

Factors associated with woody alien species distribution in a newly invaded mountain system of central Argentina

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Abstract To help determine the major factors associated with alien plant in a newly invaded mountain range; we analyzed the distribution patterns of woody alien species along the altitudinal gradient of the Córdoba mountains, in relation to biotic, abiotic and anthropogenic factors. We selected 303 plots using a Geographic Information System (GIS) covering all the variability of these factors. In the field we registered woody alien occurrence in these 303 and in 303 additional neighbor plots. We used 12 biotic, abiotic and anthropogenic variables from the GIS to predict the probability of presence of alien species through a logistic model. Then, we analyzed if neighbor alien occurrences could explain some additional variance. We created a probability map with 4 categories of alien occurrence which was then

validated by new field sampling. Occurrence of woody aliens was highest in the eastern slope (with longer history of species introduction), at low altitudes, near sources of propagule pressure (human settlements, roads and neighbor sites with established alien plants), and associated to sheltered topographies. In the upper belt of the Córdoba Mountains woody invasion is incipient and thus in a transient stage. Accordingly, propagule pressure seems to be the major factor at play, while the relevance of disturbance and biotic interactions is less clear.

Keywords Altitude · Conservation · Exotic species · GIS · Human disturbance · Invasion drivers

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Introduction

Plant invasions can produce profound changes in the structure and function of natural ecosystems, affecting a number of ecosystem services and producing high economic losses (Mack et al. 2000; Pimentel et al. 2005; Charles and Dukes 2007). To date, high-elevation environments have been less affected by invasions than lowlands because of the harsher climatic conditions and low human population densities, and it has been assumed that invasion impact in mountain areas will remain stable (MA 2005). However, in a recent review Pauchard et al. (2009), highlight that several of the factors that in the recent

past have prevented plant invasions into mountainous areas (e.g., rareness of alien species pre-adapted to harsh abiotic conditions, low propagule pressure and low human disturbances) are changing rapidly. If proved true, this has major ecological and social relevance, because mountains cover approximately 25% of the land surface, host at least a third of terrestrial plant species diversity and supply half of the human population with water (Körner 1999; Le Maitre et al. 2002). The early detection and description of invasion patterns in mountain systems is thus an essential first step in the understanding of plant invasions in these newly invaded environments (Pauchard et al. 2009).

Scientists have recognized some drivers that are expected to promote or limit plant invasions into mountain areas including propagule pressure, biotic interaction, pre-adaptation of alien species to abiotic conditions, and disturbances (Daehler 2005; Dietz and Edwards 2006; Pauchard et al. 2009 and reference therein). Distribution patterns along a particular altitudinal gradient are expected to vary depending on the relative importance of each driver in that local situation.

The upper belt of the Córdoba Mountains (central Argentina) is a local hotspot of endemism and the main water catchment area providing water to over 3 million inhabitants. A few studies have addressed invasions by herbaceous species in the area (Díaz et al. 1994; Petryna et al. 2002; Cantero et al. 2003; Paiaro et al. 2007, *in press*), but none of them consider the incipient spread of woody alien species from lower altitudes. Because most introduced woody species were originally planted below 1,500 m a.s.l., and at present are successful invaders of low-mountain ecosystems (Tecco 2006; Tecco et al. 2010; Hoyos et al. *in press*), the lowlands surrounding the Córdoba Mountains, represent an important source of propagule pressure of alien species towards higher altitudes.

In this study we aimed at obtaining a first insight into the major factors associated with plant invasions in a newly invaded mountain range, thus providing evidence which may in the future be compared to other mountain systems. This was achieved by modeling a distribution map of alien woody species along the altitudinal gradient of the Córdoba mountains, on account of their relation with certain biotic, abiotic and anthropogenic factors. In line with the

current knowledge on mountain plant invasion (Pauchard et al. 2009 and references therein) we hypothesize that propagule pressure is the main factor associated with woody alien distribution in the Córdoba mountains, as it is at its first stages of invasion. Consequently, we predict that in addition to a general pattern of decreasing abundance with altitude, alien woody species will be more abundant close to sources of propagules (e.g. towns, houses, roads and neighbor sites with established alien plants) than far away from these sources (e.g. Pauchard and Alaback 2004; Alexander et al. 2009). Additionally, as different land use histories can promote different timings of invasion and propagule pressure (Parks et al. 2005; Pauchard and Shea 2006; Wilson et al. 2007), we predict that alien woody species will be more abundant in the eastern side of the Córdoba mountain range. This side of the mountain has a longer and more intensive history of alien species introduction and forestry aided by European settlers than the western range (Verzino et al. 1999; Freytes de Vilanova 2006). At last, given the early stage of invasion, we expect to find patterns of distribution best defined by propagule pressure indicators rather than by abiotic factors or indicators of biotic interactions or disturbance.

Methods

Study area

The study was carried out in the upper portion of the Sierras Grandes, the main mountain range of Córdoba Province, central Argentina (1,500–2,800 m a.s.l., 31° 34' S, 64° 50' W). The mean annual temperatures range from 13.2°C at 1,500 m a.s.l. to 7.4°C at 2,700 m (Marcora et al. 2008). Mean annual precipitation is 924 mm, with most rainfall concentrated in the warmer months, between October and April (Cabido and Acosta 1985; Colladon et al. 2009). The main economic activity is livestock rearing (mainly cattle, but also sheep, goats, horses and camelids), which began early in the seventeenth century and completely replaced large native herbivores (*Lama guanicoe* and probably *Rhea spp.*) in the beginning of the twentieth century (Díaz et al. 1994).

Native vegetation consists of a mosaic of tussock grasslands, grazing lawns, granite outcrops, evergreen

Polylepis australis woodlands, and eroded areas with exposed rock surfaces (Cingolani et al. 2004). This vegetation arrangement is mainly explained by the interaction between livestock-related impact and abiotic factors (Renison et al. 2006, *in press*; Cingolani et al. 2003, 2008; Marcora et al. 2008). The area lacks a tree line; *Polylepis australis* woodlands can reach the highest altitudes (Cingolani et al. 2008).

In 1997, an area of 26,000 ha was declared National Park. In addition, 12,000 and 117,000 ha surrounding the Park were declared National and Provincial Water Reserves, respectively; but are under private ownership and mainly used for livestock rearing. Our study included 39,046 ha located in the southern portion of the Provincial Water Reserve (Fig. 1).

Field data collection

We used a Geographic Information System (GIS) of the area to select the sampling plots. The GIS consisted of different layers, including vegetation,

physiography, a digital elevation model, rivers, human settlements and roads (Cingolani et al. 2004, 2008). We selected 303 plots covering all the area, stratifying the selection according to the combination of GIS layers. Plots selected at each stratum were in a similar proportion as the stratum occurred in the area. Because only one road is for motor vehicles (delimiting our study area towards the south) some of the plots were reached after walking 1 or 2 days (Fig. 1b). In the field, we located the central point of each plot with GPS, and delimited a 30 × 30 m sampling area (equivalent to the resolution of the vegetation map and the digital elevation model, Cingolani et al. 2008). Within each plot we registered the presence of all woody alien species and visually estimated their cover percentage. The same variables were estimated in an additional 30 × 30 m plot located 100 m away from the first, in a randomly defined direction. This additional plot was selected to determine if the presence of woody alien species in the neighborhood of a focal plot increases the probability of finding alien woody species in that focal plot, independently of other factors considered (see data analysis).

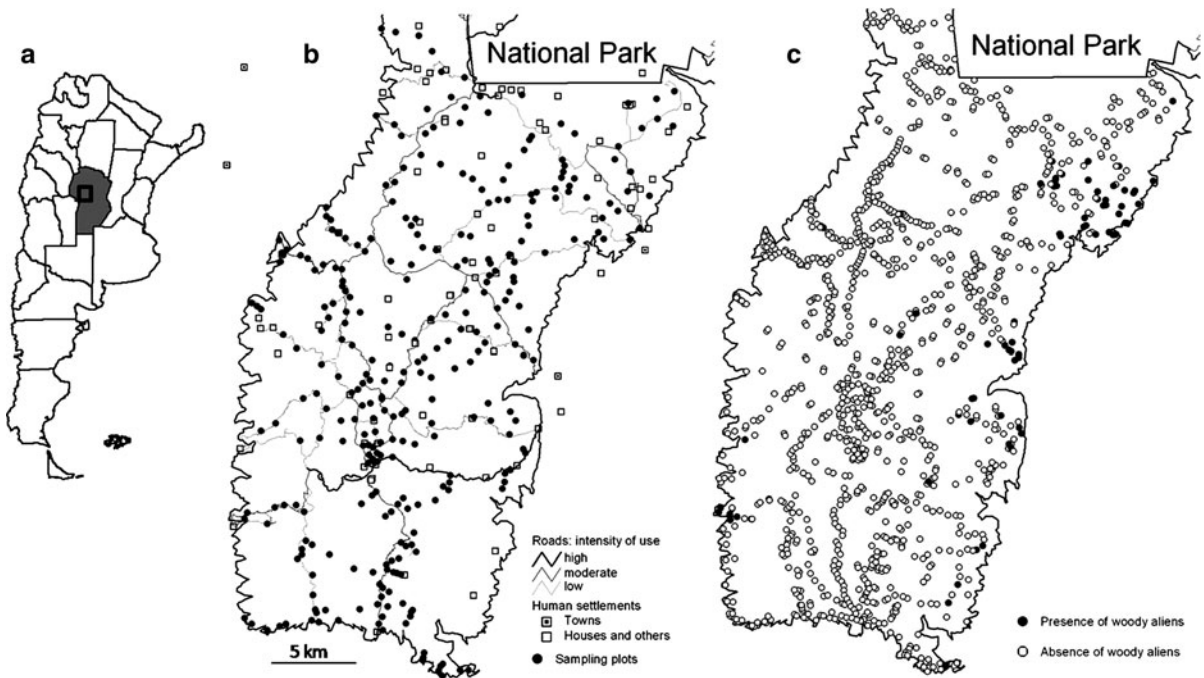


Fig. 1 **a** Location of Córdoba Province (*in gray*) and the study area (39,046 ha), indicated by a square, in Argentina. **b** Distribution of the initial 303 sampling plots, roads and human settlements in the study area. **c** Distribution of all the

1,168 sampling plots (initial 303, additional 303, and validation 562) with different color according to the presence (*black*) or absence (*white*) of alien species. For **a** and **b**, the National Park, in the northern of the study area, is indicated

GIS data sampling

We obtained predictor variables from the GIS. Native vegetation was assessed through a map of 30×30 m resolution and 87% accuracy with eight units: (1) closed woodlands, (2) open woodlands, (3) thick tussock grasslands, (4) thin tussock grasslands, (5) lawn, (6) mosaic of tussock grasslands and outcrops, (7) mosaic of eroded surfaces and outcrops, and (8) erosion pavement (Cingolani et al. 2004). No unit of the map was dominated by alien woody species. Vegetation type was considered as a biotic indicator of native plant communities which can directly affect plant invasion by biotic interactions such as facilitation (i.e., amelioration of harsh conditions) or resistance (i.e., competition). Additionally, this variable could be considered as indicator of disturbance, since the present distribution and characteristics of vegetation units is chiefly determined by present and past land use (i.e., livestock related impact; Renison et al. 2006, 2010, *in press*; Cingolani et al. 2008).

Abiotic factors were obtained from different layers. From the river layer we obtained the distance to permanent rivers. From the physiographic map we obtained four main units integrating topography, substrate and degree of dissection: (A) very steep escarpments (on granite or metamorphic rocks) (B) rocky hills, slopes and deep ravines on granite, (C) rocky hills and slopes on metamorphic rocks, and (D) plateaus, which include flat areas on granite, with low to moderate degree of dissection, and gentle valleys. From the digital elevation model we obtained various layers: slope percentage, and indices of insolation, roughness and topographic position (as in Cingolani et al. 2008). The insolation index was constructed integrating slope and aspect in a unique measure: the sine of the angle of sun rays reaching the surface in the azimuth at any equinox. This insolation index is related with the insolation received by each plot during all seasons except summer, but does not take into account the projected shadows (Cingolani et al. 2008). The index of roughness was calculated as the standard deviation of the insolation index using a circular kernel of 315 m radius. The topographic position was also calculated using a 315 m radius circular kernel, as: $(\text{height at the centre} - \text{minimum value in the circle}) / (\text{difference between the maximum and minimum height in the circle})$. In this way, for each pixel we obtained a value between zero and one, being zero

the lowest topographic position in relation with the surrounding landscape, and one the highest position.

We considered different layers as possible indicators of propagule pressure: for distance to roads (roads, tracks, horse and trekking trails) we created three alternative distance layers, one considering the distance to all roads, another considering the distance to roads with moderate or intense use, and the third one considering only the distance to roads of intense use. Roads represent a major pathway of propagule pressure for alien plant species (Pauchard and Alaback 2004; Alexander et al. 2009). Another indicator was the distance to human settlements (settler houses, abandoned houses, tourism lodges, and villages situated outside but close to the study area), that constitute the principal reservoirs of alien plant propagules. These indicators are not completely independent of disturbance, as fire and livestock are generally higher near human settlements and roads (Cingolani et al. 2008). Finally, we considered a layer with two categories: east and west mountain range slope. The Córdoba mountains run north to south for about 150 km, and the foothills and valleys below our study limits of 1,500 m a.s.l. have different land use history and slight differences in climate (mainly temperature and precipitation, Capitanelli 1979) at both sides of the range. Both sides were first settled during the seventeenth century by descendants of Spaniard conquerors, their main activity was livestock rearing and they planted few alien species. However, early in the twentieth century, large quantities of alien woody species were introduced in the eastern range of the mountains and the neighbor valley, and *Pinus* spp. plantations were promoted by immigrants from Germany, Switzerland and Czech Republic attempting to recreate their homeland in a landscape where native forests had almost disappeared (Verzino et al. 1999; Freytes de Vilanova 2006). In contrast, in the western valley, the introduction of alien species was almost absent until the late twentieth century, and even then it was not as massive as in the eastern valley. In the western valley ornamental alien species were introduced for shade in urban gardens and farm lots with the arrival of Argentinean families moving away from large cities into the countryside, and the native forest matrix was largely maintained in the remaining forest fragments.

The final number of predictor variables was 12. Three were categorical: vegetation unit (8 categories),

physiographic unit (4 categories) and range slope (2 categories). The remaining variables were quantitative: slope percentage, insolation index, roughness index, topographic position index, distance to permanent rivers, distance to human settlements and distances to the three types of roads categories (all; moderate-intense use; and intensive use—to select one as the best indicator). All distance variables were measured in pixel units (i.e. 30 m).

Data analyses

The low frequency of alien woody species in the 303 sampling plots did not allow a separate analysis for each species. Thus, we decided to pool all woody aliens for statistical analyses, but previously we tested if the most abundant species were associated in their occurrences by pair-wise χ^2 tests. Then, to detect the factors most associated with alien woody invasion, we performed a logistic regression, where the response variable was the presence or absence of at least one individual of any woody alien species. The categorical and quantitative variables obtained from the GIS (see above) and/or their quadratic and positive squared root terms were used as independent variables. These additional terms were included to represent unimodal and other non-linear relationships with the logit values (Afifi and Clark 1984; Underwood 1997). We selected the best set of variables by a forward stepwise regression (conditional), with entry of $P = 0.05$ and removal of $P = 0.1$. We discarded models that selected all three terms of the same variable (first order, square root and quadratic) and we also discarded parabolic relations with a concave (U) shape (formed by two terms of the same variable) because to our criteria these models were biologically meaningless. In these cases, to obtain an acceptable model, we repeated the selection procedure by eliminating alternatively each term. We then selected the best of the three or two possible models obtained. We proceeded in a similar way in the case of distances to roads, selecting only one of the three alternative distances.

Once the best model was selected, to check and eventually discard variables strongly associated we performed pair-wise correlations between the selected predictors of the model. Finally, we analyzed if we could significantly explain some additional variance by including in the logistic multiple regression the

presence-absence (a two-categorical variable) of alien woody species at 100 m distance from the focal sampling plot. This was done to test the importance of propagule pressure at the very local scale.

Mapping present distribution

Running the logistic model for each pixel, we generated a probability map with 30×30 m resolution, using the GIS layers as predictor variables (Erdas 1995). Once the probability map was created, we subdivided the pixels in 4 probability categories of woody alien occurrence: Class 1 = ≤ 0.019 probability, indicating nil or occasional occurrence; class 2 = 0.02–0.0999, indicating low to moderate occurrence; class 3 = 0.1–0.4999, indicating moderate to high occurrence; and class 4 = ≥ 0.5 , indicating very high occurrence.

Map validation

To validate the distribution map, we selected a total of 562 validation plots (309 in class 1, 122 in class 2, 91 in class 3, and 40 in class 4), located each sampling plot in the field, and recorded the presence or absence of woody alien species. The number of sampling plots was selected as follows: for the first class (i.e., with occasional occurrence) we selected a number of plots enough to expect 2 presences ($N = 2/\text{mean probability of the class}$). For the remaining classes we selected a number of plots enough to expect 5 presences ($N = 5/\text{mean probability of the class}$).

Using χ^2 tests, we analyzed if the distribution of presences and absences in each class was homogeneous for the three field data sets (the 303 initial plots used for the model, the 303 additional plots used to analyze the influence of the neighborhood of aliens, and the 562 validation plots). We analyzed each class separately, but when necessary to meet the assumptions, we joined classes (e.g. class 1 with 2), or data sets (the 303 initial with the additional 303 plots). In addition, to analyze if for each class the distribution of presences and absences was spatially homogeneous along the whole area, we twice subdivided the validation data in two halves: north–south and east–west, and performed χ^2 tests (we used only the validation data set for this). As before, when we could not meet the assumptions, we joined classes.

Final map

Finally, to correct the biases of the initial map (see results), we run a new logistic model using all the plots (1,168), maintaining the same variables and terms selected by the initial model. This second analysis was performed only to have a more accurate estimation of model coefficients, based in a higher number of cases. From this corrected model, we performed a new probability layer, and then, with the same criteria as before, we created the definitive map with the four classes of woody alien occurrence. Though the accuracy of the final map was not calculated (because we would need additional new field data), we assumed that its accuracy was better than the initial version as it adjusted the biases of the initial model, without changing substantially the map (see results).

Results

Alien woody species

We recorded a total of 11 alien woody species within our study plots (Table 1). Overall, the occurrence of alien woody species in the study area was low (present in 73 of the 1,168 plots, i.e., 6.2%). The most frequent species were *Cotoneaster franchetii*, *Rubus ulmifolius*, and *Rosa* spp. The species that reached the highest cover in a sample plot (30 × 30 m) was *R. ulmifolius* (70%), followed by *Pyracantha angustifolia* (50%) and *Salix viminalis* (30%). We found only four woody alien species in the western slope of the mountain range (*P. angustifolia*, *Pinus elliotii*, *R. ulmifolius* and *Morus alba*), while all the species recorded in the study area, except *M. alba*, were registered in the eastern slope. The alien which was recorded at the highest altitude above sea level was *Salix viminalis*, at 2,248 m a.s.l., with no recorded aliens above this altitude (Table 1). Most of the alien species were from Eurasian origin, and were introduced for ornamental purposes, except *P. elliotii*, used for forest industry, *Salix* spp. for shade and fuel and *R. ulmifolius* and *Rosa* spp. for fruit consumption.

Although alien occurrence in the study site was overall low, there was high co-occurrence of woody alien species, a result that support their pooling for

modeling. Almost half of the initial field plots with alien presence had more than one species within the same plot (i.e., 10 of the 23 plots with alien species in the 303 initial plots). This was consistent when considering all 1,168 sampling plots together, in which 41% of the plots with alien presence had co-occurrence of alien species. Accordingly, we found statistically significant associations between *Cotoneaster franchetii* and *R. ulmifolius* (χ^2 29.27, $P < 0.001$), between *C. franchetii* and *Rosa* spp. (χ^2 89.10, $P < 0.001$) and between *R. ulmifolius* and *Rosa* spp. (χ^2 55.35, $P < 0.001$) in the 303 initial plots.

Logistic model: factors associated with woody alien distribution

When running the logistic model using the initial 303 plots, we found the highest occurrence of woody aliens in the eastern slope of the mountain range, at low altitudes, and near sources of propagule pressure (human settlements and roads, Table 2, Fig. 2). Additionally, alien occurrence was higher at low topographic positions and on steep slopes than in habitats with the opposite characteristics. Vegetation units, physiography, landscape roughness, insolation and distance to rivers were not selected by the regression procedure. Even when most model predictors were significantly correlated, the correlation coefficients were low enough to preclude instabilities in the model (correlation coefficients ranged from 0.02 to 0.24 between the six predictors, the highest coefficients were found between altitude and slope, and between altitude and road distance, $R = 0.24$, $P < 0.05$, in both cases).

Among the four map classes obtained from the logistic model, class 1 (i.e., nil or occasional alien occurrence) covered the largest area (62%, 24,194 Ha), while class 4 (i.e., high alien occurrence) covered far less surface of the study area (6%, 2,507 Ha). Class 2 (low to moderate) and 3 (moderate to high occurrence) also covered low percentages of the area (19 and 13% respectively).

The inclusion of the categorical variable: ‘presence-absence of woody aliens 100 meters away’ proved significant when added to the logistic regression ($P < 0.05$), and increased the Nagelkerke R^2 from 0.52 to 0.57. The significance of the other variables was maintained.

Table 1 Presence of woody alien species in the upper portion of the Sierras Grandes recorded through three field data sets (1,168 sampling plots in total). First, the number of plots where each species was present in the initial data set of 303 plots (O_{plots}), and in the additional dataset of 303 plots (Add_{plots}). Then, the same information for the validation data set of 562

(Val_{plots}) and finally, for the total dataset 1,168 (Total). The maximum cover registered within a plot, in any of the datasets; and the maximum altitude at which each species were recorded is provided in the last two columns. The last row summarizes, for each data set, the number of plots with at least one woody alien species

| Species | Family | Origin | O_{plots} | Add_{plots} | Val_{plots} | Total | Maximum cover within plots (%) | Maximum altitude |
|---|------------|---------------|-------------|---------------|---------------|-------|--------------------------------|------------------|
| <i>Betula pendula</i> Roth | Betulaceae | Eurasia | 1 | 1 | 1 | 3 | 2.78 | 1.630 |
| <i>Cotoneaster horizontalis</i> Decne. | Rosaceae | Asia | 1 | 2 | 1 | 4 | 1 | 1.825 |
| <i>Cotoneaster franchetii</i> Bois | Rosaceae | Asia | 9 | 10 | 12 | 31 | 11 | 2.012 |
| <i>Morus alba</i> L. | Moraceae | Asia | 1 | 1 | 1 | 2 | 2.77 | 1.750 |
| <i>Pinus elliottii</i> Engelm. | Pinaceae | North America | 3 | 0 | 4 | 7 | 5 | 1.850 |
| <i>Pyracantha angustifolia</i> (Franch.) C. K. Schneid. | Rosaceae | Asia | 1 | 4 | 8 | 13 | 50 | 1.750 |
| <i>Rosa</i> spp.* | Rosaceae | Eurasia | 9 | 8 | 7 | 24 | 2 | 2.075 |
| <i>Rubus ulmifolius</i> Schott | Rosaceae | Eurasia | 9 | 9 | 12 | 30 | 70 | 1.920 |
| <i>Salix viminalis</i> L. | Salicaceae | South America | 3 | 1 | 2 | 6 | 30 | 2.248 |
| <i>Salix aff fragilis</i> L. | Salicaceae | Eurasia | 1 | 0 | 0 | 1 | 0.667 | 2.018 |
| <i>Spartium junceum</i> L. | Fabaceae | Europe | 1 | 0 | 0 | 1 | 3.55 | 1.551 |
| Total plots with alien occurrence | | | 23 | 20 | 30 | 73 | | |

* Two species of *Rosa* spp are abundant in the study area, *Rosa rubiginosa* L. and *R. canina* L., their identification was precluded by the absence of flower or fruits in most individuals

Table 2 Terms included in the initial logistic model with the initial 303 field plots: regression coefficient (B_i), Wald statistic value (W_i), and significance (P_i) of the initial model. In the last

column, the regression coefficient for the final map (B_f), performed with the total 1,168 field plots

| Variable | B_i | W_i | P_i | B_f |
|--|-----------------------|--------|--------|------------------------|
| Altitude ² | -2.6×10^{-6} | 24.648 | <0.001 | -2.57×10^{-6} |
| Distance to human settlements ^{0.5} | -0.406 | 7.921 | 0.005 | -0.408 |
| Range Slope (west) | -3.258 | 7.611 | 0.006 | -2.473 |
| Topographic position | -0.032 | 5.431 | 0.020 | -0.014 |
| Slope ^{0.5} | 0.553 | 5.391 | 0.020 | 0.264 |
| Distance to roads (mod-int use) ^{0.5} | -0.273 | 3.626 | 0.057 | -0.189 |
| Constant | 9.464 | 14.044 | <0.001 | 9.303 |

Map validation

The proportional occurrence of aliens in classes 1, 2 and 3 did not differ significantly across data sets (Table 3). In class 4, the initial data set had a significantly higher proportion of woody alien species than expected assuming a homogeneous distribution, and the validation data set a lower proportion than expected (Table 3). These results denoted that class 4

(as we had defined it) was overestimated in our initial map.

Using the validation data set we detected that the proportional occurrence of aliens within classes (or groups of classes) was not completely homogeneous in space. Class 4 showed a marginally significant ($P = 0.06$) difference in proportional occurrence between the northern and southern half, suggesting more presences in the northern half than would be

Fig. 2 Probability of woody alien occurrence against the independent continuous variables included in the initial model. Closed circles represent the eastern range slope, open circles the western range slope. To plot the circles, we calculated moving averages of presence-absence data between groups of 10 samples. The *trend line* was plotted using the model coefficients for each variable, fixing the remaining variables as constants equivalent to modal or mean values (*solid line, eastern range slope, dashed line, western range slope*)

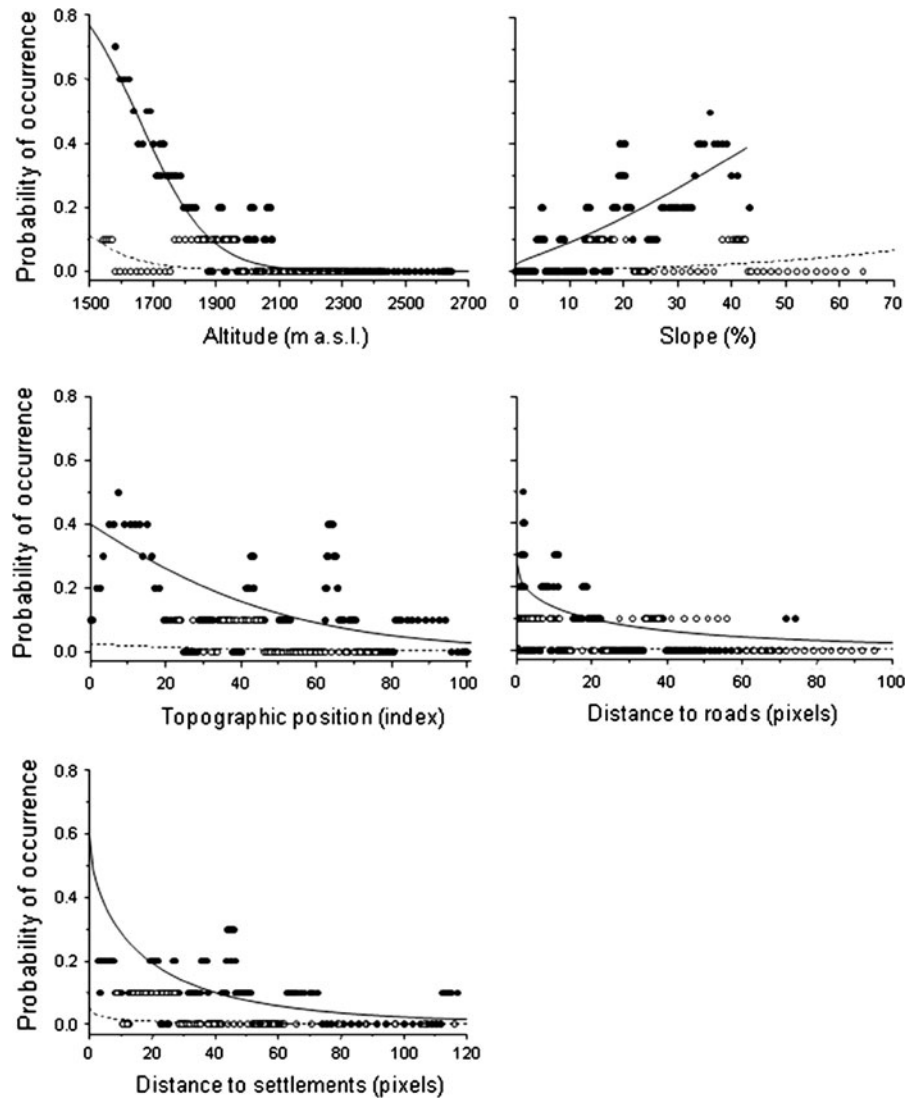


Table 3 For each class of the initial map (rows) and data set, (columns) the mean frequency (%) of plots with presence of woody aliens and the number of alien presences/total number of plots within each class (in brackets) are indicated. In the last column the significance of the χ^2 comparisons to detect if the distribution of presences and absences in each class (or group of classes) was homogeneous across data sets

| | Initial plots | Additional plots | Validation plots | P |
|---------|---------------|------------------|------------------|-----------------|
| Class 1 | 1.1 (2/180) | 0.0 (0/185) | 0.3 (1/349) | |
| Class 2 | 4.3 (3/70) | 7.8 (5/64) | 3.4 (4/117) | NS ^a |
| Class 3 | 17.9 (7/39) | 15.0 (6/40) | 18.0 (11/61) | NS |
| Class 4 | 78.6 (11/14) | 64.3 (9/14) | 40.0 (14/35) | * |

^a Merging class 1 + class 2, and initial + additional data sets
 NS no significant, *P continuity correction: 0.06

expected under the assumption of spatial homogeneity. On the other hand, merged classes 1, 2 and 3 showed a significant ($P = 0.04$) difference between the western and eastern halves of the study area, indicating more occurrences than expected in the western half (Table 4).

Final map

Nagelkerke R^2 of the new logistic model calculated with all 1,168 plots was similar to the initial model performed with the initial 303 plots ($R^2 = 0.50$ and $R^2 = 0.52$, respectively). In the recalculation of the logistic parameters some of the coefficients changed

Table 4 For each class of the initial map (rows) and halve of the area (columns) the mean frequency (%) of the 562 validation plots with presence of woody aliens and the number of alien presences/total number of plots within each class (in brackets) are indicated

| | North | South | P | West | East | P |
|---------|--------------|-------------|-----------------|-------------|--------------|-------------------|
| Class 1 | 0.55 (1/181) | 0.0 (0/168) | | 0.0 (0/223) | 0.8(1/126) | |
| Class 2 | 0 (0/53) | 6.2 (4/64) | NS ^a | 2.1 (1/46) | 4.2 (3/71) | |
| Class 3 | 20.0 (6/30) | 16.1 (5/31) | NS | 30 (3/10) | 15.6 (8/51) | 0.04 ^b |
| Class 4 | 58.8 (10/17) | 22.2 (4/18) | NS [*] | 50 (1/2) | 39.4 (13/33) | NS ^c |

Information for the north–south halves (in the left), and for the west-east halves (in the right side of the table) are provided. The significance of the χ^2 comparisons to detect if the distribution of presences and absences in each class (or group of classes) was homogeneous across space is provided in both cases

^a Merging class 1 + 2+3, ^b merging class 1 + 2+3, ^c merging class 3 + 4

NS no significant, *P continuity correction: 0.06

in magnitude, while others remained almost equal (Table 2). The final map obtained with the new model had a very similar area than the initial map for class 1, a slightly higher area for class 2, a slightly lower area for class 3, and a considerable lower area (in proportion) for class 4. Specifically, the fourth class was reduced to a 67% of the area occupied in the first map, correcting in this way the bias detected in the initial map (Fig. 3).

Characterization of the four classes

Class 1 (nil or occasional occurrence) occupied 62% of the study area according to the final map (24,236 ha, Fig. 3), and was almost free of woody alien species. Out of the 669 field plots sampled within this first class (merging the three data sets), only 2 (0.29%) had woody aliens. These occasional presences represent one individual or small population every 30.1 ha and were observed near the limits with class 2 or near to human settlements. The species registered in this class were *Salix viminalis*, *S. aff. fragilis*, *Cotoneaster franchetii* and *Rubus ulmifolius*.

Class 2 (low to moderate occurrence) occupied 19% of the study area (8,303 ha, Fig. 3). Out of the 292 field plots sampled within this class, 12 (4.11%) had woody aliens, which represent 1 individual or group of individuals every 2.19 ha. Species registered in this class were *Cotoneaster franchinetii*, *Rosa spp.*, *Pinus elliotii*, *Pyracantha angustifolia*, *Rubus ulmifolius* and *Morus alba*.

Class 3 (moderate to high occurrence) occupied 13% of the study area (4,840 ha, Fig. 3). Out of the 133 field plots sampled within this class, 30 (22.5%)

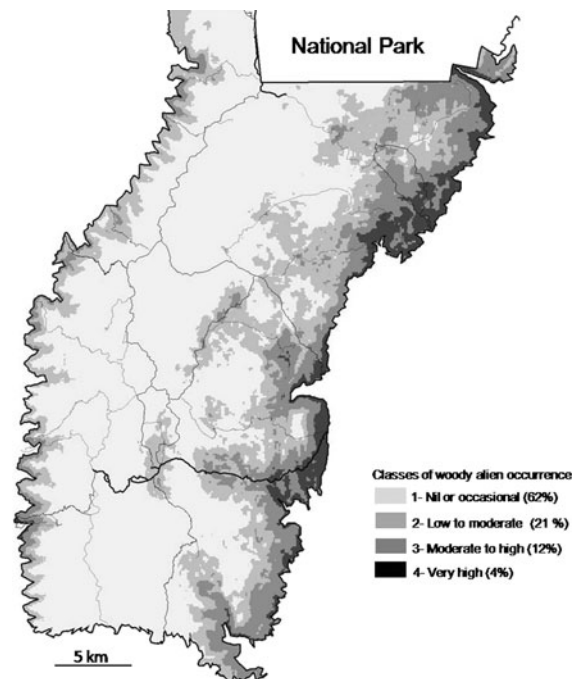


Fig. 3 Final distribution map of woody alien species in the study area (39,046 ha in the upper portion of the Cordoba mountains of central Argentina). The legend indicates the four classes of woody alien occurrence (see text for more details), and in brackets the percentage of the region occupied by each class

had woody aliens, which represent 1 individual or group every 0.4 ha. In addition to the species found in the class 2, we also registered *Cotoneaster horizontalis* and *Salix viminalis*.

Class 4 (very high occurrence) occupied 6% of the study area (1,667 ha, Fig. 3). Out of the 44 plots sampled within this class, 29 (i.e. 65.9%) had woody

aliens, which represent 1 individual or small population every 0.13 ha. We registered all the species recorded in the study area, except for *Salix viminalis*, *S. aff. fragilis* and *Morus alba*.

Discussion

The early detection and description of the major factors associated with invasion are a promising start in the research agenda of plant invasions in mountain systems (Dietz 2005; Dietz and Edwards 2006; Pauchard et al. 2009). As expected for any invasion at its first stage, in our study area propagule pressure seems to be the main factor at play in the expansion of woody aliens from lowlands to the higher altitudes. Accordingly, all variables selected to indicate propagule pressure (location in relation to the eastern valley, distance to settlements and roads and presence of woody aliens in the neighborhood) appeared as the most important predictors when modeling woody alien occurrence in the study area. These findings together with the overall low occurrence of woody alien species support the incipient state of the invasion in the Córdoba mountains.

Other factors, such as biotic interaction and disturbance, are known to influence invasion patterns in other mountain systems in addition to propagule pressure (Pauchard et al. 2009). Biotic facilitation (or alternatively biotic resistance) is expected to be at play depending on the invaders preadaptation to the more rigorous conditions of mountain ranges (Pauchard et al. 2009). Most alien species currently spreading towards higher altitudes in the Córdoba mountains are lowland invaders, and our results indicate that their occurrence at higher altitudes is significantly associated to low topographic positions. This could lead to the assumption that invaders are spreading across more sheltered (abiotic) conditions, and are likely not pre-adapted to mountain conditions. However, alien presence was not associated to vegetation units that provide climatic shelter (e.g., woodlands). The overall lack of relation between alien occurrence and vegetation units precludes us to draw definitive conclusions over the relevance of biotic interactions (either facilitation or resistance) which at this scale of analysis do not seem evident.

The recognition of disturbance as a further factor associated with woody invasion was likely to be

reflected in our study by a positive association between alien presence and vegetation communities that undergo periodic grazing and fire events (e.g., lawns). Again, as vegetation type was not selected as a predictor variable in the model, our findings do not support the idea that woody alien are spreading through the most disturbed areas. Moreover, the positive association of alien occurrence with low topographic positions and steep slopes could even suggest a preference for less disturbed sites, as these areas are related with a lower probability of fire occurrence (Renison et al. 2006). The absence of a clear relationship between alien occurrence with variables associated to disturbance and biotic interactions could be grounded on the influence of propagule pressure, which as predicted seems to be overriding this relation. This makes sense given the transient stage of the invasion.

It is worth mentioning that since the upper portion of our study area has higher temperatures than most tree-lines in the world (cfr. Körner and Paulsen 2004; Marcora et al. 2008), and considering that some of the aliens species thrive well in cold climates (e.g. *Rosa rubiginosa* and *Rubus ulmifolius*; De Pietri 1992; Morales and Aizen 2002; Zimmermann et al. 2010) it is highly probable that aliens could reach the highest altitudes of our mountains if given enough time to overcome propagule limitation. Moreover Becker et al. (2005), found that the maximum altitude reached by alien plant species in the Swiss Alps tended to increase with time since introduction, and proposed that this relationship might reflect ongoing adaptation of invading populations to the constraints imposed by the gradient. Experiments that translocate propagules or seedlings along the environmental gradient could be a powerful way to confirm our hypothesis that alien species are constrained to lower altitudes mainly due to low propagule pressure at higher altitudes rather than by abiotic or biotic conditions (Poll et al. 2009).

In addition to the proximity to sources of propagules, sheltered topographies, and low altitudes, alien occurrence increased with local slope. This was apparent in the eastern range, but was less clear in the western range, where alien occurrence was low even in steep slopes (Fig. 2). The selection of slope as predictor in the model was thus mainly driven by the trend in the eastern range. This pattern does not have a straightforward interpretation. It could be a false

inference (Palmer et al. 2008), due to the differences in land use history of both slopes, or alternatively reflect a pattern related to unknown causes, to tackle with further research efforts.

To date the major driving factors affecting native vegetation dynamics and erosion problems in the Córdoba mountains are livestock rearing and associated fires (Cingolani et al. 2003, 2008; Renison et al. 2006, 2010, in press). Here, we suggest that woody alien invasion could become, in a future, an additional driver of vegetation dynamics and ecosystem processes in the region given their incipient spread towards higher altitudes. The striking evidences on major ecosystem impacts of woody invaders in the alteration of key ecosystem processes such as water dynamics, nutrient cycling and fire regimes in other systems (e.g. Cronk and Fuller 1995; Le Maitre et al. 1996; Holmes and Cowling 1997; Reichard and Hamilton 1997; Richardson 1998; Zavaleta 2000; Farley et al. 2005) yield our findings as a matter of concern in the region. As effectiveness decreases and cost of alien management increase exponentially with the invasion process, we suggest urgent application of alien control and mitigation actions. This new distribution map might be a useful tool for forecasting spread dynamics and designing sound and effective management programs.

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