

Patterns of alien plant invasions in northwestern Patagonia, Argentina

K.L. Speziale^{a,*}, C. Ezcurra^{a,b}

^aLaboratorio Ecotono, INIBIOMA, CONICET – Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Río Negro, Argentina

^bDepartamento de Botánica, INIBIOMA, CONICET – Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Río Negro, Argentina

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ABSTRACT

Invasive plant species are a growing concern in many regions of the world, yet little information is available on the effects of habitat type and distance to urban settlements on the ability of alien plants to become established. We studied plant communities from the arid steppes to the Andean forest within two national parks and surroundings, in northwestern Patagonia, Argentina. Alien and native vascular plant species were sampled using $90 \times 100 \text{ m}^2$ plots and analyzed in relation to both climatic and environmental variables and distance to urban centres. We also compared life-forms of alien and native species. Precipitation and distance to an urban centre were important determinants of alien species community richness and composition, and shrubland sites had significantly more alien species than forest or steppe sites. Alien flora (15% of the species) was composed of a higher proportion of annuals and biennials than native flora. Our results suggest that precipitation, distance to source population, and anthropogenic disturbance influence the invasion process in this region, together with the availability of open niches. This work stresses the importance of monitoring invasive species in natural reserves, and of considering habitat types as well as idiosyncratic characteristics of the non-natives for developing management strategies.

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1. Introduction

Anthropogenic introduction of species is homogenizing the earth's biota (McKinney, 2006; Rapoport, 1990). In southern temperate latitudes many species from Eurasia, introduced since the beginning of the European occupation, have become naturalized. Ever since Darwin's time, it has been observed that invasive alien plants introduced from temperate regions of the Northern Hemisphere (NH) have had strong impacts on many habitats in the Southern Hemisphere (SH) (e.g., Arroyo et al., 2000; Darwin, 1845; Lambertucci and Speziale, 2011; Hauman, 1925; Richardson et al., 1994; Speziale and Lambertucci, 2010; Webb et al., 1988; Zalba and Villamil, 2002). For example, several species of pine, a mostly NH genus, are spreading rapidly in several countries of the SH (Rejmánek and Richardson, 1996). These dramatic *Pinus* invasions have occurred in habitats that can support life-forms that are not present in local floras for historical and/or evolutionary reasons, e.g., trees in the South African shrubby fynbos (Higgins et al., 1999; Richardson and Brown, 1986) or in the Argentine grassy open pampas (Zalba et al., 2008). Invasive plants are therefore a special concern in nature reserves in the SH (e.g., Alston and Richardson,

2006; Jesson et al., 2000; Pauchard and Alaback, 2004; Simberloff et al., 2002).

Recent studies in the Northern Hemisphere that used continental and regional data bases of vegetation plots have shown that habitat type is a good predictor of plant invasion (e.g., Chytrý et al., 2009; Vilà et al., 2007). In general, high levels of invasion have been found in lowland areas of the temperate zone in western and central Europe, and low levels in the boreal zone and mountainous regions across the continent (Chytrý et al., 2009). At a smaller scale, the highest levels of invasion have been predicted for agricultural, urban and industrial areas, lower levels for most woodlands and grasslands, and the lowest for alpine and sclerophyllous vegetation, heathlands and peatlands (Chytrý et al., 2009; Pyšek et al., 2002; Vilà et al., 2007). This is important for the assessment of invasion trends within habitats, and for future modelling of the effects of climate changes on levels of invasion (Chytrý et al., 2009). Until now, the relationship between plant invasions and habitat type has only been assessed in few areas of temperate South America (but see Pauchard and Alaback, 2004).

Cities present near or within natural reserves bear a special threat to biodiversity conservation (Alston and Richardson, 2006; Botham et al., 2009; Timmins and Williams, 1991). Human movements and activities associated with urban places increase disturbance and exotic propagule pressure, and as such, provide favourable environments for exotic species (Alston and Richardson,

* Corresponding author. Tel.: +54 2944 428505; fax: +54 2944 22111.

E-mail addresses: kspeziale@crub.uncom.edu.ar (K.L. Speziale), cezcurra@crub.uncoma.edu.ar (C. Ezcurra).

2006; Botham et al., 2009; Bulleri and Chapman, 2010; Pennington et al., 2010; Ricotta et al., 2010). Two large natural reserves in northern Patagonia, Nahuel Huapi and Lanín national parks, have shown a noticeable increase in exotic species (e.g., Ezcurra and Brion, 2005; Margutti et al., 1996). Both have cities near or within their limits that have experienced dramatic increases in human population over the last 30 years. In these cities, diverse horticultural and ornamental plants sometimes escape and grow wild, as has been observed in other places of the SH (Sullivan et al., 2005). Many appear only as casuals (*sensu* Richardson et al., 2000, i.e., non-native species that sometimes grow wild but do not reproduce regularly), but several have naturalized, and some have become problematic invaders, such as sweetbrier rose (*Rosa rubiginosa*) and scotch broom (*Cytisus scoparius*) (Damascos and Gallopin, 1992; Simberloff et al., 2003).

Currently, the flora of northern Patagonia comprises approximately 300 alien species (Rapoport and Brion, 1991) representing about 20% of the total species in this region (Zuloaga et al., 1999). In addition, 25% of the flora of Nahuel Huapi National Park region has been reported as non-native (Ezcurra and Brion, 2005), whereas in natural reserves in temperate Europe the proportion of non-natives is generally much lower (e.g., Czech Republic mean 6.1%, range 0–25%, Pyšek et al., 2002). The high richness of alien plants found in northern Patagonia (particularly within biodiverse natural reserves) makes the area especially suited to the study of the characteristics and determinants of plant invasions.

At large scales, areas with high species richness are especially prone to invasions (Stohlgren et al., 2003), contradicting a long-held ecological paradigm (Elton, 1958) and experimental evidence from small scales (e.g., Kennedy et al., 2002) of higher invasion in

low richness sites. Northwestern Patagonia is climatically and topographically diverse, producing habitats that may have varying susceptibility to invasion. In addition, alien species with dissimilar characteristics may find different niches to occupy in this type of diverse landscapes. This paper aims to answer the following questions related to the factors affecting plant invasions in northern Patagonia: Are there life-history traits that characterize invasive flora that differ from the characteristics of native flora? Which habitat types are most invaded, and what are the associated environmental variables? What is the effect of urban settlements in these areas? Is alien species richness correlated with native species richness at regional and/or local scales? By answering these questions, we not only aim to obtain information with useful implications for the long-term management and conservation of these Southern Hemisphere temperate reserves, but also to contribute to theoretical plant invasions principles from a southern perspective.

2. Methods and materials

2.1. Study area

We conducted this study in northwestern Patagonia, Argentina (approximately between 39°47' – 41°27'S and 70°26' – 71°32'W; Fig. 1), a region comprising temperate forests, shrublands and steppe. The different habitat types exist along an abrupt precipitation gradient resulting from the rain-shadow produced by the westerly winds from the Pacific on the southern Andes (Cabrera and Willink, 1973; Ezcurra and Brion, 2005). Precipitation mainly occurs from April to September and ranges from about 3000 mm/year to the west, to 200 mm/year to the east. It is an area of high

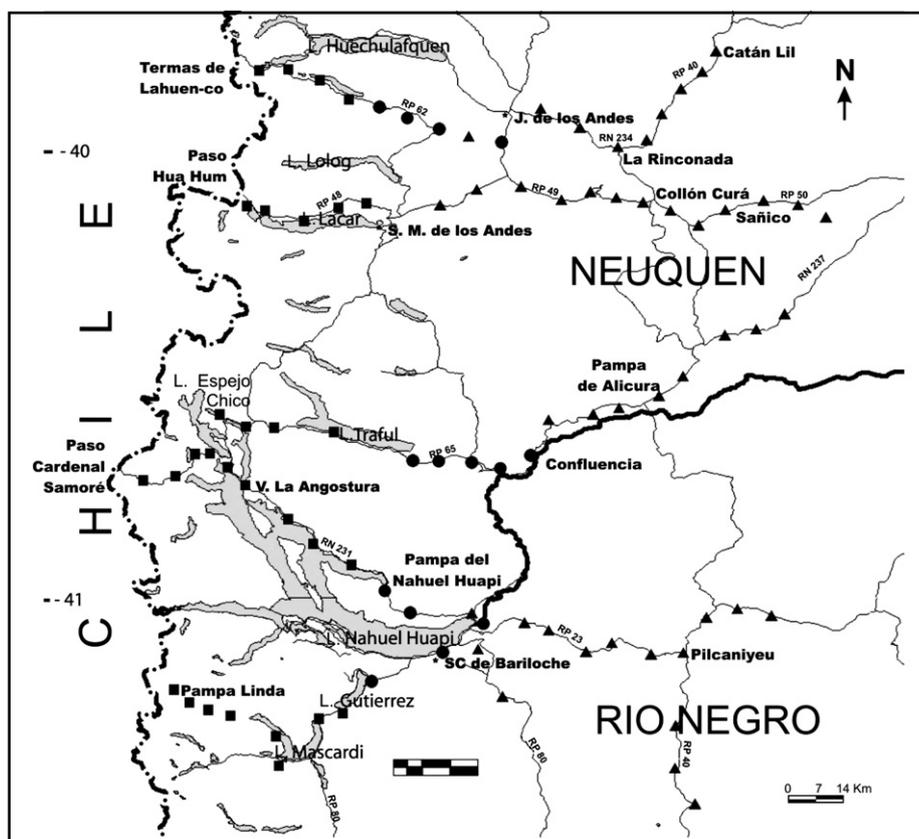


Fig. 1. Study area showing sampling plots in Lanín and Nahuel Huapi National Parks, northwestern Patagonia, Argentina. Forest plots are shown with squares, shrubland plots with circles and steppe plots with triangles.

floristic diversity including portions of two different phytogeographical regions, the Subantarctic and Patagonian (Cabrera and Willink, 1973).

Two of Argentina's largest nature reserves are also found in the region: Lanín (412,000 ha) and Nahuel Huapi (705,000 ha). Even though the first European settlements in temperate South America began in the mid XVI century in Chile, it was not until the 20th century that permanent urban settlements began to develop. Currently, the largest city in the area is San Carlos de Bariloche, with about 130,000 inhabitants while the smaller towns in the region have less than 25,000 people (INDEC, 2001). Most of these cities have generally doubled or tripled in size in the last 30 years, and they are centres for the main economic activities in the region, including tourism, cattle ranching, and forestry.

2.2. Field sampling

Samples were taken along five west-east transects of approximately 100 km in length using national or provincial roads that traversed all the vegetation types present in the region: mesic forest, transitional shrubland, and xeric steppe (Fig. 1). Transects were restricted in altitude from 600 to 1100 m a.s.l., to reduce the confounding effects of elevation. In total, $90 \times 100 \text{ m}^2$ ($10 \times 10 \text{ m}$) sampling plots were established, with an average of 17 plots in each transect, and placed approximately equidistantly (Fig. 1). The 100 m^2 plot size is commonly used in the determination of species richness and composition for forest, shrubland and herbaceous vegetation (Otypková and Chytrý, 2006). Plots were located in places that were representative of local native vegetation and away from bogs, wet meadows, and lake or river shores. Plots were separated at least 200 m from roads, 3 km from urban settlements, and in places without recent signs of fire, overgrazing, or other anthropogenic influences. Plots were sampled during the growing seasons (austral spring and summer) between November 2003 and January 2004. The plots were classified as forest (F), shrubland (Sh) or steppe (St) sites on visual examination. Throughout the manuscript we used the word site to refer to our sampling units and the word habitat when referring to the natural environments in general.

2.3. Environmental variables

We recorded every plant in each plot and calculated total native and alien species richness. Mean annual temperature, annual temperature variation, mean annual precipitation, and annual precipitation variation were taken for each plot from the WorldClim database (Hijmans et al., 2005, available at <<http://www.worldclim.org/current.htm>>), which has a spatial resolution of 1 km^2 . As measures of local heterogeneity, we measured soil slope (using a clinometer), and qualitatively assigned a value of substrate heterogeneity according to the scale: 0 = no rocks; 1 = rocks mostly less than 1 cm in diameter, 2 = between 1 and 10 cm, 3 = between 10 and 30 cm, and 4 = larger than 30 cm. We also recorded altitude above sea level, latitude and longitude using a GPS (Global Positioning System). Distance to the closest city or town was calculated in Google Earth.

2.4. Data analysis

To analyze traits characteristic of alien species in the study area we compiled a list of all the species found in the sampled plots and recorded data on their native or alien status (Correa, 1969–1996), biogeographical origin (Correa, 1969–1996; Wiersma and León, 1999), and life-form (i.e., herbaceous annual, biennial or perennial, and woody; Correa, 1969–1996). Species found in more

sampling sites were considered most invasive, assuming the invasion process requires distant dispersal (Richardson et al., 2000). The probability of invasion also increases with the time since introduction, i.e., residence time (e.g., Pyšek et al., 2004; Richardson and Pyšek, 2006), however there is very little or no information on the exact residence time of each species in this area.

G-tests were used to compare the relative proportion of life-forms of alien and native herbaceous species. Differences in alien and native species richness among the three studied habitats (forest, shrubland and steppe) were compared with a Kruskal–Wallis nonparametric test, as our data did not conform to parametric assumptions. The relationship between native and alien herbaceous species richness and the influence of environmental variables on alien herb species richness was determined using linear simple regression and multiple regression analysis.

We present a model to explain alien species richness using native species richness, slope, substrate heterogeneity, altitude, precipitation, temperature, and distance to the closest city or town as predictors. Correlations among these variables were lower than 0.45. The model was tested using backward multiple regression procedure for the whole gradient and separately for forests, as well as for the whole set of shrubland–steppe plots together due to their similarities (Speziale, 2006; Speziale et al., 2010). We selected the significant variables for each set of plots and used standard multiple regression for the final model estimates.

To determine gradients in community composition and their relationship with environmental variables and to assess the position of the most invasive species in these gradients, we used Detrended Correspondence Analysis (DCA). For this, we constructed a presence–absence matrix of all the species (native and alien, $N = 299$) and all the plots (forest, shrubland and steppe, $N = 90$), and a matrix of environmental variables and plots. The species and plots data were analyzed using CANOCO, and the environmental data were treated as supplementary in the same analysis (ter Braak and Smilauer, 1998). In this way, the plots were ordinated on a factorial plane according to species composition, and then environmental variables were subsequently projected onto the same plane.

We also performed Canonical Correspondence Analysis (CCA) to analyze the importance of environmental variables for alien species composition ($N = 46$ species) in the sites with the highest count of aliens, i.e., shrubland and steppe sites ($N = 60$ sites). CCA detects gradients in environmental variables and determines their relative importance in the ordination of plots based on their species composition. In this way it links correspondence analysis with multiple regression methodology (ter Braak and Verdonschot, 1995). The statistical significance of these relationships was determined by a Monte Carlo permutation test. Detrended Canonical Correspondence Analysis (DCCA) was also performed on the same data to obtain a better graphical output.

3. Results

3.1. Characteristics of the alien flora

In the study area we identified a total of 299 vascular plant species, of which 46 (15.35%) were aliens. The most frequent non-native species (those present in more than 33% of the plots) were *Bromus tectorum*, *Cerastium arvense*, and *Rumex acetosella* (Table 1). Families with more invasive genera and species were Asteraceae (9 genera, 9 species), Poaceae (6 genera, 7 species), and Caryophyllaceae (5 genera, 6 species). Regarding their origin, 82.61% are native to Eurasia, 15.22% to North America, and 2.17% are considered cosmopolitan northern temperate species. Most of the species were anemochorous or autochorous.

Table 1

List of the 35 most frequent alien species (present at least in two plots of the study area) ranked by frequency of occurrence.

| Alien sp | Family | Common name (English/Spanish) | OR ^a | LF ^b | DT ^c | OCC ^d |
|-------------------------------|------------------|-------------------------------------|-----------------|-----------------|-----------------|------------------|
| <i>Bromus tectorum</i> | Poaceae | Downy brome/– | EA | Ann | Anem | 53.33 |
| <i>Cerastium arvense</i> | Caryophyllaceae | Field chickweed/Cerastio | EA | Per | Auto | 44.44 |
| <i>Rumex acetosella</i> | Polygonaceae | Sorrel/Vinagrillo | EA | Per | Auto | 42.22 |
| <i>Draba verna</i> | Brassicaceae | Whitlow grass/– | EA | Ann | Anem | 28.88 |
| <i>Taraxacum officinale</i> | Asteraceae | Dandelion/Diente de león | EA | Per | Anem | 26.66 |
| <i>Holosteum umbellatum</i> | Caryophyllaceae | Jagged Chickweed/– | EA | Ann | Auto | 25.55 |
| <i>Hypochaeris radicata</i> | Asteraceae | Flatweed/Hierba del chancho | EA | Per | Anem | 24.44 |
| <i>Microsteris gracilis</i> | Polemoniaceae | Slender phlox/– | NA | Ann | Epiz | 23.33 |
| <i>Apera interrupta</i> | Poaceae | Dense silkybent/– | EA | Ann | Epiz | 15.55 |
| <i>Lactuca serriola</i> | Asteraceae | Prickly lettuce/Lechuga salvaje | EA | Ann | Anem | 14.44 |
| <i>Carduus thomeri</i> | Asteraceae | Musk thistle/Cardo de caballo | EA | Ann | Anem | 14.44 |
| <i>Plantago lanceolata</i> | Plantaginaceae | Buckhorn plantain/Llantén | EA | Per | Epiz | 13.33 |
| <i>Rosa rubiginosa</i> | Rosaceae | Sweet brier/Mosqueta | EA | Shr | Endo | 12.22 |
| <i>Erodium cicutarium</i> | Geraniaceae | Red-stem filaree/Alfilerillo | EA | Ann | Epiz | 12.22 |
| <i>Myosotis stricta</i> | Boraginaceae | grassland forget-me-not/– | EA | Ann | Auto | 11.11 |
| <i>Epilobium brachycarpum</i> | Onagraceae | Annual fireweed/– | NA | Ann | Anem | 10 |
| <i>Cynoglossum creticum</i> | Boraginaceae | Blue Hound's Tongue/Lengua de perro | EA | Ann | Epiz | 10 |
| <i>Prunella vulgaris</i> | Lamiaceae | Common selfheal/Hierba mora | EA | Per | Auto | 8.88 |
| <i>Tragopogon dubius</i> | Asteraceae | Yellow salsify/– | EA | Ann | Anem | 7.77 |
| <i>Stellaria media</i> | Caryophyllaceae | Chick weed/Capiquí | EA | Ann | Epiz | 7.77 |
| <i>Holcus lanatus</i> | Poaceae | Velvet grass/Pasto miel | EA | Ann | Anem | 7.77 |
| <i>Veronica serpyllifolia</i> | Plantaginaceae | Thyme-leaf speedwell/Veronica | NT | Per | Auto | 6.66 |
| <i>Trifolium repens</i> | Fabaceae | White clover/Trébol blanco | EA | Per | Auto | 4.44 |
| <i>Dactylis glomerata</i> | Poaceae | Orchard grass/Pasto ovillo | EA | Per | Anem | 4.44 |
| <i>Verbascum thapsus</i> | Scrophulariaceae | Common mullein/Tabaco de indio | EA | Ann | Auto | 3.33 |
| <i>Poa pratensis</i> | Poaceae | Kentucky bluegrass/Pasto de mallin | EA | Per | Anem | 3.33 |
| <i>Claytonia perfoliata</i> | Portulacaceae | Miner's lettuce/Lechuga de minero | NA | Ann | Auto | 3.33 |
| <i>Cerastium glomeratum</i> | Caryophyllaceae | Clammy chickweed/Media de chivo | EA | Ann | Auto | 3.33 |
| <i>Cardamine hirsuta</i> | Brassicaceae | Hairy bittercress/Berro cimarrón | NA | Ann | Auto | 3.33 |
| <i>Bromus hordeaceus</i> | Poaceae | Soft brome/– | EA | Ann | Anem | 3.33 |
| <i>Vulpia bromoides</i> | Poaceae | Vulpia hair grass/Pasto cedilla | EA | Ann | Anem | 2.22 |
| <i>Pseudotsuga menziesii</i> | Pinaceae | Douglas fir/Pino oregón | NA | Tre | Anem | 2.22 |
| <i>Descurainia sophia</i> | Brassicaceae | Herb-Sophi/Sofia | EA | Ann | Epiz | 2.22 |
| <i>Cirsium vulgare</i> | Asteraceae | Bull thistle/Cardo negro | Eur | Ann | Anem | 2.22 |
| <i>Arenaria serpyllifolia</i> | Caryophyllaceae | Thyme-leaf sandwort/– | Eur | Ann | Auto | 2.22 |

^a Biogeographical origin: EA: Eurasia, NA: North America, NT: north temperate.

^b Life-form: Ann: annual or biannual herbs, Per: perennial forbs and grasses, Shr: shrubs, Tre: Trees.

^c Dispersal type (Anem: anemochory, Auto: autochory, Epiz: epizoochory, Endo: endozoochory).

^d Percentage of occurrence.

The mean number of alien species per plot was 4.07 ± 0.30 (\pm SE; Fig. 2) ranging from 0 to 10, but this varied among habitats: $H_{2,90} = 13.63$, $p = 0.001$. Forests and steppes had lower values of alien species than shrublands, with means of $2.87 (\pm 0.58)$ and $4.22 (\pm 0.34)$ respectively (differences between forest and steppes not significant). In contrast, shrublands were richer in non-native species and had 6 ± 0.63 alien species per plot. There was also a higher number of native species in the shrublands: 21.93 ± 1.95 , whereas both steppes and forests had a lower number of natives: 13.87 ± 0.76 and 15.01 ± 0.96 (mean \pm SE) respectively (difference between forest and steppes not significant) (Fig. 2). Alien herb species did not differ in dispersal types, but had a higher proportion of annuals and biennials compared to herbaceous natives ($G = 42.82$, $p < 0.001$).

3.2. Determinants of alien species richness

Multiple regressions for the whole gradient included native species richness, precipitation and distance to the closest city as best predictors, together explaining 33% of the observed variation in alien species richness (Table 2). Alien species richness was positively correlated with native species richness but negatively correlated with precipitation and distance to the closest city (Table 2). Forest data did not fit the model. The same model explained 36% of the observed variation in alien species richness for the shrubland to steppe gradient (Table 2). In shrub and steppe habitats, native species richness and distance to the closest urban centre were the best predictors, with positive and negative relationships respectively.

3.3. Gradients of community composition

The ordination of all the species (native and alien) and sites (forest, shrubland and steppe) on the first two axes of the DCA (Fig. 3) showed a clear west-east floristic gradient along axis 1 of the analysis. The alien flora changed from species typical of forest in the west, such as *Sagina procumbens*, *Potentilla anserina* and *Prunella vulgaris*, to species of more arid places in the east such as *Descurainia sophia*, *Erodium cicutarium* or *Vulpia bromoides*. The centroid of the distribution of most frequent and extended non-native species, *B. tectorum*, *C. arvense* and *R. acetosella*, appeared in the centre-east of the gradient where shrubland and steppes occur. The supplementary environmental variables (Fig. 3) showed precipitation increasing in forest sites to the west, and variation in temperature and precipitation increasing in steppe sites to the east, both associated with axis 1. Temperature increase appeared negatively associated with axis 2, with the warmest sites towards the lower part of the figure.

The CCA and DCCA (Fig. 4) for alien species composition in shrubland and steppe sites also showed a west-east gradient for alien species composition. The model resulting from the forward selection procedure identified three most relevant variables in relation to composition (Table 3): precipitation and temperature variation associated with axis 1, and temperature related to axis 2. Native species richness and distance to the nearest city showed a lower relationship to species composition gradients but still significant (Fig. 4), with native species richness related to axis 1, and distance to the closest city equally related to the first two axes.

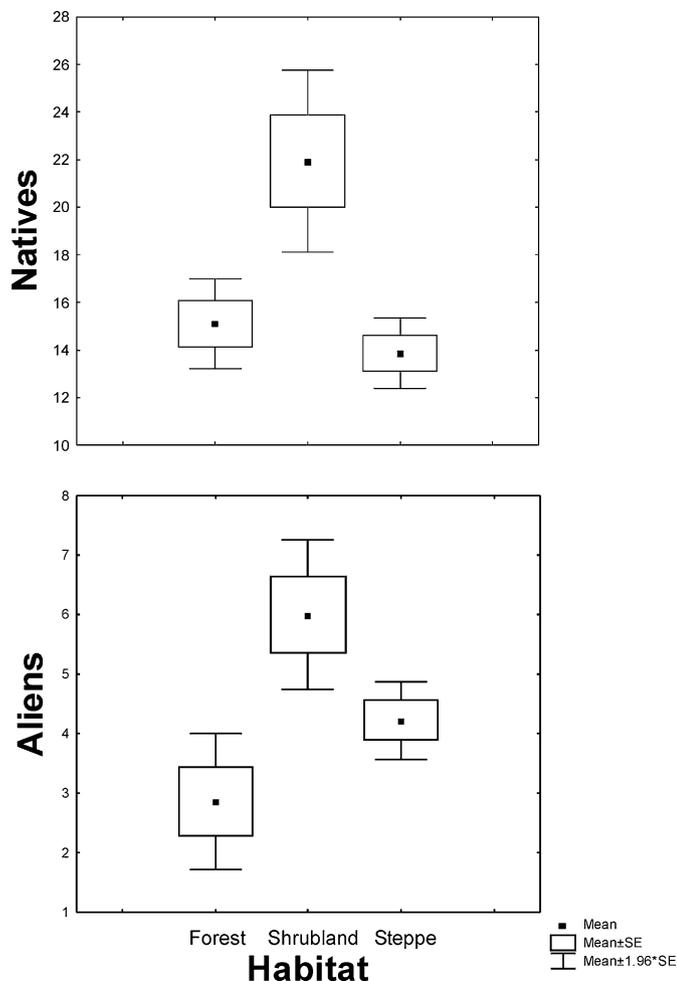


Fig. 2. Box-plots of average alien richness (top) and native species richness (bottom) for forest, shrubland and steppe plots in Lanín and Nahuel Huapi National Parks and surroundings, northwestern Patagonia, Argentina.

4. Discussion

4.1. Invasive species and their characteristics

Our study showed that the alien herbaceous flora was dominated by annuals and biennials, whereas the native herb flora was dominated by perennials. This suggests a vacant or open niche. Open niches are habitats that can support life-forms that are not present in local floras for historical and/or evolutionary reasons, in which exotics may be successful because they have access to resources that are not exploited by local species (Hierro et al., 2005; Rejmánek et al., 2005). In general, the floras of New Zealand and southern Chile have been described as having a lower percentage of annuals than floras from similar climates in the Northern Hemisphere (e.g., Arroyo et al., 2000; Wardle, 1991). The very low proportion of annuals and biennials found for native species in this study has also been shown in the high-Andean flora of southern Argentina (Ferreyra et al., 1998a). A continental climate with longer growing seasons, characteristic of the alien species geographic origin, has been proposed as a probable driver of the evolution of species with short generation times (Ferreyra et al., 1998b). Longer summers favour the evolution of annual species as they allow plants to complete their life-cycle within one season (Ferreyra et al., 1998b). Accordingly, the temperature increases observed in

northern Patagonia during the last decades due to climate change (SAyDS, 2006) could benefit annual alien plants.

4.2. Habitat types most invaded

Even though many studies show that different types of habitat present different levels of invasion (e.g., Chytrý et al., 2009; Guirado et al., 2007; Richardson et al., 1994; Vilà et al., 2007), few studies address the habitat characteristics that favour invasibility (Richardson and Pyšek, 2006; Woham, 2006). Native and non-native diversity were both greatest in the shrubland community. This habitat type also showed higher values of alien cover ranging from 3 to 65% of the plot with a mode value of 19% (Forest: 0–38%, mode 0%; Steppe: 0–60%, mode 7%). This ecotonal shrubland is associated with intermediate levels of precipitation that are less limiting for biological activity and therefore result in highest native richness (Speziale et al., 2010). Climatic conditions that favour natives can also be productive areas for alien species (Richardson and Pyšek, 2006; Stohlgren et al., 2003). Nurse effect of shrubland native species could also affect aliens positively, as has been observed for high-Andean native cushion plants (Arredondo-Núñez et al., 2009). Together with high disturbance in these areas (through fire and other human-related activities) and the resulting fluctuations in resource availability, these are likely determinants of the observed pattern of highest alien species richness within shrublands (cf. Brooks et al., 2004; Davis et al., 2000; Richardson and Pyšek, 2006). However, other variables not considered in our analyses that could also be playing a role, including land use, resource availability, soil nutrients, propagule pressure or an interaction among these variables (Burke and Grime, 1996; Harrison, 1999; Huenneke et al., 1990; Lonsdale, 1999; Pauchard and Alaback, 2004; Stohlgren et al., 1999).

Important human activities in the shrubland area include plantation forestry and breeding of introduced herbivores such as sheep, cattle and horses, which do best with moderate levels of precipitation. Even though steppe environments are also used for raising livestock, these areas are more arid and thus less productive. Sites grazed by livestock in the analogous central Chilean Matorral have shown a higher relative abundance of alien plants than sites without grazing (Arroyo et al., 2000; Holmgren et al., 2000). The presence of large herbivores (domestic or wild) may increase the rate of successful introductions by acting as major seed vectors across the landscape (Pauchard and Shea, 2006). Nevertheless, the relationship between grazed habitats and alien species richness is complex, and not only includes increased seed dispersal, but also the faster recovery of aliens post grazing as a result of better adaptation, among other factors (Keeley et al., 2003; Kimball and Schiffman, 2003).

Table 2

Forward stepwise regression coefficients of the significant variables included in the models for the 90 plots along the complete gradient, for the shrubland–steppe, and separately for the forest, the shrubland and the steppe.

| Variables include ^a | Beta | Multiple R ^b | p-level |
|------------------------------------|-------|-------------------------|---------|
| Whole gradient (90) ^b | | 33% | |
| Dist | −0.34 | 0.16 | <0.001 |
| Nat | 0.29 | 0.12 | 0.003 |
| Prec | −0.37 | 0.05 | <0.001 |
| Shrubland–steppe (60) ^b | | 36% | |
| Dist | −0.44 | 0.15 | <0.001 |
| Nat | 0.28 | 0.15 | 0.02 |

^a Nat: native species richness, Prec: precipitation, Dist: distance to the closest city or town.

^b N values for each habitat.

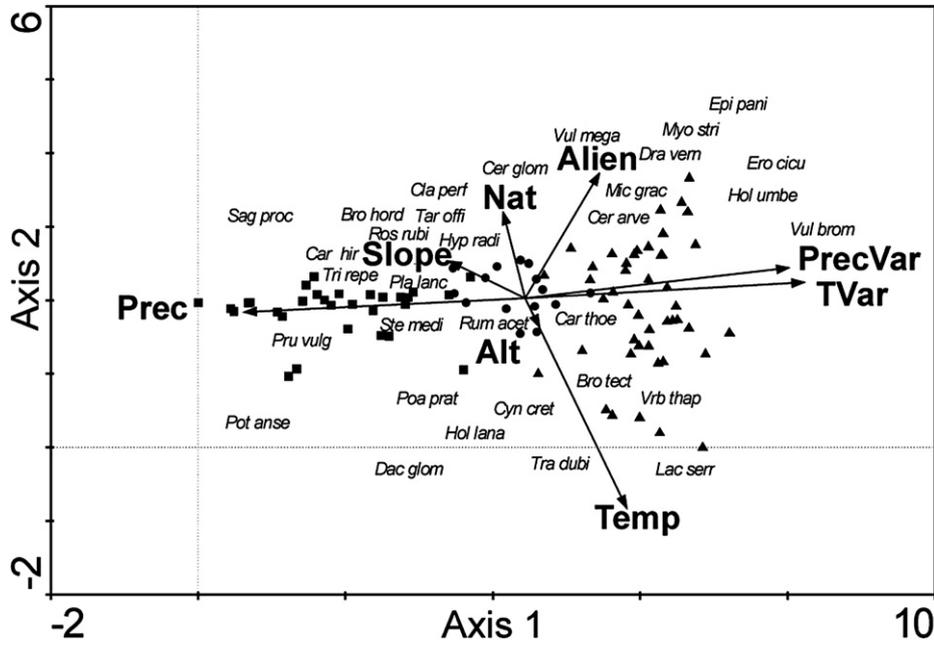


Fig. 3. Detrended Correspondence Analysis (DCA) diagram of axes 1 and 2 grouping plots ($N = 90$) by their species composition ($N = 299$). Cumulative percentage of variation explained by both axes is 8.5%. Eigenvalue for axis 1 is 0.799 and for axis 2 is 0.375. Forest plots (squares) separate from steppe plots (triangles) along the first axis, whereas shrubland plots (circles) appear in an intermediate position. Total inertia is 13.893. Species names shown correspond to the most frequent alien species present in more than 3 plots. Variables analyzed included mean annual precipitation (PREC), annual precipitation variation (PRECVAR), mean annual temperature (TEMP), altitude above sea level (ALT), slope of the terrain (SLOPE), native species richness (NAT), and alien species richness (ALIEN) and were treated as supplementary.

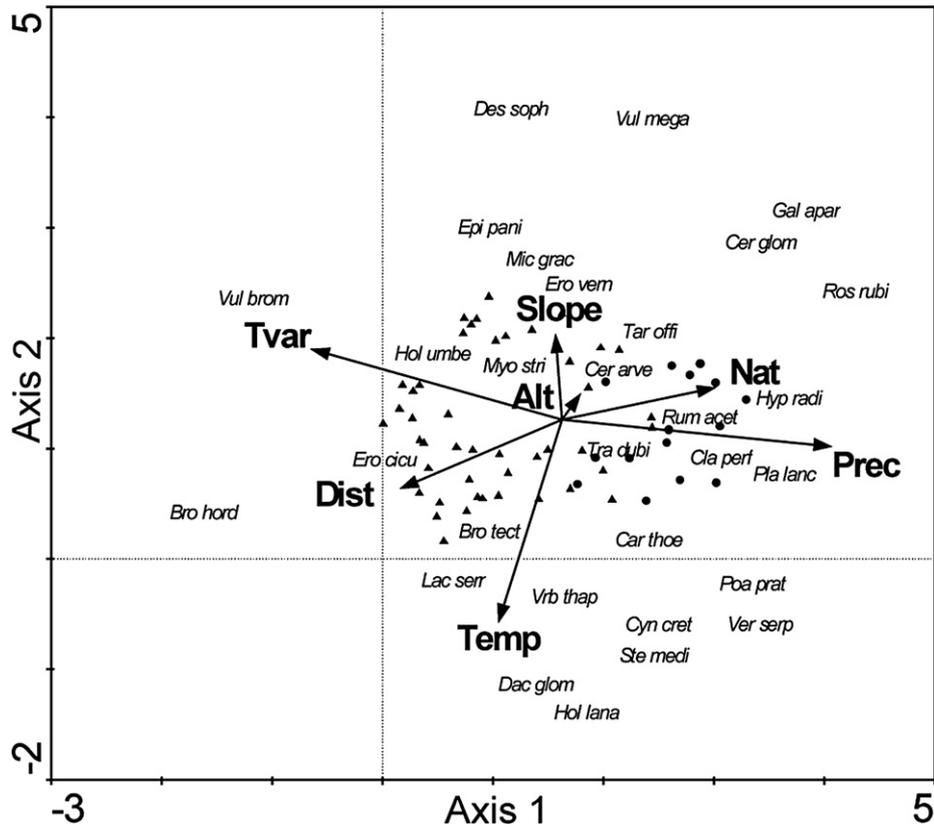


Fig. 4. Detrended Canonical Correspondence Analysis (DCCA) grouping plots classified as shrubland (circles) and steppes (triangles) ($N = 60$) by their alien species composition ($N = 46$) and environmental characteristics. Species names shown correspond to the most frequent alien species present in more than 3 plots. The forward selection procedure resulted in a model in which slope (Slope) and altitude (Alt) were not significant. Eigenvalue for axis 1 is 0.494 and for axis 2 is 0.246. Total inertia is 9.09 and the cumulative percentage variance of species–environment relation explained by both axes is 44.2. Variables analyzed included: mean annual precipitation (Prec), mean annual temperature (Temp), annual temperature variation (TVar), altitude above sea level (Alt), slope of the terrain (Slope), native species richness (Nat), alien species richness (Alien), and distance to the nearest town/village.

Table 3

Conditional effect (i.e., ability to explain composition patterns in the species data considering the effect of other explanatory variables) of each variable on the CCA ordination of alien species composition.

| Variable ^a | λA_{ξ}^b | F |
|-----------------------|---------------------|--------|
| Prec | 0.49 | 3.27** |
| Temp | 0.26 | 1.8** |
| Tvar | 0.22 | 1.52** |
| Nat | 0.17 | 1.53* |
| Dist | 0.20 | 1.37* |
| Alt | 0.16 | 1.12 |
| Slope | 0.12 | 0.87 |

** $p < 0.005$.

* $p < 0.05$.

^a Prec: Mean annual precipitation, Temp: Mean annual temperature, Alien: Alien species richness, Tvar: Temperature variation, Nat: Native species richness, Dist: distance to the closest city or town, Alt: Altitude above sea level (see methods for a complete description of each variable).

^b λA_{ξ} = additional variance each variable explains at the time it was included in the model.

4.3. Effect of distance to urban settlements

Urban and suburban areas may act as foci of alien species propagules and human disturbance (Alston and Richardson, 2006; Botham et al., 2009; Foxcroft et al., 2008; Sullivan et al., 2005). Our results showed that distance to the closest city or town had a consistent relation with alien species richness, even though the urban settlements considered were present in each of the three different studied environments. As shown for other areas, urban places within natural parks harbor the highest number of alien species due to the presence of gardens with many introduced horticultural species and weeds, possibly acting as foci for their spread (e.g., Alston and Richardson, 2006; Botham et al., 2009; Sullivan et al., 2005). In Chile, areas with the highest density of aliens have been attributed to dense human population and other human activities (Arroyo et al., 2000; Bustamante et al., 2005; Fuentes et al., 2008). It is interesting to note that human densities as low as 500 inhabitants were correlated to an increase in alien plant richness, showing that high human densities are not needed to begin an invasion.

4.4. Alien and native species richness

As seen for total species richness in this area (Speziale et al., 2010), alien species richness is associated with different variables at different scales. In general, our results showed a positive relationship between alien and native species richness both at regional and local scales in northwestern Patagonia. This is supported by previous studies in other areas (e.g., Guirado et al., 2007; Higgins et al., 1999; Pauchard and Shea, 2006; Pino et al., 2005; Robinson et al., 1995; Stohlgren et al., 2003; Vitousek et al., 1996). Although observational and experimental studies have shown contrasting results regarding this relationship (e.g., Kennedy et al., 2002; Stohlgren et al., 1999; see also Richardson and Pyšek, 2006 and references therein), it has generally been found that at larger scales, places with more native species appear more heavily invaded than areas with lower plant diversity (e.g., Pauchard and Shea, 2006; Pino et al., 2005; Pyšek et al., 2002; Stohlgren et al., 2003). It has been suggested that native species richness acts as a proxy variable for other habitat characteristics (e.g., abiotic conditions that promote high native species richness can also support diverse alien floras) (Richardson and Pyšek, 2006; Stohlgren et al., 1999). Furthermore, at larger scales extrinsic factors and habitat diversity tend to vary (e.g., there is a wider range of latitudinal, elevational and climatic variation which favour native and non-native diversity alike (Lonsdale, 1999; Pauchard and Shea, 2006)).

5. Conclusions

In temperate regions with high species richness, shrubland habitats are especially prone to invasions. This is associated with intermediate precipitation conditions. Urban settlements within these temperate regions, together with the availability of open niches, also influence the invasion process. Due to severe consequences invasions can have in some areas (Brooks et al., 2004; D'Antonio and Vitousek, 1992; Levine et al., 2003) and to the latency period before introduced species can actually become invasive (Richardson and Pyšek, 2006), screening and monitoring of introduced species within species rich areas of natural reserves of southern latitudes is crucial for prevention and management of the invasion process.

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