Do climatically similar regions contain similar alien floras? A comparison between the mediterranean areas of central Chile and California

Alejandra Jiménez[1,4], Aníbal Pauchard[1,4*], Lohengrin A. Cavieres[2,4], Alicia Marticorena[2] and Ramiro O. Bustamante[3,4]

[1]*Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, Chile,* [2]*Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Chile,* [3]*Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Chile,* [4]*Instituto de Ecología y Biodiversidad (IEB), Chile*

ABSTRACT

Aim Taxonomic comparisons of alien floras across climatically similar regions have been proposed as a powerful approach for increasing our understanding of plant invasions across scales. However, detailed comparisons between the alien biotas of climatically similar regions are scarce. This study aims to compare the taxonomic patterns of alien species richness in mediterranean-type climate areas of central Chile and California, in order to better understand how climatically similar regions converge or diverge in terms of their alien flora.

Location Central Chile and California, United States.

Methods We compared the alien floras of the state of California in the United States and central Chile, considering within-region variation and taxonomic composition up to the species level. To test for within-region variation, administrative units and counties were grouped within seven latitudinal bands for each region. We tested for differences in the relative contributions of the various origins of the naturalized species to each region. We used a family naturalization index to establish which families had relatively higher numbers of naturalized species in each region. We evaluated the similarity, using cluster analyses with Jaccard's similarity index, of alien taxa between regions and latitudinal bands using presence–absence matrices at the species, genus and family levels. We used principal components analysis to determine the presence of a compositional gradient including all latitudinal bands.

Results We recorded 1212 alien plant species in California and 593 in central Chile, of which 491 are shared between the two regions. These figures include 25 species that are native to California and 37 that are native to Chile. A comparison between the alien floras of central Chile and California reveals three major trends: (1) higher naturalized species diversity for California than for Chile, at all taxonomic levels; (2) differences in the proportion of species according to origin, with America, Africa, Asia and Australia providing a larger number of species in California than in Chile; (3) segregation between regions in terms of taxonomic composition of their alien flora, and a rather weak differentiation within regions; and (4) a trend towards higher similarity between the alien floras of latitudinal bands associated with higher levels of human disturbances.

Main conclusions The alien floras of central Chile and California are significantly different, but this difference diminishes in highly disturbed areas. Thus, the current high levels of species movement caused by globalization, together with increasing levels of anthropogenic disturbances, should reduce the

Correspondence: Aníbal Pauchard, Facultad de Ciencias Forestales, Universidad de Concepción, Casilla 160-C, Concepción, Chile.
E-mail: pauchard@udec.cl

differentiation of the alien floras in these regions, increasing overall biotic homogenization.

INTRODUCTION

Large-scale taxonomic comparisons of alien floras have provided interesting insights into the patterns of invasiveness across plant taxa. For example, Pyšek (1998) compared the alien floras from 26 regions of the world and established that some families (e.g. Papaveraceae, Chenopodiaceae and Amaranthaceae) contain a relatively higher number of successful invasive species with respect to the total pool of potential alien species. However, these global-scale comparisons often do not take into account differences between climatic regions, which may lead to overgeneralization and to contradictory results regarding the invasiveness of certain taxa.

The comparison of alien floras across climatically similar regions has been proposed as a powerful approach to understanding the various aspects of plant invasion processes, particularly the identification of large-scale drivers other than climate (Pauchard *et al.*, 2004a). Detailed comparisons between the alien biota of climatically similar regions would better establish which taxa are more invasive, by reducing the overall variability caused by regional climatic peculiarities. Such comparisons would also facilitate the identification of highly invasive species, making it easier to monitor their expansion in climatically matched environments in which invasion has not yet occurred (Weber, 1997). At the same time, comparisons between regions with similar climates could elucidate the role of anthropogenic introductions, and the effects of specific human disturbances associated with a historical or cultural setting, on invasion processes (e.g. Kruger *et al.*, 1989; Aschman, 1991). Ideally, once these factors are accounted for, studies could focus on more local factors, such as the characteristics of the invader species and their interactions with native ecosystems (Pauchard *et al.*, 2004a).

Given the currently high rates of globalization and homogenization of human activities, resulting in more intensive propagule exchange, climatically similar regions should have higher chances of receiving similar sets of alien species than in historic times (Mack *et al.*, 2000). Once a species has arrived in a new region, the local climate should impose a comparable barrier across climatically similar regions, resulting in the homogenization of the alien floras in these regions (Pauchard *et al.*, 2004a). However, historical differences in the rate and type of introductions, and cultural differences in land use, could still have major effects on the current composition of the alien flora of a region, resulting in differences even for climatically similar regions. Furthermore, in natural and semi-natural environments, interactions between introduced and native biotas with different evolutionary histories may also define the composition of the alien flora.

In order to advance with a comparative approach, detailed comparisons among regions with similar climates are needed to elucidate more accurate patterns of taxa invasiveness. Although several attempts have been made to compare climatically similar regions (e.g. Kruger *et al.*, 1989; Aschman, 1991), detailed taxonomic comparisons among climatically similar regions are scarce. The assumption that areas with similar climates have similar alien floras has seldom been tested using comparable data sets, and within-region variation has often been ignored (Pauchard *et al.*, 2004a).

The mediterranean-type climate areas of California and central Chile represent particularly interesting systems for testing a comparative taxonomic approach between climatically similar regions. Of the five mediterranean-type climate regions of the world, central Chile and California have the highest similarity in terms of climate and geomorphology (Mooney *et al.*, 1970; Mooney, 1977; di Castri, 1991; Arroyo *et al.*, 1995; Sax, 2002). The two regions also show a parallel latitudinal-climatic gradient, with higher precipitation and lower temperatures at higher latitudes, which shapes the patterns of distribution of natural vegetation (Mooney *et al.*, 1970; Arroyo *et al.*, 1995). Furthermore, coastal and interior mountain ranges and central valleys are remarkably comparable between Chile and California, having equivalent local climatic effects (Mooney *et al.*, 1970).

Both central Chile and California have been substantially invaded by alien plants (Arroyo *et al.*, 2000). Over 1100 alien plant species have been recorded in California (cf. approximately 5000 native species; Hickman, 1993), and more than 700 alien plants are found in central Chile (cf. nearly 2500 native species; Matthei, 1995). Furthermore, both sites contain a highly endemic flora, and are considered hotspots for biodiversity (Myers *et al.*, 2000). Most of these invasions are associated with a long history of human immigration and settlement, which was similar in the two regions in terms of magnitude and origin until the mid-1800s. During the last century, however, California has seen a much higher rate of immigration and international trade than Chile, thus increasing the opportunities for biotic exchange (Schrag, 2007).

This study aims to compare the taxonomic patterns of alien species richness in central Chile and California, in order to better understand how climatically similar regions converge or diverge in terms of their alien flora. For this purpose, we use floristic data bases that are comparable across regions, and a multi-scale approach that recognizes within-region variation.

To explore patterns of similarity of the naturalized alien floras of Chile and California, we compare taxonomic richness at the species, genus and family levels, as well as comparing the biogeographic origin of each species. We test whether these taxonomic differences are consistent on a smaller, within-region spatial scale. Specifically, we use latitudinal bands to address within-region variation. Based on these analyses, we hope to elucidate patterns of similarity and differentiation between alien floras of climatically similar regions, and to establish the basis for more specific studies that could illuminate the causal factors of such patterns.

METHODOLOGY

Study sites

We compared the alien floras from two climatically similar regions: the State of California in the United States (32°–42° N latitude and 114°–125° W longitude), covering an area of 410,000 km^2, and central Chile (29°–44° S latitude and 72°–73° W longitude), covering an area of 256,500 km^2. California comprises 58 counties, and central Chile comprises eight administrative units (Fig. 1). The two regions experience similar seasonal variation in precipitation and temperature (Mooney et al., 1970; di Castri, 1991; Arroyo et al., 1995), being characterized by a temperate climate with cold, rainy winters and hot, dry summers. Furthermore, intense coastal fog, resulting from the influence of the cold Humboldt current in Chile, and the California current in the Northern Hemisphere, is a common climatic feature of both regions (di Castri, 1991). The geography of both central Chile and California is characterized by a longitudinal valley trenched between two mountain ranges. These climatic and geographic similarities have placed California and Chile among the regions with higher potential for biological comparisons (Arroyo et al., 1995).

Chile and California have received high numbers of alien plant species during recent centuries. In California, alien plants have had an extensive and severe impact (Bossard et al., 2000). The vegetation of coastal dunes, swamps, grasslands and oak savannas has been the most strongly invaded (di Castri, 1991; Dark, 2004; Seabloom et al., 2006). Forested regions and chaparral habitat have been impacted to a lesser extent (Kruger et al., 1989; di Castri, 1991; Bossard et al., 2000). Alien species continue to be introduced, and some of them become invasive, especially those introduced for ornamental purposes (Bossard et al., 2000). Although less affected by globalization, central Chile is especially sensitive to invasions because of its high
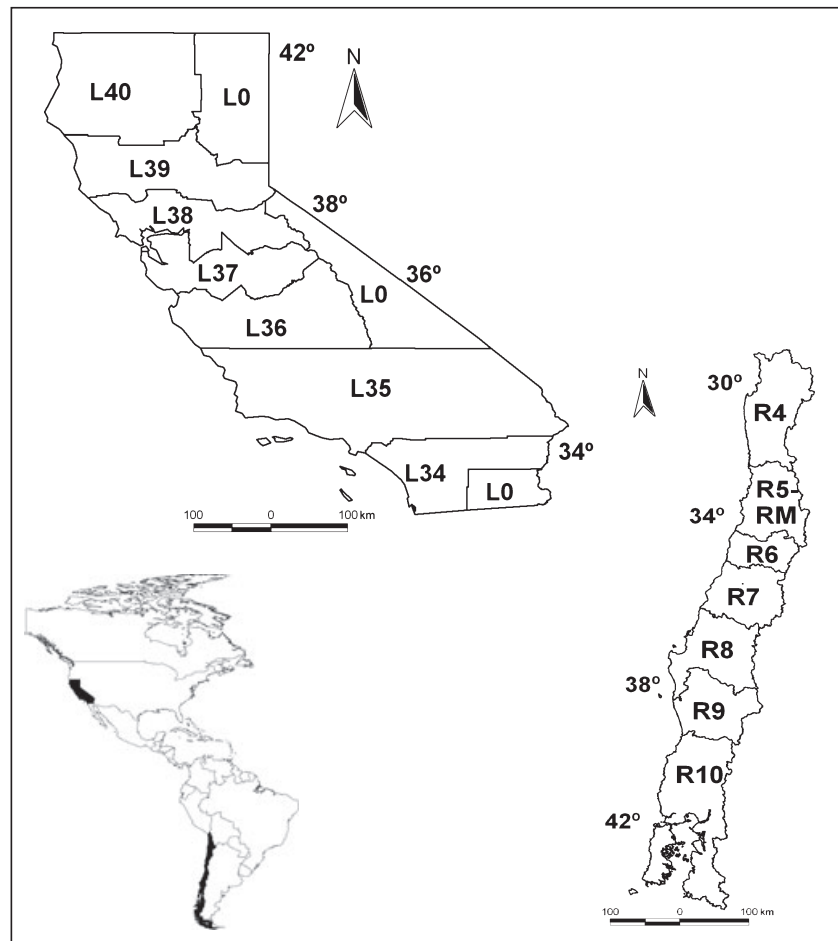
Figure 1 Locations of central Chilean and Californian regions. Latitudinal bands are indicated for Chile (R) and California (L). L0, in California, represents counties not considered in the analyses.

levels of endemism (Armesto *et al.*, 1998, 2001; Arroyo *et al.*, 2000; Pauchard *et al.*, 2004b; Castro *et al.*, 2005). In recent decades, this region has been heavily impacted by intensive agriculture and plantations of exotic pine and *Eucalyptus*, as well as by an exponential increase in urban development, making this region progressively more susceptible to alien plant invasions (Lewis & Ferguson, 1993; Arroyo *et al.*, 2000; Pauchard *et al.*, 2004b, 2006).

Data

Data on naturalized alien species were obtained from the Calflora data base (http://www.calflora.org) for California and from the data base of the Herbarium of the Universidad de Concepción (CONC) for Chile. Data were geographically assigned to counties (California) or administrative regional units (Chile). We conducted an exhaustive review of the data bases, eliminating repeated species, merging subspecies taxa, corroborating synonymies, and verifying and standardizing scientific names. Species, genus, and family names were also verified to ensure that they were compatible for the two regions, prioritizing the name synonymies assigned in the Chilean data base (C. Marticorena, personal communication, 2005), following current classification schemes (Stevens, 2001; IPNI, 2004; MBG, 2005). Hybrid species were considered as valid species. Those species listed for the study area but not linked to specific distribution records were not considered for the analysis. Finally, where doubts existed regarding the distribution of a species, these doubts were verified using literature records and expert opinion. For species identification we consulted the *The Jepson Manual: Higher Plants of California* (Hickman, 1993) and M. Rejmánek (personal communication, 2005) for California, and C. Marticorena (personal communication, 2005) for Chile.

A species was considered to be a naturalized alien for a region if: (1) it was not a native of the region; (2) it was recorded in the selected data bases; and (3) its naturalization was confirmed by experts (using Richardson *et al.*, 2000). Species were classified according to their continent of origin (Africa, America, Asia, Australia and Europe), and for some species Eurasia was considered as a separate unit when the literature did not differentiate between Asia and Europe origins (Bailey, 1942; Chittenden, 1965; Hickman, 1993, Matthei, 1995). Species were classified as 'Others' when information regarding their origin was inconclusive.

For regional analyses, owing to significant differences in size between counties in California and administrative units in central Chile, Californian counties were grouped within seven latitudinal bands, each covering approximately one degree of latitude, analogous to the administrative units in Chile (Fig. 1, Table 1). In Chile, administrative regional units R5 and RM were combined into one latitudinal band because of their size and latitudinal overlap (Table 1). For California, counties located on the western slopes of the Sierra Nevada mountains, which do not have a maritime influence, were not considered in the analyses (Alpine, Imperial, Inyo, Lassen, Mono, Modoc, Plumas, Sierra – denoted L0 in Fig. 1). These counties were excluded on the basis of a preliminary cluster analysis with all alien species for both regions (Chile and California), which indicated significant differentiation between counties located east of Sierra Nevada from the other counties of California.

Analyses

Herbarium records provide an accessible data source for exploring large-scale patterns of plant distribution (Kühn

Table 1 Attributes for latitudinal bands in central Chile and California. Latitudinal bands were used to group local administrative units to allow for comparisons between the two regions. Variables included are approximate latitude, population, and numbers of naturalized alien species, genera and families (including the logarithmic correction by area).

Latitudinal band	Aproximate latitude	Area (km^2)	Population	No. of species	Species/ log area	No. of genera	Genera/ log area	No. of families	Families/ log area
California									
L34	33°–34°	31,604	6,078,985	602	134	328	73	88	20
L35	34°–36°	103,996	12,080,807	776	155	418	83	103	21
L36	36°–37°	43,740	1,473,237	572	123	315	68	83	18
L37	37°–38°	25,857	5,031,392	849	192	449	102	111	25
L38	38°–39°	30,106	3,646,668	785	175	396	88	100	22
L39	39°–40°	36,725	854,113	702	154	373	82	93	20
L40	40°–42°	53,829	395,833	602	127	313	66	79	17
Chile									
R4	29°–32°	40,580	603,210	249	54	159	35	44	10
R5-RM	32°–34°	31,799	7,601,037	428	95	246	55	58	13
R6	34°–35°	16,387	780,627	266	63	166	39	45	11
R7	35°–36°	30,296	908,097	312	70	195	44	47	10
R8	36°–38°	37,063	1,861,562	381	83	213	47	52	11
R9	38°–40°	31,842	869,535	318	71	188	42	49	11
R10	40°–44°	67,013	1,073,135	299	62	185	38	58	12

et al., 2004; Pauchard & Shea, 2006; Seabloom et al., 2006). Nonetheless, we recognize that the use of herbarium and other botanical data bases has limitations, mostly because of the different criteria and sampling effort for collections in independent data bases. Specific analyses, such as comparing the shared species, can help to shed light on any differential bias between data bases.

For each region and latitudinal band, we calculated the species, genus and family richness of naturalized species. Taxa were also classified according to whether they were exclusive to one region (present in only one region) or shared (present in California and central Chile). To test for differences in the numbers of species in families and genera between Chile and California, we conducted a Wilcoxon test ($P < 0.05$) for the most diverse taxa.

We used the family naturalization index (F) based on Rejmánek et al. (1991) to calculate the proportion of naturalized species per family, weighted by the total number of naturalized species in the region (total number of species per family from Stevens (2001 onwards)):

Table 2 Naturalized alien taxon richness (families, genera, species) for central Chile and California. Taxa were classified as exclusive to Chile or California, shared between the two regions, and total.

Taxa	Chile	California	Exclusive to Chile	Exclusive to California	Shared	Total
Families	69	128	2	27	65	132
Genera	301	571	26	235	275	610
Species	593	1212	139	746	491	1376

maintained the higher taxonomic richness, even after correction for area (Table 1). In both regions, central latitudinal bands showed the highest diversity of naturalized flora.

California had the higher taxonomic richness for families, genera and species. However, both Chile and California presented common patterns for the most diverse families: Poaceae (Chile: 120 species, California: 192), Asteraceae (87,

$$F = \frac{\text{Number of naturalized species in the family}}{\text{Total number of species in the family} \times \text{Total number of species naturalized for the region}} \times 100.$$

To test for differences in the relative contributions of the various regions of origin of the naturalized species of each region (central Chile and California), the percentages of species by origin were compared using a proportion test (STATISTICA 6.0).

To evaluate alien taxa similarity between the two regions at a more detailed spatial scale, we conducted two similarity analyses. First, we generated presence–absence matrices using latitudinal bands, of both regions, for all the species, genera and families. Species native to one region but alien in the other were considered in these similarity analyses. In addition, a presence–absence matrix containing only species shared by the two regions was compiled. Cluster analyses were performed for each of the matrices with average linkage using the unweighted pair-group method (UPGMA) and Jaccard's similarity index. The statistical significance of the resulting clustering was established using the critical value of Jaccard's similarity index at the 95% confidence level (Real, 1999). Finally, to test for compositional gradients in the alien floras between and within central Chile and California, we performed a principal components analysis (PCA) with the presence–absence matrix for species in latitudinal bands.

RESULTS

Taxonomic richness

We recorded 1212 alien species in California and 593 alien species in central Chile, of which 491 are shared between the two regions (Table 2). These figures include 25 species that are native to California and 37 species that are native to Chile. At the scale of latitudinal bands, California

165), Fabaceae (48, 84), Brassicaceae (31, 67) and Caryophyllaceae (27, 44) (Fig. 2). The best-represented genera for Chile and California were Trifolium (Chile: 13, California: 18), Bromus (12, 15) and Polygonum (9, 16) (Fig. 2). Other less diverse genera were distinctly better represented in one region, for example Chenopodium (7, 16), Solanum (6, 14), Centaurea (5, 13), Veronica (9, 12), Euphorbia (8, 13) and Acacia (4, 12). Overall, when we corrected for the total number of alien species in each region, genus and family richnesses were significantly different between the two regions (Wilcoxon test, $P < 0.05$).

Family naturalization index

Polygonaceae, Geraniaceae, Scrophulariaceae, Onagraceae, Caryophyllaceae, Poaceae and Amaranthaceae showed the highest family naturalization index values for both regions (Fig. 3). However, subtle differences were detected for all families. Rosaceae, Iridiaceae, Solanaceae and Myrtaceae were among the families that showed disproportionally higher family naturalization indices in California compared with those in Chile, whereas Malvaceae and Apiaceae showed the opposite pattern.

Species origins

Central Chile and California presented significant differences in the proportions of species according to origin (proportion test, $P < 0.01$), with the exception of Eurasia (13.2% in Chile and 12.8% in California). Europe was the most important source of alien species in both regions, although
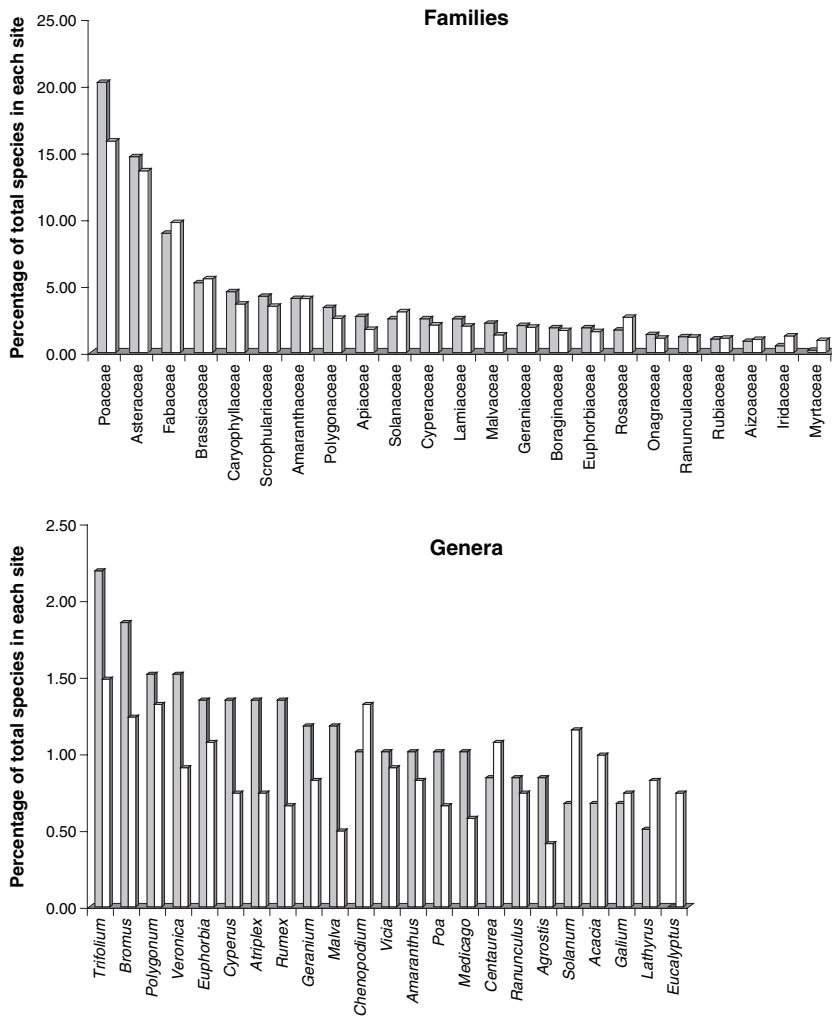
Figure 2 The most abundant families and genera of naturalized alien species in Chile and California. Bars indicate the percentage of the total alien flora for each site: grey, Chile; white, California.

its relative contribution in central Chile was significantly higher than that in California (48.7% compared with 38.5%, Fig. 4). America (11.9%, 21.5%), Africa (4.3%, 7.8%), Asia (1.6%, 6.5%), and Australia (2.4%, 4.8%) were significantly larger contributors to the alien flora of California.
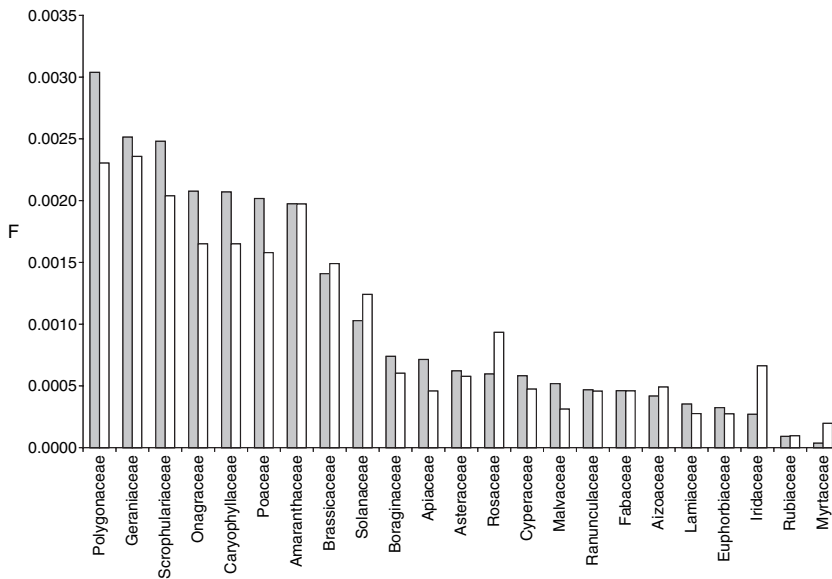
Figure 3 Family naturalization index for families with the largest numbers of alien species. The family naturalization index (*F*) is the number of naturalized species in a family divided by the total species diversity for that family worldwide, weighted by the total number of naturalized species in the region, multiplied by 100 (see text for formula). Families shown have at least ten species in each region. Bars: grey, Chile; white, California.
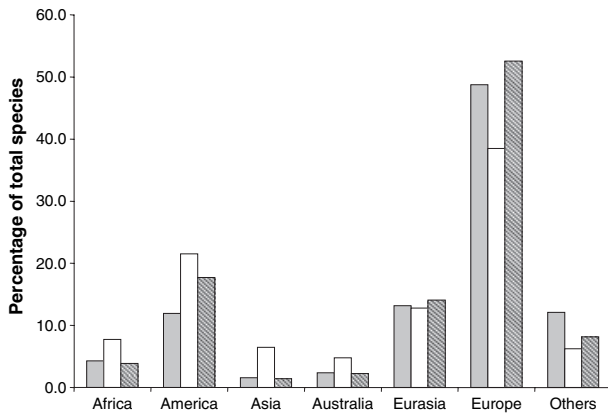
Figure 4 Continents of origin for alien species in California and central Chile. Percentage of species in the total alien flora. Bars: grey, Chile; white, California; hatched, shared species.

Similarity at the regional scale

Cluster analyses showed significant differences in taxonomic composition between Chile and California at the family, genus and species levels, and, in some cases, within-region segregation (Fig. 5). At the family level, three clusters were detected: one including all Chilean latitudinal bands, one containing northern Californian latitudinal bands, and one with central and southern Californian bands (Fig. 5a). The results suggest a fairly homogeneous distribution of families of alien species in central Chile, but a clear differentiation between the northern and southern latitudes in California. At the genus level, latitudinal bands for central Chile and California formed two separate clusters joined at a low similarity value (0.42, Fig. 5b). Within the Chilean cluster, the regions with the most extreme latitudes (R4 and R10) were not included in clusters with higher similarity. Administrative units R6 to R9 formed a cluster significantly separated from R5-RM. For California, most extreme latitudinal bands also showed a low similarity with the cluster formed by the central latitudinal bands (Fig. 5b). At the species level, higher variation was observed, but the pattern of cluster formation for California and central Chile continued to exceed inner-region variation (Fig. 5c). When only shared species were considered, six groups were detected (Fig. 5d). With the exception of one single latitudinal band (L34), the rest of the latitudinal bands for California formed a single cluster. Interestingly, this cluster of Californian bands included the R5-RM Chilean band, which is the area with the highest levels of introduction and anthropogenic disturbance. The other four groups, containing only Chilean bands, appeared distinctly grouped in the analyses, but R04, the most desertic Chilean latitudinal band, did not form part of any cluster. This clustering of California and the most invaded region of Chile indicates a higher degree of homogenization in the alien flora compared with other less disturbed areas of central Chile (Fig. 5). The PCA analysis shows
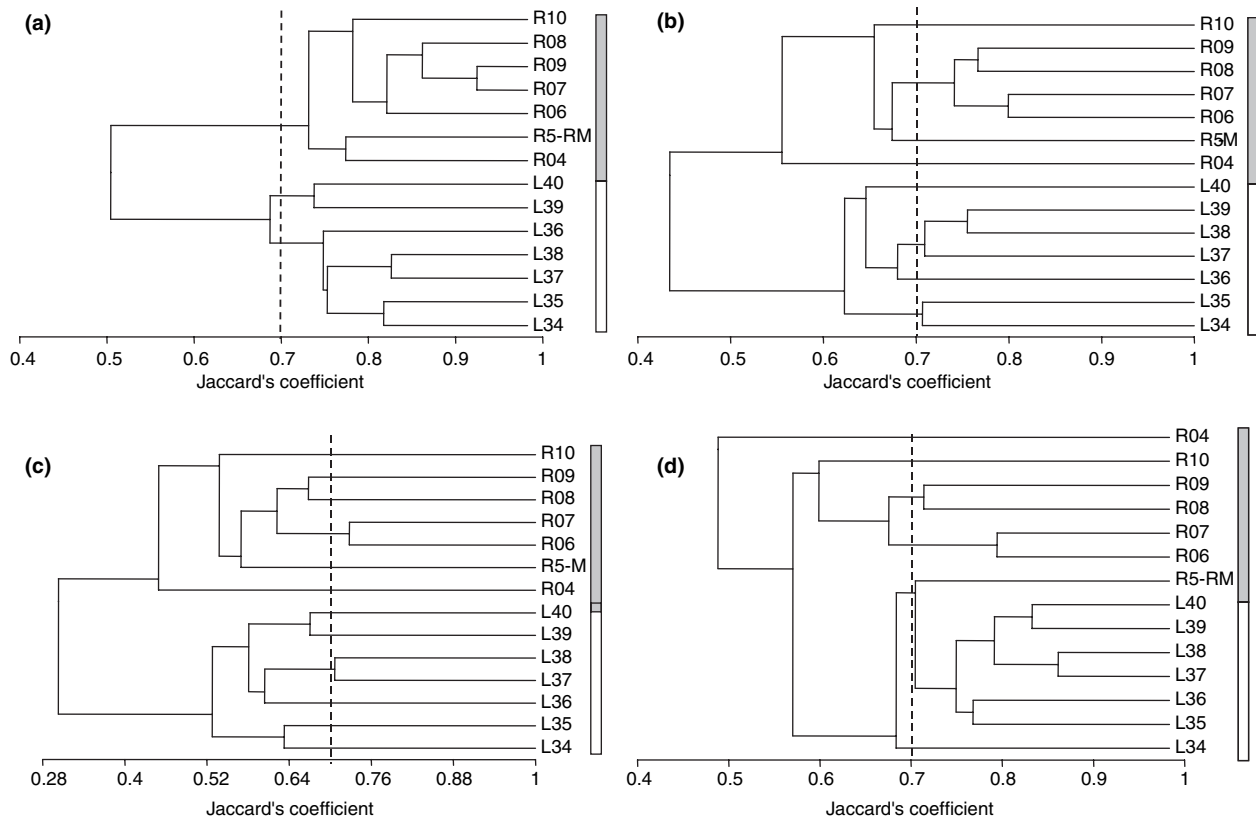
Figure 5 Cluster analysis of alien floras in latitudinal bands in central Chile and California. (a) families, (b) genera, (c) species, and (d) shared species. Bars: grey, Chile; white, California. The dotted line indicates significant clustering (Real, 1999).
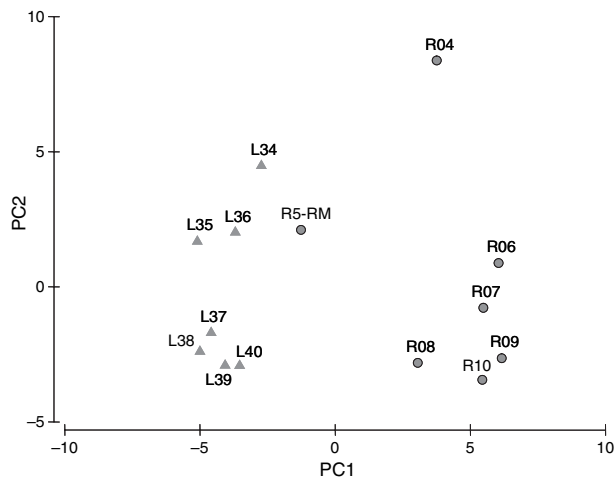
Figure 6 PCA ordination of latitudinal bands in Chile (circles) and California (triangles), based on the composition of their alien floras at the species level.

separation between the latitudinal bands of Chile and California (Fig. 6; axis 1, Explained Variation = 27.5%; axis 2, E.V. = 15.2%). However, bands towards the geographic centre of California and central Chile were closer in the diagram, denoting higher composition similarity.

DISCUSSION

The comparison between the alien floras of central Chile and California reveals three major biogeographical trends: (1) higher naturalized species diversity for California compared with Chile, at all taxonomic levels; (2) differences in the proportion of species according to origin, with America, Africa, Asia and Australia providing a larger number of species to California; (3) segregation between regions in terms of taxonomic composition, and a rather weak differentiation within regions; and (4) a trend towards higher similarity between the latitudinal bands with higher indices of human disturbances.

Overall, California has a much more diverse naturalized alien flora than central Chile. California has more than double the number of species recorded in Chile, and the vast majority of the species that grow in Chile are also found in California. Accordingly, at the genus and family levels, California presents a higher diversity for most taxa. This trend may be partly explained by a more complete set of plant collections for California, but other more fundamental causes, such as a higher rate of introductions and stronger antropogenic influence on the landscape, are probably responsible for these differences. At a regional scale, there is a clear relationship between greater alien taxonomic richness and centres of human population and disturbances (e.g. high levels of agriculture and silviculture, and the existence of important maritime ports) (Arroyo *et al.*, 2000). In Chile the latitudinal bands R5-RM and R08, and in California the bands L37 and

L38 correspond to areas with higher population densities and important internationals ports. In both regions, coastal areas appear to be more prone to alien invasions, probably owing to the greater propagule pressure caused by maritime exchange, higher levels of human disturbance, and a longer history of human settlements (Arroyo *et al.*, 2000; Dark, 2004; Castro *et al.*, 2005).

The analysis of alien species origins shows both convergence and divergence between central Chile and California. Most alien species in both regions originated on the European continent, and specifically in the Mediterranean basin, which was the historical source of modern human immigration associated with the Spanish colonization (di Castri, 1991; Figueroa *et al.*, 2004). In Chile, Spanish colonization started earlier than in California (mid-1500s), strongly modifying the landscape and causing the deliberate and accidental introduction of alien plants and animals (Aschman, 1991). In California, the first (Spanish) settlement occurred in the late 1700s, but quickly extended to the whole state, leaving an important legacy of alien species (Aschman, 1991; Bossard *et al.*, 2000).

The divergence in alien floras between the two regions may be explained by distinct immigration patterns after the early Spanish settlements. Overall, California has a larger proportion of species from other continents (e.g. Africa, Asia and Australia) than has Chile, which partly explains the higher total naturalized species diversity. This pattern may be related to the diverse and large array of immigrants from these areas to California. There has even been an exchange of species between the two compared regions, with a greater number of species exported from Chile to California as a result of intense 19th-century oceanic trade during the Gold Rush (Davis 1894). The inclusion of California into the United States territories in 1848 generated a large economic boom, increasing trade from all over the world. A large number of immigrants came from Asia, especially China, and Europe during the Gold Rush period (Aschman, 1991; OIS, 2003). This trend continued during the 20th century, with a continuous immigration of people of diverse origins (e.g. Japan, India) (OIS, 2003). The resulting exponential growth in population and international trade has transformed California into one of the world's largest and most diversified economies (Aschman, 1991; OIS, 2003). On the other hand, in the last two centuries the relative number of European immigrants to Chile (e.g. from Germany and Italy) has been significantly smaller than that to California, and Asian immigrants have been almost absent (Frías-Valenzuela, 1993). The Chilean economy has only recently been internationalized, and trading is now increasing the risk of introductions of new species.

Despite differences in the diversity and origin of naturalized species between central Chile and California, differences in the numbers of species in families and genera are subtle. Poaceae, Asteraceae, Fabaceae, Brassicaceae and Caryophyllaceae account for the greatest number of naturalized species. These results, except for the Caryophyllaceae family, coincide

with the global analysis of Pyšek (1998) for multiple alien floras.

Central Chile and California show similar trends in naturalized species richness by family when weighted by the total number of naturalized species in each region. Polygonaceae, Geraniaceae and Scrophulariaceae are, proportionally, the most successful families. Asteraceae and Fabaceae contain relatively fewer invaders, supporting the notion that the number of species in a family is not directly correlated with invasion potential (Pyšek, 1998). For example, Rubiaceae and Lamiaceae show low invasiveness but high numbers of species in native biotas. Nevertheless, species-rich families such as Poaceae, Brassicaceae and Caryophyllaceae are among the top ten families with greatest invasiveness (Rejmánek et al., 1991; Pyšek, 1998).

The naturalized flora of Chile and California differ not only in diversity, but also in composition at the family, genus and species levels. Our analyses indicate that the two regions are significantly different at the family level. At the genus and species levels there is higher within-region variation than at the family level, but bands of California and Chile remain in separated groups. Differentiation between Chile and California tends to disappear when considering only shared species, and the latitudinal band containing the Chilean capital, Santiago, and the largest port, Valparaiso, are grouped together with most Californian bands. The closer similarity between the developed areas of the two regions is confirmed by the PCA, suggesting that the convergence of alien floras between regions is enhanced by increasing levels of human disturbance.

Differences in the alien floras of central Chile and California are consistent for the multiple analyses. Apart from differences in human immigration, the factors that differ between California and central Chile, and which may be responsible for the observed patterns, are difficult to isolate. Factors such as disturbance and microclimatic variability may play roles in determining plant invasions in climatically similar regions. Therefore, approaches at finer scales are needed to understand those mechanisms (e.g. Sax, 2002; Pauchard & Shea, 2006). For California, Seabloom et al. (2006) recognize that most alien species are associated with human disturbances, but that increasingly they are moving into more pristine habitats.

Overall, our results indicate that, given a high level of anthropogenic disturbance across a region and increased levels of human transportation of alien species, there is a trend towards more homogeneous assemblages of alien species. Thus, as human settlements and booming economic development expand across the globe, the risk of biotic homogenization caused by alien species increases.

This paper aids in the comparison of alien floras of climatically similar regions because it incorporates the within-region spatial variation and uses comparable data sets containing detailed information about the taxonomic composition of the alien floras up to the species level. Using this approach, we have found novel trends in the convergence and differentiation of alien floras in climatically similar regions. Our results may appear to contradict the notion that climatically similar regions should share similar alien floras. However, this differentiation between alien floras can be largely explained by differences in propagule pressure (quantity and diversity) and land use, which are closely related to divergent human immigration histories. Additional studies are needed to elucidate the specific influence of each of these factors in determining the differentiation in local alien floras in climatically similar regions. Future research should trace particular species and their patterns of distribution using a comparative approach, adding information to comparisons of native vs. introduced ranges. This would improve our understanding of the causes of invasion and the potential habitat of the species and shed light on the mechanisms, other than climate, that promote or restrain plant invasions.

ACKNOWLEDGEMENTS

REFERENCES

Armesto, J., Rozzi, R., Smith-Ramirez, C. & Arroyo, M.T.K. (1998) Conservation targets in South American temperate forests. *Science*, **282**, 1271–1280.

Armesto, J., Rozzi, R. & Caspersen, J. (2001) Past, present, and future scenarios for biological diversity in South American temperate forests. *Future scenarios for biological diversity* (ed. by T. Chapin and O. Sala), pp. 223–249. Springer Verlag, New York, NY.

Arroyo, M.T.K., Cavieres, L., Marticorena, C. & Muñoz-Schick, M. (1995) Comparative biogeography of the mediterranean floras of central Chile and California. *Ecology and biogeography of mediterranean ecosystems in Chile, California and Australia* (ed. by M.T.K. Arroyo, P. Zedler and M.D. Fox), pp. 43–88. Springer-Verlag, New York, NY.

Arroyo, M.T.K., Marticorena, C., Matthei, O. & Cavieres, L. (2000) Plant invasions in Chile: present patterns and future predictions. *Invasive species in a changing world* (ed. by H.A. Mooney and R.J. Hobbs), pp. 385–421. Island Press, Washington, DC.

Aschman, H. (1991) Human impact on the biota of mediterranean-climate regions of Chile and California. *Biogeography of mediterranean invasions* (ed. by R.H. Groves and F. di Castri), pp. 33–41. Cambridge University Press, Cambridge.

Bailey, L.H. (1942) *The standard encyclopedia of horticulture*, Vols I, II and III. The Macmillan Company, New York, NY.

Bossard, C., Randall, J. & Hoshovsky, C. (2000) *Invasive plants of California's wildlands*. University of California Press, Berkeley, CA.

di Castri, F. (1991) An ecological overview of the five regions of the world with Mediterranean climate. *Biogeography of Mediterranean invasions* (ed. by R.H. Groves and F. di Castri), pp. 3–15. Cambridge University Press, Cambridge.

Castro, S.A., Figueroa, J.A., Muñoz-Schick, M. & Jaksic, F.M. (2005) Minimum residence time, biogeographical origin, and life cycle as determinants of the geographical extent of naturalized plants in continental Chile. *Diversity and Distributions*, **11,** 183–191.

Chittenden, F.J. (ed.) (1965) *Dictionary of gardening*. The Royal Horticultural Society. Vols I–IV. Clarendon Press, Oxford.

Dark, S. (2004) The biogeography of invasive alien plants in California: an application of GIS and spatial regression analysis. *Diversity and Distributions*, **10,** 1–9.

Davis, H. (1894) California breadstuffs. *The Journal of Political Economy*, **2,** 517–535.

Figueroa, J.A., Castro, S.A., Marquet, P.A. & Jaksic, F.M. (2004) Exotic plant invasions to the mediterranean region of Chile: causes, history and impacts. *Revista Chilena de Historia Natural*, **77,** 465–483.

Frías-Valenzuela, F. (1993) *Manual de historia de Chile*. Editorial Nascimento, Santiago, Chile.

Hickman, J.C. (1993) *The Jepson manual: higher plants of California*. University of California Press, Berkeley, CA.

IPNI (2004) *The International Plant Names Index*. http://www.ipni.org/.

Kruger, F.J., Breytenbach, G.J., Macdonald, I.A.W. & Richardson, D.M. (1989) The characteristics of invaded mediterranean-climate regions. *Biological invasions: a global perspective* (ed. by J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson), pp. 181–213. John Wiley & Sons, New York, NY.

Kühn, I., Durka, W. & Klotz, S. (2004) BiolFlor – a new plant-trait database as a tool for plant invasion ecology. *Diversity and Distributions*, **10,** 363–365.

Lewis, N.B. & Ferguson, I.S. (1993) *Management of radiata pine*. Inkata Press, Melbourne.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10,** 689–710.

Matthei, O. (1995) *Manual de las malezas que crecen en Chile*. Editorial Universidad de Concepción, Concepción, Chile.

MBG (2005) *Missouri Botanical Garden*. http://www.mobot.org/.

Mooney, H.A. (1977) *Convergent evolution in Chile and California mediterranean climatic ecosystems*. Dowden, Hutchinson & Ross, Stroudsburg, PA.

Mooney, H.A., Dunn, L., Shropshire, F. & Song, L. (1970) Vegetation comparisons between the mediterranean climatic areas of California and Chile. *Flora*, **159,** 480–496.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403,** 853–858.

OIS (2003) *Yearbook of Immigration Statistics: 2003*. http://www.uscis.gov/graphics/shared/statistics/yearbook/YrBk03Im.htm

Pauchard, A. & Shea, K. (2006) Integrating the study of non-native plant invasions across spatial scales. *Biological Invasions*, **8,** 399–413.

Pauchard, A., Cavieres, L. & Bustamante, R. (2004a) Comparing alien plant invasions among regions with similar climates: where to from here? *Diversity and Distributions*, **10,** 371–375.

Pauchard, A., Cavieres, L., Bustamante, R., Becerra, P. & Rapoport, E. (2004b) Increasing the understanding of plant invasions in southern South America: First symposium on Alien Plant Invasions in Chile. *Biological Invasions*, **6,** 255–257.

Pauchard, A., Aguayo, M., Peña, E. & Urrutia, R. (2006) Multiple effects of urbanization on the biodiversity of developing countries: the case of a fast-growing metropolitan area (Concepción, Chile). *Biological Conservation*, **127,** 272–281.

Pyšek, P. (1998) Is there a taxonomic pattern to plant invasions? *Oikos*, **82,** 282–294.

Real, R. (1999) Tables of significant values of Jaccard's index of similarity. *Miscellània Zoològica*, **22,** 29–40.

Rejmánek, M., Thomsen, C.D. & Peters, I.D. (1991) Invasive vascular plants of California. *Biogeography of mediterranean invasions* (ed. by R.H. Groves and F. di Castri), pp. 81–101. Cambridge University Press, Cambridge.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6,** 93–107.

Sax, D.F. (2002) Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions*, **8,** 193–210.

Schrag, P. (2007) The old history and the New California. *Rethinking History*, **11,** 31–49.

Seabloom, E.W., Williams, J.W., Slayback, D., Stoms, D.M., Viers, J.H. & Dobson, A.P. (2006) Human impacts, plant invasion, and imperiled species in California. *Ecological Applications*, **16,** 1338–1350.

Stevens, P. F. (2001 onwards) *Angiosperm Phylogeny Website, Version 7, May 2006*. http://www.mobot.org/MOBOT/research/APweb/.

Weber, E.F. (1997) The alien flora of Europe: a taxonomic and biogeographic review. *Journal of Vegetation Science*, **8,** 565–572.

BIOSKETCH

Alejandra Jiménez is a doctoral student at the Faculty of Forest Sciences at the Universidad de Concepción. She received her Master's degree in botany at the same university, and defended this research as part of her Master's thesis. Her interests include invasive species, conservation biology and plant taxonomy.