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ORIGINAL PAPER

Alien plants in Chile: inferring invasion periods from herbarium records

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Abstract We used 71,764 specimens (14,988 alien and 56,776 native) from the herbarium CONC at Universidad de Concepción, Chile to identify alien invasion periods. We assumed that the pattern of accumulation of specimens can be used for tracing back the distribution in time of alien species introductions in the Chilean territory. To assess this we constructed Invasion Curves (IC) of native and alien species and specimens recorded in the complete territory and we adapted this methodology to draw Proportion Curves (PC). Increments in the proportion of alien vs. native species can be interpreted as expansions in population size of alien species, either locally or by invasion of new areas. To visualize surface expansions consistent with changes in PC we arranged four maps broadly coincident with inflexions in PC: before 1900, 1940, 1980 and 2004. Invasion curves from both native and alien species produced a first step of positive and rapid increment followed by an extended, apparently stable phase. The first expansion phase of alien flora (1910–1940) coincides with a first period of strong growth of Chilean agriculture as indicated by increments in wheat and other cereals production. A more recent second maximum showed by PC (approximately between 1980 and 2000) occurs in a period when: (i) wheat surface goes down but (ii) wheat production increases, and (iii) forestry exports increases. These changes are coincident with increased mechanization making possible more wheat production in fewer surfaces. The expansions of alien plant species in Chile are evident on geographical distribution maps. In only one century alien species expanded to nearly all the territory. Both the North and South extremes however, seem to be an exception to this general trend as shown by the gaps on maps.

Keywords Herbarium specimens · Invasion periods · Alien species · Historical reconstruction · Chile

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Introduction

The effects of human-caused biological invasions threaten efforts to conserve biodiversity (di Castri et al. 1990; Vitousek et al. 1997; Mooney and Cleland 2001). Thus, learning to identify plant species invaders could reveal the most effective means to prevent future invasions (Sala et al. 2000). In this context, data stored in herbarium labels is at present the main source of historical information available about alien plant species in a given zone. Herbarium records are heterogeneous in terms of locations and habitat descriptions (Pyšek and Prach 1993; Delisle et al. 2003; Lavoie and Dufresne 2005), but they at least provide us with collection dates and geographical location to approach arrival and establishment of alien species.

Herbarium data has been widely used to study plan invasions (e.g., Pyšek and Prach 1993, 1995; MacDougall et al. 1998; Stadler et al. 1998; Mihulka and Pyšek 2001; Lienert et al. 2002; Delisle et al. 2003; Lavoie et al. 2003; Willis et al. 2003; Gimaret-Carpentier et al. 2003; Mandák et al. 2004; Wu et al. 2004; Lavoie and Dufresne 2005). Pyšek and Prach (1993) prepared invasion curves methods (IC) for reconstructing the propagation history of four alien species in Czech Republic. They adjusted an exponential model to the accumulated number of locations against time. The slope of the corresponding regression line was used as a measure of the invasion rate (Mihulka and Pyšek 2001). Abrupt inflexions on the invasion curve would indicate expansion periods of the alien species involved (Pyšek and Prach 1993).

Later Delisle et al. (2003), aiming to account for variability in sampling effort, employed proportion curves (PC). They used proportions of accumulated locations of alien species on accumulated locations of native species. Increments in the proportion of alien vs. native species can be interpreted as expansions in population size (either locally or by invasion of new areas). A faster than normal accumulation of alien herbarium specimens associated to specific locations is interpreted as an invasion period (Delisle et al. 2003).

Chile is identified as a hotspot of world biodiversity (Ormazabal 1993) due to its remarkable high levels of endemism and biogeographic isolation (Myers et al. 2000), raising concerns on its susceptibility to invasions (Arroyo et al. 2000). However, little is known about the history of introductions and fluctuations of abundance of alien plant species. They have been reported in Chile since colonial times in the 16th century (Arroyo et al. 2000; Figueroa et al. 2004) but they have not been systematically recorded up until the 18th century (review and references in Figueroa et al. 2004).

In this research we aimed to identify alien plant species invasion periods in Chile using herbarium records. In order to do that, we accept that the pattern of accumulation of specimens can be used for tracing back the distribution in time of alien species introductions.

Methods

Data source and analysis

We used an extensive database of 71,764 specimens (14,988 alien and 56,776 native) from the herbarium database at Universidad de Concepción (CONC, founded 1924). Total numbers of species and specimens collected in Chile (hereafter-sampling effort) were plotted against time in 10 years periods. A Kendall's rank correlation procedure was used to correlate the number of alien and native species and specimens. Chi-square Goodness of Fit (Sokal and Rolf 1992) was employed to test for differences in sampling effort distribution.

We modified the procedure in Pyšek and Prach (1993) for constructing invasion curves (IC) of native and alien species and specimens. We plotted the cumulative number of species and specimens collected in Chile against time in 10 years periods. Pyšek and Prach (1993) reconstructed the invasion history of four species using dates and locations. While we used instead specimens for invasion curves of the total of species and for the whole country. We assumed that the curve for native and alien species reflect the spatio-temporal sampling distribution of herbarium specimens. In other words, we expected that specimen's accumulations of native and alien in a collection should follow the same tendency. As in Mihulka and Pyšek (2001), the slope b of the regression line of the logarithms of cumulative number of species on time was used as a measure of the invasion rate. Differences between alien and natives due to a faster rate of accumulation of alien than the "normal" for natives indicate an invasion period. A t-test of parallelism of regression lines (Sokal and Rohlf 1992) was employed to test differences between the slopes of alien and native species and specimens.

Also we adapted the methodology in Delisle et al. (2003) to draw proportion curves (PC). We divided the cumulative numbers of alien species by cumulative numbers of native species. The proportion obtained was then plotted against time in 10 years periods. As for IC, we modified the procedure in Delisle et al. (2003), constructing PC for the total species number and not for a reduced set. Then we searched for inflexions corresponding to periods when alien species were more collected than natives. It is worth to note that our PC was constructed using species number and a not specimens as in Delisle et al. (2003). Increments in the proportion of alien vs. native species are interpreted as expansions in population size of alien species, either locally or by invasion of new areas (Delisle et al. 2003). This process should result in a faster than normal accumulation of alien herbarium specimens, over those of native species, thus accounting for an invasion period.

To visualize expansions in area consistent with changes in PC we arranged four maps broadly coincident with inflexions in PC: before 1900, 1940, 1980 and 2004. Sampling locations and collection dates for the alien plant specimens were obtained from herbarium labels and processed with a geographical information system (ArcView GIS 3.2, ESRI, USA).

Results

A total of 71,764 herbarium specimens (14,988 alien, 56,776 native) were examined in this study corresponding to 629 alien and 1,997 native species. Eventhough the distribution of sampling effort for alien and native species were significantly different ($\chi^2_{(1,9)} = 38.14$; $P < 0.001$), both were positively correlated (Kendall's-Tau = 0.818; $P < 0.001$). Most of alien species were collected between 1920 and 1940 (Fig. 1a) and during the decades of 1960 and 1990. The vast majority of native species were also obtained between 1920 and 1940 (Fig. 1a), but diminished during the 1950 decade and incremented again in 1960.

Sampling efforts for native and alien specimens were significantly different on the last 90 years (Fig. 1b) ($\chi^2_{(1,9)} = 52.75$; $P < 0.001$). However, both were positively correlated (Kendall's-Tau = 0.745; $P < 0.001$). Variation in sampling effort, in species and specimens, is evident when examining shorter periods. For instance, during the 1930 decade 400 native species were recorded (Fig. 1a) from near 2,000 specimens (Fig. 1b) while for the year 2000 from approximately 8,000 specimens only 60 species were registered. Similar tendency is evident for alien species, during the 1930 decade 100 species (Fig. 1a) in 800 specimens were obtained (Fig. 1b), while during the year 2000, 50 species were recorded on 2,000 specimens.

Slopes of IC for alien species (Fig. 2a) and specimens (Fig. 2b) did not differ significantly from that of native species and specimens, respectively, suggesting similar rates on species accumulations. However, IC for alien species and specimens shows a notorious increment between 1910 and 1940 (Fig. 2a, b). The same inflexion was evident on PC (Fig. 3) between 1910 and 1940. During that period the predominant families collected were Poaceae, Asteraceae and Fabaceae (Fig. 3, inset). Additionally, a second period of increment is evident on PC (Fig. 3) from 1980 on. However, this is of lower magnitude as compared with the first one.

To broadly visualize the spatial dimension on alien expansion in Chile 13,827 specimens were used to prepare distributions maps (Fig. 4). They are presented in four steps. First, before 1900 (Fig. 4) 28 specimens were collected only in the Mediterranean climate in central Chile. By 1940 it reached 2,300 specimens (Fig. 4), most of them from the central Mediterranean zone but incorporating some exemplars from north and south extremes. Subsequently, towards 1980, a proportionally large number of alien specimens are added to reach 10,478 (Fig. 4) with a significant increments in area. Again, they are concentrated on the Mediterranean central zone but now with a significant participation of exemplars collected on the temperated rainy forest, southern from the Bio-Bio river; also extremes North and South increment noticeably. Lastly, by 2004 it reaches 13,827 specimens (Fig. 4) without noticeable increments in the area covered, suggesting stabilization or "saturation." From a broad perspective, both the northern and southern portions exhibit areas of significant size without records (Fig. 4). They broadly correspond to the Atacama desert on the north and to ice-covered areas on the south.

Discussion

We identified invasion periods of alien plant species in Chile from the collection dates of specimens

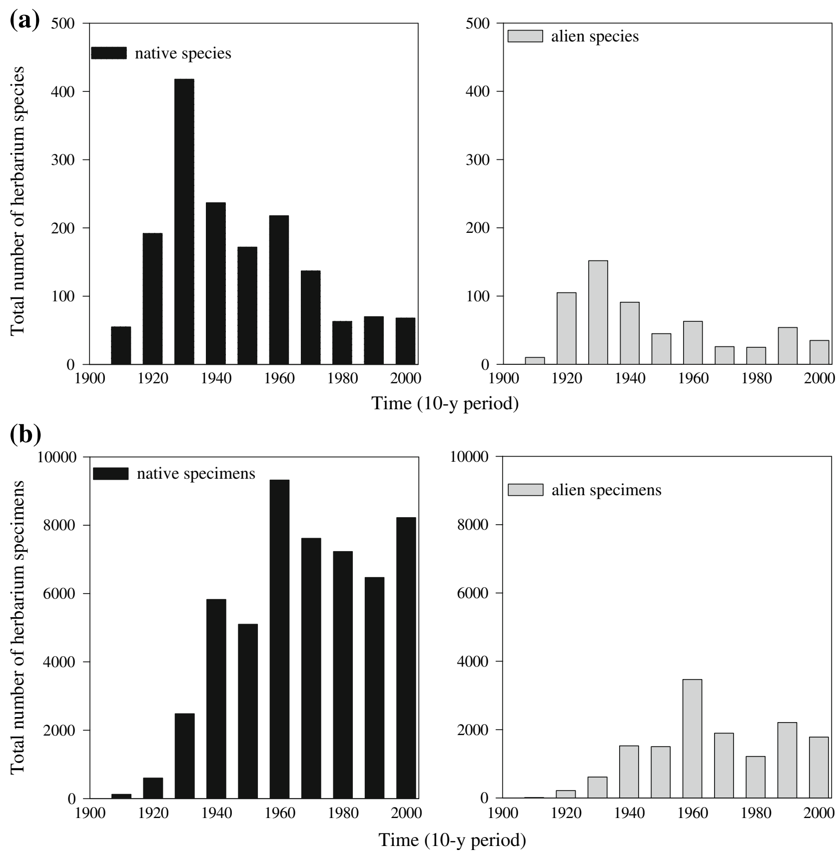

Fig. 1 Total number of herbarium species (**a**) and specimens (**b**) recorded in the Herbarium of the Universidad de Concepción, Chile (CONC) plotted against time (10-year periods)

deposited on CONC herbarium in Concepción Chile. We corroborate that alien species and specimens accumulate in relation to alien species introductions into new areas. Undoubtedly, herbaria are at the present times the one of the most reliable source of information to document past changes in a given flora. The more than 70,000 well-checked specimens used in this study should be sufficient to diagnose the situation in Chile in the past and for the evaluation of future risks.

We adapted invasion and proportion curves by Pyšek and Prach (1993) and Delisle et al. (2003), respectively, and used them with full collections and specimens, and not only for a reduced group of species and their localities. We acknowledge all known "drawbacks" and peculiarities of information registered on herbarium labels mainly in terms of the quality of habitat description and geographical distribution (Wu et al. 2005). But also we accept that having a location, a date of collection and well-checked taxonomy should grant the use of that information to inquire on the accumulation process and, by it, on the dynamics of establishment and expansion of aliens in Chile.

Additionally, we accepted that the accumulation of native specimens corresponds to a "normal," expected situation for increments on a collection. We are also assuming that, first, there is a definite pattern and, second, that both native and aliens follow the same pattern of accumulation. Consequently, by comparison of both, it is possible to detect changes in the rates of accumulation of species evidencing periods of increments of new species into the flora.

When accumulated as IC, both native and alien species produced a first step of positive and rapid increment followed by an extended, apparent plateau phase. Steep increments on the first phase of IC for native species are related with increments in floristic sampling intensity (associated to the foundation and increments in collection efforts at CONC in our case) and, in part, to higher levels of floristic richness and endemism in the Mediterranean climate region in central Chile (Myers et al. 2000). Delisle et al. (2003) argue that this initial phase in the native

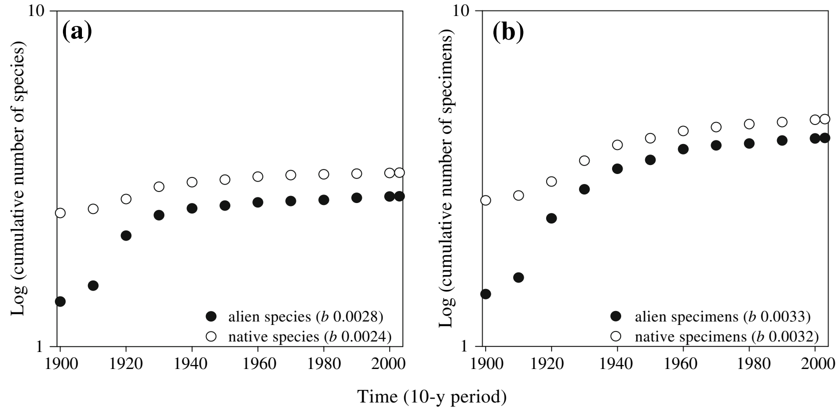

Fig. 2 Invasion curves (sensu Pyšek and Prach 1993) for alien and native species (**a**) ($P > 0.01$; $R^2 = 0.89$; $R^2 = 0.91$, respectively; $P = 0.08$ test of parallelism) and for alien and native specimens (**b**) ($P > 0.01$; $R^2 = 0.96$; $R^2 = 0.97$, $P = 0.16$ test of parallelism). Invasion rate (slope *b*) is given for each alien and native species and specimens. Records were obtained from Herbarium of the Universidad de Concepción, Chile (CONC)

species represent the history of the state of knowledge of the range occupied by these species. Both, species and specimens leveled off and follow a similar pattern from 1940 on. Also, it is evident the lack of collections before 1900. Moreover, a second inflexion not present in IC was evident in the PC curve. Since PC is constructed using a proportion (alien vs. native species), it should be more responsive to changes in alien flora. For a curve of natives increasing to some sort of normal rate, any unusual increase or leap of alien species would result in an inflexion on the curve. Also, alien vs. natives proportions cancel out the effects of fluctuations in year to year sampling effort. We assume that there is no bias towards any of both natives or alien species and they accumulate independently.

The first expansion phase of alien flora (1910–1940) coincides with a first period of strong growth of Chilean agriculture (Cariola and Sunkel 1982) as indicated by increments by wheat and other cereals production (Fig. 5). Also Matthei (1995) reports on sustained increments in the collection of weeds from 1894 to 1934 (100 new alien species) associated to wheat imports. Aronson et al. (1998) recognizes a "first wave" of species introduction in the drier central Mediterranean climate area

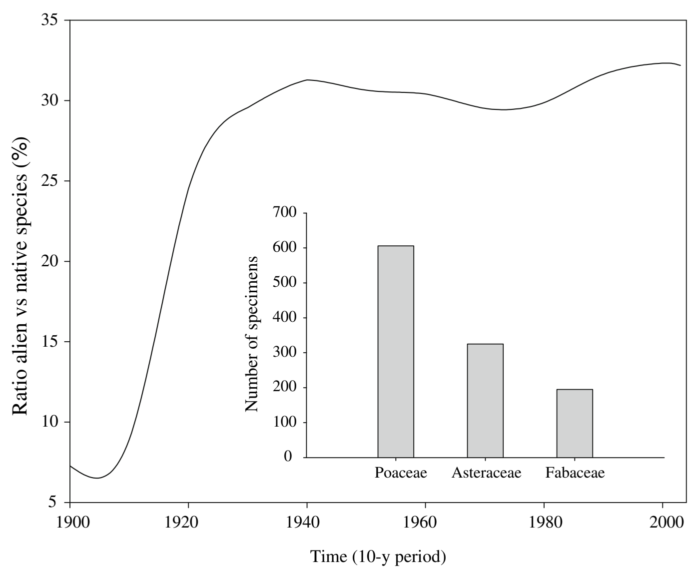

Fig. 3 Proportion curve (sensu Delisle et al. 2003) i.e., cumulative number of alien species divided by cumulative number of native species in Chile, calculated for every 10 years intervals. Proportions obtained were then plotted against time. Inset Family with more alien specimens in the period 1910–1940. Records were obtained from Herbarium of the Universidad de Concepción, Chile (CONC)

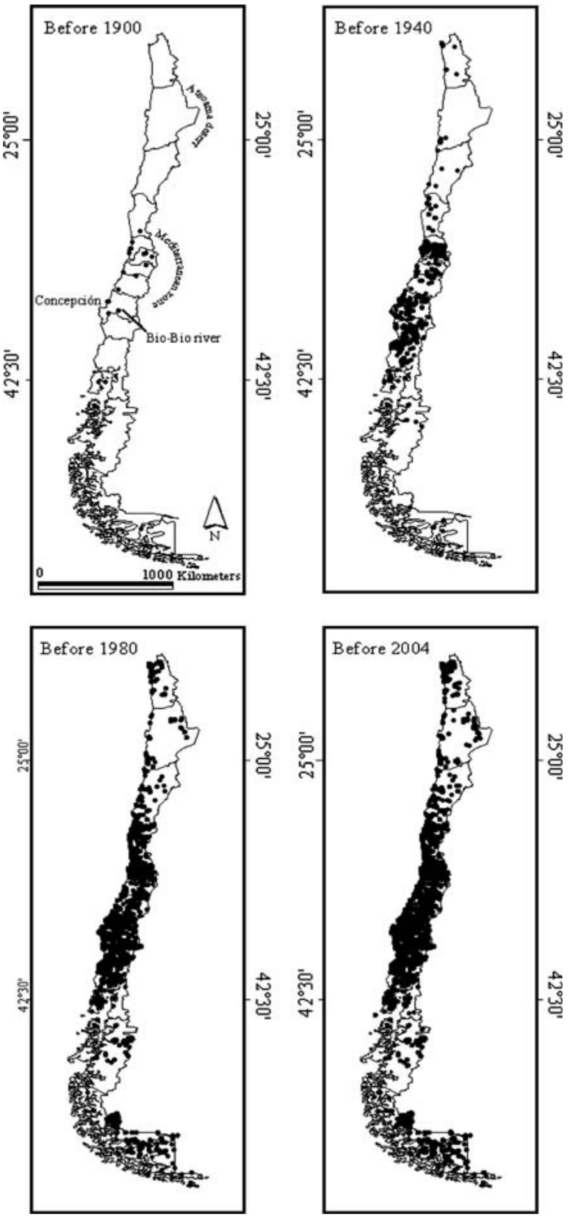

Fig. 4 Location of alien specimens (black dots) with place names cited in the text-collected before 1900 (28), 1940 (2,300 specimens), 1980 (10,487) and 2001 (13,827), respectively. Sampling locations and collection dates were obtained from Herbarium of the Universidad de Concepción (CONC), Chile

starting on colonial times (1880) and ending by early 1920s, associated to landscape transformations. There is reasonable correspondence between that phase and the expansion phase recognizable between 1910 and 1940 in our results. In general the areas under Mediterranean climate and temperate rainy influence have a well-documented history of pervasive human influence, landscape degradation and losses in diversity (Aronson et al. 1998; Arroyo et al. 2000).

In contrast, the more recent second maximum showed by PC (approximately between 1980 and 2000; Fig. 3) occurs in a period when: (i) wheat surface goes down (Fig. 6a) but (ii) wheat production increases (Fig. 6b) and at same time (iii) volume of forestry plantations and forestry exports increases (Fig. 7). Those changes are coincident with increased of mechanization that made possible more wheat production in less surface. It is known also that during that period part of the land dedicated to wheat has been changed into forestry plantations. Moreover, Fuentes et al. (unpublished data) found non-significant relationship between alien species richness and forestry plantations activities, but a significant positive one with agriculture at provincial level. Recent changes in land-use could be then promoting a new phase in alien species arrival and expansion in Chile. That tendency is, with our data, not possible to project for the future.

The expansion of alien species in Chile is clearly evident on spatial changes visualized by geographical distribution maps (i.e., the four periods in Fig. 4). In only one century alien species expanded to nearly all the territory. Both the North and South extremes however, seem to be an exception to this general trend as shown by the gaps on maps (Fig. 4). This can

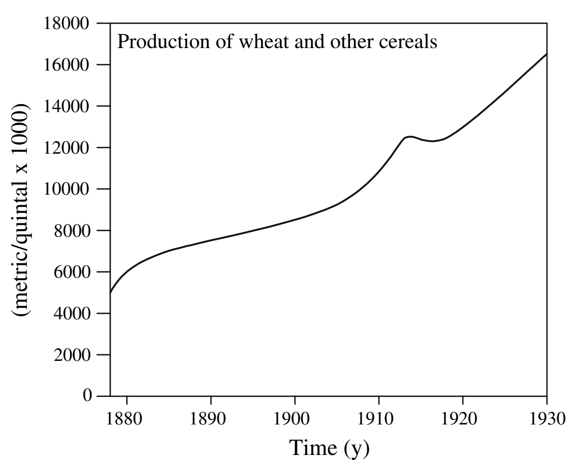

Fig. 5 Production of wheat and other cereals (metric/quintal × 1000) in Chile from 1878 to 1930. Data were obtained from Cariola and Sunkel (1982)

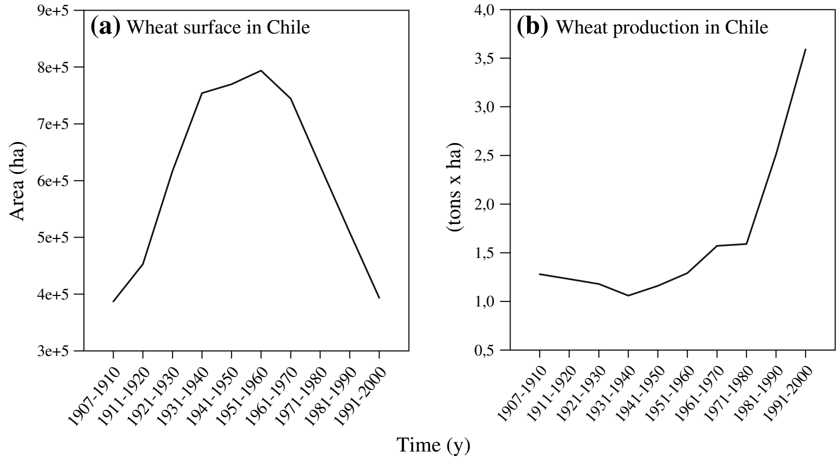

Fig. 6 Surface of wheat (ha) cultivated in Chile (**a**) and production of wheat (tons × ha) (**b**). Data were obtained from Mellado (2007)

be explained by different circumstances. First, the North has been thoroughly explored and collected during the last three decades and gaps there are then attributable to the harsh hot desert there. Gaps in the southern extreme area could be instead the result of a combination of less intensity in collection efforts due to inaccessibility as well as to the big sections of land covered with permanent ice or natural forest.

Both curves give rise to questions like: How can we understand the curves in historical terms? Are changes concordant with relevant historical events in Chile? It is widely accepted that the spread of native

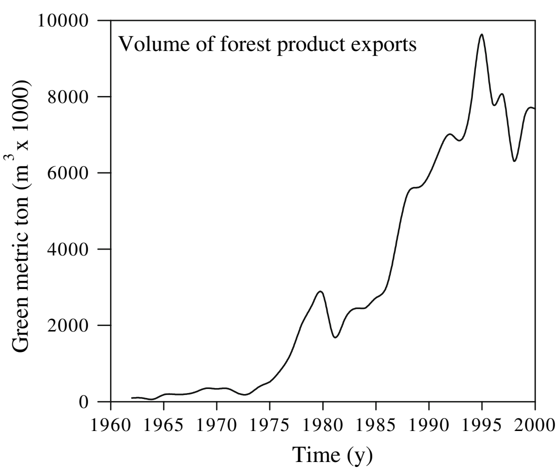

Fig. 7 Volume of forestry products exports (Green metric tons), (lumber, pulpwood, periodic paper, elaborate wood, moldings, furniture and chips) in Chile ($m^3 \times 1{,}000$). Data were obtained from Corporación Nacional Forestal and Instituto Forestal (CONAF—INFOR, 2005. http://www.conaf.cl)

plant species from refuge after last glaciations event ca. 10,000 years ago with different success in terms of colonized area (Hinojosa and Villagrán 1997). While aliens species have been present only for four and a half centuries (from around 1520–2000) when Spanish conquerors brought agriculture to the Mediterranean climate area in Chile. It is important to take into account that the Spanish colonization period embraces two distinct steps in Chile (Aronson et al. 1998). (i) The Spanish were able to control and settle only the territory located to the north of the Bio-Bio river for three and a half centuries (Aronson et al. 1998). (ii) Only during the last century the territory was secured for settling southern from the Bio-Bio river. Consequently, for three and a half centuries alien species were restricted to the territory north from the Bio-Bio river. Only during the 20th century the whole Chilean territory was open for alien species to establish and disperse, when clearing of the southern temperate forest was massive and intensive (Donoso and Lara 1996). The difference on the first phases of IC curves then is at least in part explained by the expansion of alien species to the territory southern of the Bio-Bio river when new land was available to them. They could originate from aliens already present north of the Bio-Bio and from new species finding new opportunities under the new temperate rainy conditions, or new ones through new ports opened at the south. The differentiation of origin should be correlated with present distribution ranges (Fuentes et al. unpublished data).

In summary, we identified two periods of increment in alien species in Chile both related to changes in agriculture and forestry plantations. Historically in the first period to phases are confounded: the Mediterranean zone gave aliens opportunities to expand during three centuries while the temperate rain zone has been open only during the last century. There is a second increment suggested by a peak on the PC which could be a response to changes in agriculture and probably to an intensification of forestry plantations activities. Consequences and risks in terms of spreading and invasions of individual species will require to be documented by an efficient combination of herbarium records with well designed, specifically oriented, sampling programs.

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