



# Minimum residence time, biogeographical origin, and life cycle as determinants of the geographical extent of naturalized plants in continental Chile

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## ABSTRACT

The geographical extent of exotic plant species is a major component of invasiveness, which has been explained by intrinsic attributes of the plants, such as growth rate, reproductive type, life form, and biogeographical origin. We assessed quantitatively life cycle and biogeographical origin as determinants of the geographical distribution of naturalized plants in continental Chile, using minimum residence time (MRT) as an estimator of introduction date. We assembled a database with information on 428 plants (principally herbs) in continental Chile, corresponding to 61% of the exotic naturalized flora. For each species we recorded: (1) minimum residence time (introduction date or first recorded date in the country); (2) biogeographical origin (American, Eurasian, others); (3) life cycle (annual, perennial, others); (4) number of Chilean regions occupied by the plant. We found that 82 species (19%) have been recorded in only one region of Chile, while only three species have been found in all 13 regions of the country. About 89% of the species (381) have been found only in central Chile (Regions IV to VIII), while the remaining 11% (47) are found only in the northern (Regions I to III) or southern parts of the country (Regions IX to XII). We detected significant differences in regional spread of naturalized plants according to minimum residence time: those species with shorter MRT had more limited spread ranges than those with longer MRT. Biogeographical origin and life cycle did not explain geographical extent in Chile. This study shows that historical factors are more important than biological ones in determining the geographical extent of naturalized plants in continental Chile. Thus, caution should be exercised when assigning value to biological attributes that may confer invasiveness to naturalized plants.

## Keywords

Biological invasions, exotic plant distribution, geographical spread, introduced plants, introduction date.

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## INTRODUCTION

Biological invasion may be thought of as a colonization event wherein a species succeeds in crossing biogeographical barriers, thus becoming able to establish viable populations in a new region (Lodge, 1993; Williamson, 1996; Sakai *et al.*, 2001). Once established, those populations may reach different abundances from their original ranges and increase their geographical extent in their new homeland (Richardson *et al.*, 2000). Invasive species are those that reach high abundances and/or broad geographical distribution (or range), as opposed to non-invasive species that are less abundant or show a limited geographical distribution (Kolar & Lodge, 2001).

What factors determine the spread of exotic plant species? Among terrestrial plants, efforts have been centred on the search of attributes or morpho-functional traits that determine the 'ideal invader' (*sensu* Noble, 1989). This approach, originally developed for weeds by Baker (1965), hypothesizes that some intrinsic traits (or a combination of them) determine the abundance and geographical extent that a given species shows in a recipient community. Thus, growth traits (Richardson *et al.*, 1990; Richardson & Bond, 1991; Mack, 1996; Rejmánek & Richardson, 1996; Richardson *et al.*, 2000; Davis *et al.*, 2001; Grotkopp *et al.*, 2002), reproduction type (Huenneke & Vitousek, 1990; Reichard, 1996; Rejmánek & Richardson, 1996; Reichard & Hamilton, 1997), original range and biogeographical

origin (Di Castri, 1989; Rejmánek, 1995; Thebaud & Simberloff, 2001) have been proposed as factors that determine whether a plant will become invasive or not. Nevertheless, there is little agreement among researchers on the generality and predictive power of these traits (Newsome & Noble, 1986; Crawley, 1987; Noble, 1989; Goodwin *et al.*, 1999).

Alternatively, other researchers have proposed that characters extrinsic to a given species determine their success as an exotic species. Among these, the biological diversity of the recipient community (Elton, 1958; Tilman, 1997; Crawley *et al.*, 1999; Stohlgren *et al.*, 1999; Naeem *et al.*, 2000; Troumbis *et al.*, 2002; Kennedy *et al.*, 2002), attributes of the native populations that interact with the exotics (Zavaleta *et al.*, 2001; Keane & Crawley, 2002), and patterns of landscape disturbance and soil use (D'Antonio & Vitousek, 1992; Mack & D'Antonio, 1998; Dukes & Mooney, 1999; Silveri *et al.*, 2001; Pauchard & Alaback, 2004). While this view is not opposed to the preceding, it urges caution when assigning value to biological attributes that may confer invasiveness to exotic plants, because the abundance or geographical spread of an exotic may be more related with the initial circumstances of colonization than with specific morpho-functional traits (Lonsdale, 1999; Kolar & Lodge, 2001). Thus, the search for extrinsic factors that may determine the abundance and distribution of exotic plants contributes to broadening our understanding of biological invasions.

As an extrinsic factor, the historical circumstances during which exotic plants were introduced may have affected their current spread (Mack, 1986, 1996; Daehler, 1988; Groves, 1991; Rejmánek & Richardson, 1996; Mack *et al.*, 2000). Some authors have demonstrated that introduction date (ID, year when the exotic plant was inoculated) and/or minimum residence time (MRT, time since the first record until to present) contribute to determine the abundance of exotic species (Rozenfelds & Mackenzie, 1999; Rejmánek, 2000; Pyšek *et al.*, 2003). Closely related to ID and MRT are demographic and genetic processes in small populations, influx of new propagules through time, time lag events, and the opportunities for dispersal afforded by the landscape (Kolar & Lodge, 2001; Sakai *et al.*, 2001; Shigesada & Kawasaki, 2001). Still, there are few empirical studies assessing the effect of ID or MRT on distributional and abundance patterns of exotic plants, because dates have usually been recorded in a discontinuous and incomplete manner (Mack, 1986; Lonsdale, 1999).

Continental Chile has an exotic vascular flora consisting of 707 naturalized species (Arroyo *et al.*, 2000), equivalent to 11.6% of the native terrestrial vascular flora ( $n = 5364$  species; Marticorena & Quezada, 1985). Most of the exotic species are European annual herbs (Montenegro *et al.*, 1991), which are assumed to have attributes that favour their colonization as a consequence of a '... history on a large continental mass that suffered major upheavals during the glacial period and a longer association between humans and plants in the Old World' (Arroyo *et al.*, 2000). This notion, originally proposed by di Castri (1989) and broadly accepted in the literature (see Rapoport, 2000), suggests that in continental Chile, European annuals should have larger geographical ranges than plants with other origins (Australia, Africa, South-America). This, as a consequence of intrinsic

attributes that facilitate their invasiveness in a changing landscape: fast growth and high reproductive rate, which coupled with a relatively low number of annual species in the native flora of Chile (Arroyo *et al.*, 2000).

Within continental Chile, naturalized plants are distributed along a wide climatic gradient that stretches along 40° of latitude (Di Castri & Hajek, 1976). The regional distribution of these exotic plants reveals a broad variation in their geographical extent; some plants being found in only one region, while others are found in all 13 administrative regions of the country (Fig. 1; Matthei, 1995). Arroyo *et al.* (2000) reported that 430 alien weeds occupy a mean of five administrative regions, while 260 alien non-weeds occur on average in only two regions. Additionally, alien weeds appearing before 1900 tend to be more widely distributed than those recorded for the first time after 1900, while those registered for the first time only since 1950 have the narrowest distribution range (Arroyo *et al.*, 2000; Pauchard *et al.*, 2004a). Further, central Chile accumulates the largest proportion of naturalized plants, in association with a large human population, vast modification of the landscape, intensive agricultural practices, and high road density (Arroyo *et al.*, 2000). Recently, Pauchard & Alaback (2004) documented that diversity and abundance of naturalized plants are negatively correlated with elevation, but positively correlated with grazing and logging in two protected areas of southern Chile.

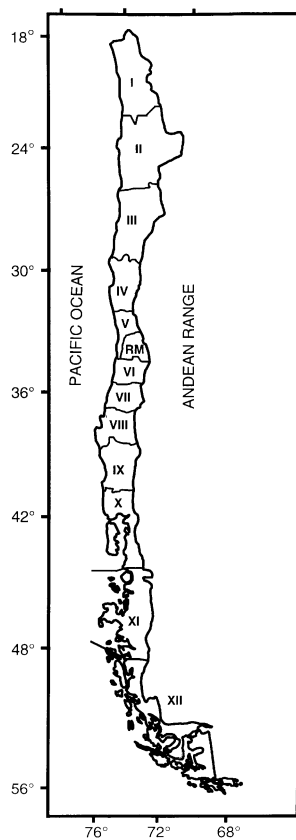
The main objective of this investigation is to evaluate the relative importance of biogeographical origin, life cycle, and minimum residence time as determinants of geographical spread of naturalized plants in continental Chile. We hypothesize that naturalized plants of European origin, with annual life cycle, and introduced early should present more broad geographical ranges than other plant species.

## METHODS

### Continental Chile and its naturalized flora

Continental Chile lies along the south-western coast of South America, between latitudes 17°30' and 56°30' S and longitudes 68° to 72° W. It extends as a narrow belt of land 4270 km long, comprising a broad north–south latitudinal gradient, covering an area of approximately 756,626 km<sup>2</sup> (Fig. 1). Politically, the country is divided into 13 administrative regions, stretching from the Andean Ranges westward to the Pacific Ocean, all sequentially laid southwards along the territory (Fig. 1), which closely correlates with precipitation increases and temperature decreases with increasing latitude (di Castri & Hajek, 1976). Additionally, this linear arrangement of regions renders them useful to estimate the range of geographical and latitudinal distributions of plant species. Regions are identified with numbers from I to XII, and with the acronym RM for the Metropolitan Region, which is landlocked between Regions V and VI in the central part of the territory (Fig. 1).

In geographical terms, the presence of the Andes Ranges on the East, the Atacama Desert on the North, and the Pacific Ocean on the West and South impose severe biogeographical barriers



**Figure 1** Geographic location and political map of continental Chile. The regions are identified with numbers from I to XII, and with the acronym RM for the Metropolitan Region.

that have kept the biota in Chile relatively isolated from that of the rest of the South America (Jaksic, 1998; Arroyo *et al.*, 1999). Thus, the Chilean vascular flora is composed of 5364 native taxa (including species and subspecies; Marticorena & Quezada, 1985; Marticorena & Rodríguez, 1995; Marticorena & Rodríguez, 2001) with high national and local endemism (Axelrod *et al.*, 1991; Arroyo *et al.*, 1993, 1999; Cowling *et al.*, 1996; Myers *et al.*, 2000).

The naturalized flora in Chile derives from introductions carried out since the beginning of the 16th century (Montenegro *et al.*, 1991), mostly involuntarily (Arroyo *et al.*, 2000). The presence of naturalized plants was systematically and continuously documented since Bertero (1828, 1829) and Gay (1845–1854). Additionally, institutions such as the Museo Nacional de Historia Natural in Santiago have kept plant collections since 1828, with over 50,000 specimens in the Herbario de Plantas Nativas and 40,000 in the Herbario de Plantas Exóticas (Muñoz-Schick, 1991). Other valuable sources of information are the anecdotal records of travellers, chroniclers, collectors and naturalists that visited Chile since the 16th century, making relevant observations regarding the presence and distribution of exotic plants.

### Assembling a database of naturalized flora

We assembled a database consisting of the 707 exotic naturalized plants recorded in Chile, using published information (Arroyo

*et al.*, 2000). For each species we determined: (a) regional distribution in continental Chile; (b) minimum residence time (*sensu* Wu *et al.*, 2003), using the introduction date or, in its absence, first recorded date in the country; (c) biogeographical origin; (d) life cycle. This information was incorporated into the database to evaluate the role of extrinsic and intrinsic attributes on geographical spread of exotic plants. From the initial database, we obtained a complete data set for 428 species (60.5% of 707 species), > 95% being herbs. Currently, the Museo Nacional de Historia Natural is in the process of georeferencing its collections, but that information is not available for the moment. It is already known that some specimens do not have an accurate record of their geographical location, and some just indicate nearby towns or cities. Thus, it has not been possible to obtain precise records about location and biological community type in which the collections were made. Therefore, we used administrative regions as estimates of distribution range. This information is provided in Appendix S1.

The year of introduction or first recorded date in the country was determined from the literature, using information available in Bertero (1828, 1829), Gay (1845–1854), R. Philippi (1882), F. Philippi (1884), Reiche (1896–1911) and Matthei (1995). We also incorporated information available in the Herbarium of the Museo Nacional de Historia Natural and in records of collectors and naturalists who visited Chile through its history (S.A. Castro, unpublished data). Information concerning the geographical distribution of naturalized plants was obtained from Navas (1973, 1976, 1979), Marticorena & Quezada (1987), Marticorena & Rodríguez (1995, 2001), and Matthei (1995), recording presence/absence by administrative region of Chile, and then tallying the number of regions occupied by each naturalized species.

### Statistical analyses

To determine whether extrinsic or intrinsic factors affected the geographical spread of naturalized plants in continental Chile, we carried out a three-way ANOVA. Factors were: (a) minimum residence time (b) biogeographical origin, and (c) life cycle of the naturalized plants. For the first factor, we grouped data in periods of 50 years, establishing four levels:  $\leq 1849$ , 1850–1899, 1900–49 and 1950–2000. These groupings reduced the historic bias in the exotic plant record. For life cycle, we distinguished three levels: annual, perennial, and others, this latter category including a minority group of facultative species with annual/perennial cycles ( $n = 10$ ), annual/biennial ( $n = 24$ ), biannual/perennial ( $n = 3$ ), and biannual ( $n = 13$ ). In our essentially herbaceous database, other life forms such as shrubs and trees yielded insufficient numbers for comparative purposes. For biogeographical origin, we recognized: American Continent (including North, Central and South America), Eurasian (including Europe and West Asia), and other (including East Asia, Africa, and Oceania). As dependent variable we considered the number of administrative regions (as an arcsine-transformed proportion) that each naturalized plant occupied in continental Chile. Raw values were originally computed as the arithmetic sum of the number of regions in which each plant was recorded as present.

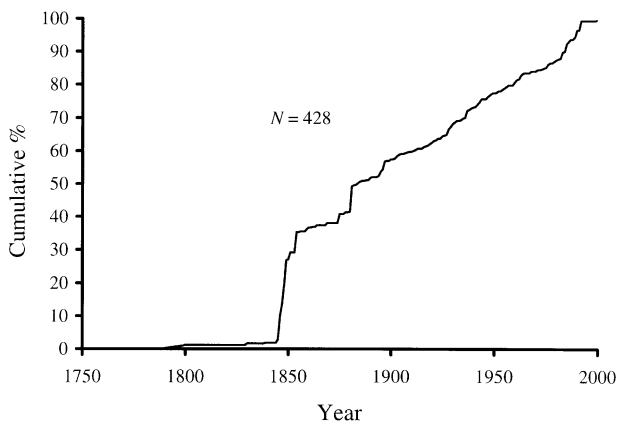


Figure 2 Cumulative distribution (%) of naturalized plant records in continental Chile.

## RESULTS

### Temporal patterns

Historical records show that until 1845 only four naturalized species had been recorded in continental Chile, < 3% of the currently naturalized species (Fig. 2). These naturalized plants, which were introduced to continental Chile between the 16th and 18th centuries were *Cardamine hirsuta*, *Medicago polymorpha*, *Spartium junceum* and *Bromus hordeaceus*. Between 1845 and 1849, the record increased markedly to 111 species, 30% of the presently naturalized plants. Since the latter date, that figure has shown a steady increase by 2–3 species year<sup>-1</sup> (Fig. 2). For instance, by 1885 the record of naturalized plants increased to 50%, and by 1944 to 75% of current figures (Fig. 2).

### Distribution patterns

All 13 administrative regions of Chile have naturalized flora, although the frequency distribution shows a greater concentration in the central area of the country, from Regions III to VIII (Fig. 3a). Particularly, Region VIII has the largest number of naturalized plants (282), followed by Regions V and Metropolitan, with 246 and 245 species, respectively (Fig. 3a). On the other hand, regions with the smallest number of naturalized species were XI (southernmost Chile), II and I (northernmost Chile), with 41, 54, and 58 species, respectively (Fig. 3a). Out of the 428 species considered in this study, 82 (19%) were found in only one region of Chile (Fig. 3b), which represents the modal value of the frequency distribution (Fig. 3b). Only three species were found in all 13 regions of the country: *Erodium cicutarium*, *Medicago sativa* and *Chenopodium album*. On average, the 428 naturalized species had a geographical extent of 4.7 regions.

### Regional distribution vs. minimum residence time

Until 1849, 115 naturalized species had been recorded but their precise date of introduction was not established. For those species,

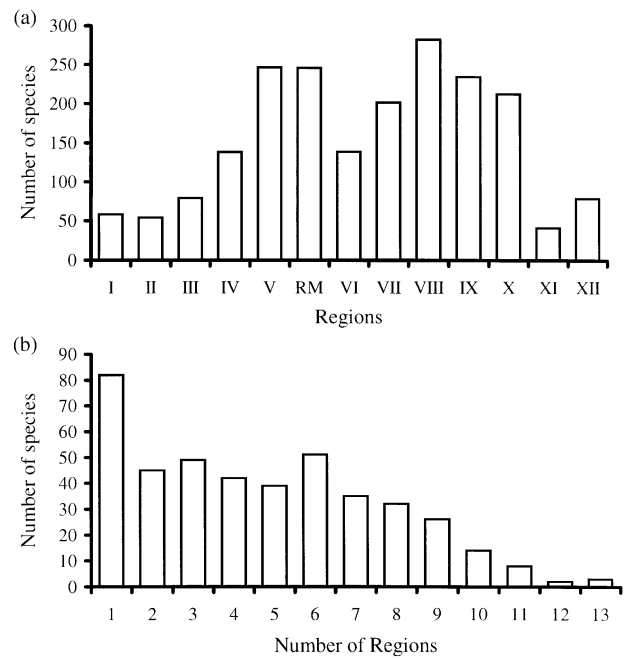


Figure 3 Patterns of regional distribution for naturalized plant species in continental Chile. (a) Number of exotic species in each region. (b) Frequency distribution of 428 exotic species among regions.

Table 1 Statistical descriptors for naturalized plant distributions in continental Chile, according to minimum residence time, life cycle, and biogeographical origin

Factors/Levels	X ± S.D.	Mode	Range	N
Minimum residence time				
≥ 150 year	6.1 ± 3.02	6	1–13	115
101–149 year	5.7 ± 2.69	6–7	1–12	128
51–100 year	4.1 ± 2.50	1	1–10	87
50 year	2.3 ± 1.71	1	1–8	98
Life cycle				
Annuals	4.6 ± 3.07	1	1–10	230
Perennials	4.7 ± 2.85	1	1–13	148
Others	5.2 ± 2.77	6	1–11	50
Biogeographical origin				
American	4.4 ± 2.92	1	1–10	63
Eurasian	4.8 ± 2.95	1	1–11	323
Others	4.2 ± 3.06	2	1–12	42

the distribution ranges varied between one and 13 regions, with a mean of 6.1 regions (Table 1). In this group were species with broad geographical distribution and high abundance, such as *Vulpia myuros*, *Bromus lanceolatus*, *Erodium cicutarium*, *E. malacoides*, *E. moschatum*, *Medicago arabica*, *M. lupulina*, *M. minima* and *M. sativa*. Interestingly, species such as *Spartium junceum*, *Calendula officinalis* and *Cardamine hirsuta* still have a narrow distributional range in spite of long residence time in continental Chile (> 151 years). Between 1850 and 1899, 128 new naturalized plants were recorded. These occupied a mean of 5.7 regions, with ranges from 1 to 12 regions (Table 1). Species such

as *Acacia dealbata*, *Eschscholzia californica*, *Centaurea jacea* and *Veronica persica* are included in this group. From 1900 to 1949, 87 new species were recorded with a mean of 4.1 regions, a range from 1 to 10 regions and a modal value of 1 (Table 1). In this group were species such as *Alyssum plantago-aquatica*, *Carduus pycnocephalus* and *Cotula australis*. Finally, from 1950 to the present, 98 species occupied a mean of 2.3 regions, a mode of 1, and a range from 1 to 8 regions (Table 1). Here are species with limited geographical distributions such as *Ammannia latifolia*, *Ammi majus* and *Crepis pulchra*.

### Regional distribution vs. life cycle and biogeographical origin

Among plants naturalized in Chile we recorded 230 annual species, 148 perennials and 50 species with facultative life cycle duration ('others'). Annual plants present a distributional range that varies from 1 to 10 regions, with a modal value of 1 region (Table 1), while the perennial species have the same modal value but with a range between 1 and 13 regions (Table 1). The species with other life cycles present a distribution range between 1 and 11 regions, with modal value of 6 regions (Table 1). On the other hand, we classified 63 exotic species as of American origin, 323 as Eurasian, and 42 species with other origins. The regional distribution of these species is indicated in Table 1, where similar mean (4.8–4.2 regions), range (1–12 regions), and modal values (1 and 2 regions) were observed for plants with the three origins determined.

### Determinants of distributional range of naturalized plants in continental Chile

Comparing the number of regions occupied by naturalized species between different periods, we found significant differences in their geographical range (Table 2). Plants recorded earlier showed a broader distributional pattern than those introduced later. Tukey tests yielded significant differences between all distributions, except < 1849 and 1850–1899 (Table 1). Life cycle (annual, perennial, other), biogeographical origin (Eurasian, American, other), and interaction between factors (including minimum residence time), did not display significant statistical effects with regard to the regional range of naturalized plants in continental Chile (Table 2).

**Table 2** Three-way ANOVA for life cycle, biogeographical origin, and introduction year as determinants of geographical distribution of naturalized plants in continental Chile

Source	SS	d.f.	MS	F	P
Year	2.19	3	0.73	12.5	< 0.000
Life cycle	0.04	2	0.02	0.32	0.726
Biogeographical origin	0.09	2	0.04	0.74	0.478
Life cycle × Biogeographical origin	0.15	4	0.04	0.63	0.643
Year × Biogeographical origin	0.13	6	0.02	0.38	0.890
Life cycle × Year	0.13	6	0.02	0.38	0.894
Error	23.42	404	0.058		

## DISCUSSION

Studies such as this are scarce in literature on biological invasions (Kolar & Lodge, 2001) due to the inherent difficulty in accessing historical records on exotic plants (Wu *et al.*, 2003; Pauchard *et al.*, 2004a,b). Interestingly, there is a good database on introduction events of naturalized plants in Chile, because numerous naturalists and botanists have made valuable observations and collections since mid-19th century. Nevertheless, uncertainty exists for plants introduced in previous years (Pauchard *et al.*, 2004a,b), specifically between 1550 and 1849. We have reduced this bias by using the concept of minimum residence time and grouping the data in categorical variables for analytical purposes.

The minimum residence time (MRT) corresponds to time between present and first observation or collection of exotic species in their new homeland, and is broadly used when there is an incomplete historical record (Wu *et al.*, 2003). MRT involves some time lag phases because the first collected sample is obtained only when the exotic population becomes detectable in the wild. According to theoretical and empirical studies, the lag time phases have magnitudes of years to decades, but not centuries (Sakai *et al.*, 2001; Shigesada & Kawasaki, 2001), so that MRT is a valuable estimator of introduction date for exotic flora.

### Historical effects and geographical distribution

Mack *et al.* (2000), Rejmánek (2000) and Sakai *et al.* (2001) proposed that introduction date or MRT may be a deciding factor in the direction of colonization and invasion of exotic plants, but few studies have tested this proposition (Kolar & Lodge, 2001: 200–201). Arroyo *et al.* (2000) reported that the distributional pattern of alien weeds is associated with the time of establishment classified in three periods (pre 1900, 1900–50, post 1950). Our analyses also point out to the importance of the MRT as a decisive factor in the current geographical distribution of naturalized plants, unlike intrinsic attributes of the species, such as life cycle and biogeographical origin.

Scott & Panetta (1993) documented that the introduction year of exotic plants determines invasiveness in weeds, and their overall abundance (Pyšek *et al.*, 2003). Toney *et al.* (1998) reported that 288 species of exotic plants introduced between 1950 and 1966 in the north-western United States show different spreads of counties occupied, but they did not specifically mention a relationship between introduction date and invasiveness. To the contrary, Wu *et al.* (2003) reported that time since introduction did not always correlate with the number of localities of collection of naturalized Fabaceae in Taiwan.

Minimum residence time as estimator of date of introduction constitutes a historical factor that may account for at least three relevant ecological–evolutionary processes (Sakai *et al.*, 2001). First, newly introduced plants are usually represented by a small number of individuals (or colonies) that may require some time before developing self-sustained populations (Mack, 1986, 1996; Kowarik 1995, cited in Sakai *et al.*, 2001). A certain time may be required for the operation of micro-evolutionary processes leading to the expression of invasive traits and the

elimination of deleterious genetic variations that emerge in small populations (Ellstrand & Schierenbeck, 2000; Mack *et al.*, 2000).

Secondly, some authors have suggested that a longer period since introduction to the time of first recording may provide a greater opportunity for spread in the host region (Lodge, 1993; Kolar & Lodge, 2001). To reach regional distribution a given exotic species may require the existence of spread vectors and routes, which are not always available (Parendes & Cones, 2000; Novak & Mack, 2001). For the naturalized flora Arroyo *et al.* (2000) documented that the density of roads is positively correlated with the number of naturalized plants in each region of the country.

Thirdly, the subsequent arrival of new propagules that are added to the initial exotic population may constitute an important contribution to escape from demographic bottlenecks (Kolar & Lodge, 2001; Sakai *et al.*, 2001). Further, the longer the time elapsed from the initial colonization, the greater is the probability of arrival of new individuals of the exotic population. Pyšek *et al.* (2003) documented that the introduction date was a determinant factor of the abundance of exotic flora in the Czech Republic. Interestingly, they showed that morpho-functional attributes considered favourable for colonization (Rejmánek, 2000; Sakai *et al.*, 2001) were not related to invasiveness of the European neoflora. In concordance with our results, Pyšek *et al.* (2003) found that life cycle (annual/perennial) was not associated with invasiveness. To the contrary, Baker (1974) reported that life cycle might be associated with invasiveness, although he did not control for introduction date.

We did not find any effect of biogeographical origin on the spread of naturalized plants in Chile. Di Castri (1989) proposed that species of the Eurasian flora are highly invasive. According to him, this invasiveness would have evolved in response to drastic climatic and other environmental changes in Eurasia, including intensive agriculture. This hypothesis is not supported by our study, because the naturalized flora in Chile originating from American, African, European, East Asian or Oceanian regions does not show differences in their regional spread. Thus, an alternative explanation for the ample spread of Eurasian flora around the globe may be associated to the high historical availability of plants of this origin, due to an asymmetrical exchange in imports and exports to and from that region.

### Plant naturalization in continental Chile

The 707 exotic plant species in continental Chile show a distribution pattern that encompasses between one and all of the 13 administrative regions of the country. Most naturalized species concentrate in central Chile (Matthei, 1995), with a lower representation in the northern and southern extremes. This pattern may occur because these regions were the first occupied during the Spanish colonization, and have experienced the highest human population levels and most intense land use for five centuries (Montenegro *et al.*, 1991; Matthei, 1995; Arroyo *et al.*, 2000).

According to Arroyo *et al.* (2000: 390), the accidental and involuntary introduction of plants to continental Chile was the chief arrival mode of exotic flora. Nevertheless, this proposition

requires some qualification, because a considerable number of naturalized species in Chile have medicinal, nutritional, or ornamental use (F. Philippi, 1884; Castro, unpublished data), suggesting that their former usage in Europe might have motivated their import and release. In fact, before the 1850s many exotic plants were introduced as agricultural crops, therefore this type of alien should have a broad distribution just because Chile is a highly agricultural country. On the other hand, recent introductions are primarily of ornamental species that do not have vectors to spread broadly. Therefore, many of the patterns that we observe today may be related to functional type of alien species or the kind of human activity that promotes their dispersal.

It should also be noted that during the second half of the 19th century, the Chilean government actively promoted the introduction of exotic plants to the country. The import to and cultivation of more than 2000 exotic plants in the Jardín Botánico de Santiago (the first botanical garden in Chile) had the purpose of using those plants to teach Botany, in fields such as medicine or pharmacy, as well as in search of new crops (R. Philippi, 1882; F. Philippi, 1884). Through time, most of the attempts to cultivate those plants were unsuccessful (R. Philippi, 1882), but in the process 43 species escaped to the wild and became naturalized (Matthei, 1995). According to our estimations, these deliberate introduction events resulted in a proportion of naturalized species of 2%, lesser than the 10% figure reported in others studies (Kolar & Lodge, 2001).

Although the total number of exotic plants that arrived to Chile is difficult to estimate, we may extrapolate it by using the 2–10% 'rule' for naturalized species. Thus, we estimate that between 7070 and 35,400 exotic species may have arrived to the country, values that are in line with the actual number (*c.* 700) of naturalized plants. The exotics have naturalized with an apparently constant rate of 2–3 species year<sup>-1</sup>, lower than the 4–6 species year<sup>-1</sup> estimated for Mediterranean regions of the world (Groves, 1991; Kloot, 1991; Rejmánek *et al.*, 1991; Wu *et al.*, 2003). Interestingly, the naturalization of exotic plants in continental Chile shows a linear growing tendency similar to that documented by Pyšek *et al.* (2003) for the Czech Republic, and by Wu *et al.* (2003) for the Taiwanese Fabaceae.

Traditionally, studies of invasions have focused on intrinsic plant factors that determine exotic invasiveness or on native habitat factors associated to invasibility. Nevertheless, here we emphasize that purely historical factors may contribute to a better understanding of the process of biological invasion, which subsequently affect the exotic population spread and abundance.

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## SUPPLEMENTARY MATERIAL

The following information is available from  
<http://www.blackwellpublishing.com/products/journals/suppmat/DDI/DDI145/DDI145sm.htm>

**Appendix S1** Checklist of 428 naturalized plants in continental Chile, their first record date (FRD), life cycle (LC), biogeographical origin (BO), and number of administrative regions occupied (ARO)

Am: America; Eu: Europe; As: Asia; Af: Africa; Australia; N.Z. New Zealand; Pan: Pantropical; Cosmo: Cosmopolitan; Tro: Tropical.

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