining predicted plant distribution area (Schulze et al. 1987; Turnbull et al. 2000). Most of the species we examined have a herbaceous life form (with the exception of two *Atriplex* species); these plants have regeneration tissues that are more sensitive to thermal stress than to water limitations, contrary to expectations for woody plant species (Turnbull et al. 2000). In particular, reproductive phenology – specifically flower development, pollen release and germination and seed and fruit maturation in herbaceous plants – are particularly sensitive to temperature variation (Körner et al. 2016). Despite the important influence of temperature on plant performance, there are only



Figure 3. Relation of niche traits and Potential distribution size (×10000) in km2, for a set of 49 exotic plants occurring in Chile **A** Thermal niche breadth **B** Thermal niche position **C** Hydric niche breadth **D** Hydric niche position. We detected significant effects for Thermal niche breadth and position. The p-values were obtained from GAMLSS. Confident intervals were constructed with LOESS regression analysis.

a few studies that have scaled the effect of temperature on the biogeography of plants (Bykova et al. 2012; Pigott 1989; Rasmussen and Kollmann 2004).

Climatic niche breadth has frequently been used to predict invasiveness ("niche breadth-invasion success hypothesis") (Granot et al. 2017; Vazquez 2006). Similar results have also been obtained for native plants, where climatic niche traits are good predictors of the biogeographic expansion of native trees (Vela Díaz et al. 2020). Our results showed that this is the case for alien species in Chile. Specifically, using thermal niche traits (breadth and position), we propose a suitable classification scheme to categorise the invasive status of alien plants in Chile: a) species in Quadrant IV (Fig. 4) are the best candidates to be highly invasive and b) species in Quadrant I (Fig. 4) will probably be less invasive.

Determining which traits promote plant invasiveness is a central issue in biological invasion research (Daehler 2001; Duncan et al. 2001; Rejmánek et al. 2005). However, evaluating these factors implies a lengthy effort that does not match the timetable required for management practices, especially if anticipation is the most fundamental strategy to control species invasions (Leung et al. 2005). In our study, we found that thermal niche traits can be used for a rapid assessment of the invasive status of alien species in Chile, thereby helping to provide information for management practices.

Incorporating global climate data into GSDMs is essential for a reasonable approximation of a species' potential to invade across different regions beyond its native



Figure 4. Summary of species position in a bidimensional-plane whose axes are standardized thermal niche breadth and thermal niche position from a sample of 49 exotic plants in Chile. Niche values were standardized using the expression $((NT)_{-i}aNT))/\sigma NT$. The point (0, 0) represents the average values of both niche traits. Quadrant I represent the area of low invasiveness; Quadrant IV represents the area of high invasiveness. Dots represent the position of species within the two-phase plane. Dots size represents species distribution size. Gray dots: species with distribution size lower than average: black dots: species with distribution size higher than average.

ranges (Kambach et al. 2019; Lombaert et al. 2011). GSDMs can help us to understand the big picture of biogeographic patterns; however, they are unable to show the role of local processes in the details of species distribution, such as topography (elevation and slope exposure (Önol 2012)); anthropogenic disturbances such as deforestation, fires and fragmentation (Franklin 2010); and biotic interactions and dispersal limitation (Boulangeat et al. 2012).

Caveats

Invasiveness assessment is an important input for alien species management; however, for a more comprehensive approach, we need to know impacts. For most people (i.e. stakeholders and policy-makers), invasiveness and impact are synonymous (Colautti et al. 2004; Ricciardi and Cohen 2007), despite weak evidence for a connection between these two concepts (Ricciardi and Cohen 2007; Williamson and Fitter 1996). In our study, we did not find a significant association between invasiveness and impact (Table 3), although we are aware that our analysis is preliminary and requires further

examination of a larger number of species. However, for application purposes, we can propose target species for management to prevent detrimental effects on crop agriculture, livestock or biodiversity, based on our literature review (Table 2).

We propose to focus primarily on the 12 species that were predicted to be highly invasive and, at the same time, were documented to have impacts (see Table 2): *Aira caryophyllea, Bromus catharticus, Cirsium vulgare, Erodium cicutarium,* (outcompete native plants); *Convolvulus arvensis, Sonchus asper* (crop weed or pest); *Medicago sativa, Polipogon mosnpeliensis, Spergula arvensis, Stellaria media* (allelophatic effects) and *Hordeum jubatum, Sonchus asper* and *Vicia villosa* (poisonous to livestock) (for details and references, see Suppl. material 2).

The issue of the impact of invasive plant species is the subject of an ongoing interdisciplinary research programme (Settele et al. 2005); however, the basic questions remain open up to date ; namely, what are the impacts of invasion and are there some traits that can be used to anticipate impacts? The search for species attributes seems to be an interesting avenue. For instance, in plants, life form, stature and pollination syndrome together with the network structure formed between plants and pollinators are regarded as useful predictors of impacts (Gibson et al. 2012; Hejda et al. 2017; Pyšek et al. 2012; Valdovinos et al. 2018).

Conclusions

In our study, we have demonstrated the importance of thermal niche traits for predicting alien plant invasiveness. Based on these results, we have proposed a conceptual framework that classifies species according to their anticipated level of invasiveness. For management purposes and to assess comprehensive risk, it is mandatory to also implement impact assessment because higher invasiveness does not necessarily imply higher impact.

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Supplementary material I

Table S1. Exotic species located in Quadrant 1 (see Figure 3) and impacts on biodiversity, agriculture and cattle raisng

Authors: Ramiro O. Bustamante, Lúa Alves, Estefany Goncalves, Milen Duarte, Ileana Herrera

Data type: occurrence

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Link: https://doi.org/10.3897/neobiota.63.50049.suppl1

Supplementary material 2

Table S2. Basic information obtained for 49 exotic plants in Chile

Authors: Ramiro O. Bustamante, Lúa Alves, Estefany Goncalves, Milen Duarte, Ileana Herrera

Data type: species data

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Link: https://doi.org/10.3897/neobiota.63.50049.suppl2

Supplementary material 3

Map of the species

Authors: Ramiro O. Bustamante, Lúa Alves, Estefany Goncalves, Milen Duarte, Ileana Herrera

Data type: occurrence

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