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Altitudinal distribution of native and alien plant species in roadside communities from central Argentina

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Abstract Roadsides may homogenize the distribution of native species and act as corridors for the spread of alien taxa. We examined the variation in native and alien plant species richness and composition at two spatial scales defined by altitude and habitat type (edges and fill slopes), as well as the relationship between native and exotic species richness in roadside plant communities in mountains from central Argentina. Following a gradient from 1100 to 2200 m a.s.l. along a mountain road, plant species cover was recorded within sample plots of 30 m × 10 m systematically located at 100-m altitude intervals on both roadside habitats. Although native species richness decreased with altitude and composition changed accordingly, the number of alien species peaked at both extremes of the elevation gradient and did not reflect an altitudinal replacement of chorological groups. The number of both native and alien species was higher in roadside edges, but a negative association between the richness of native and alien species occurred only on fill slopes, suggesting that roadside habitats differ in their susceptibility to plant species colonization and in the mechanisms driving native and alien species richness. Our results highlight the importance of altitude and roadside habitat as factors controlling plant species richness and composition along roadside communities in central Argentina. Although altitude acts as a filter for native plants, it apparently did not constrain the establishment of alien species along the studied roadsides, indicating that the influence of this road as a plant species corridor may increase with time, promoting the opportunities for aliens to expand their current distribution.

Key words: alien species, altitudinal gradient, fill slope, mountain grassland, road edge, species composition, species richness.

INTRODUCTION

Roadsides are disturbed areas with a strong linear structure potentially allowing the unimpeded dispersal of plant species (Tikka *et al.* 2001). By facilitating dispersal, roads may homogenize the regional distribution of native species and act as corridors for the spread of alien taxa, providing a major conduit for plant invasion (Forman & Alexander 1998; Tikka *et al.* 2001; Harrison *et al.* 2002; Christen & Matlack 2006). The distribution and abundance of plant species along roadsides may be affected by many factors acting at different spatial scales on native and alien species, such as altitude, microsite conditions, and resource or competitive release (e.g. Parendes & Jones 2000; Gelbard & Harrison 2003; Arévalo *et al.* 2005).

On a regional scale, altitude plays a fundamental role in plant species distribution, with many environmental factors varying simultaneously along elevation gradients (Körner 2007). In temperate mountain systems, species richness of both native (Kitayama 1992; Odland & Birks 1999) and alien plants (Pauchard & Alaback 2004; Daehler 2005; Mcdougall *et al.* 2005; Kalwij *et al.* 2008) generally decreases with altitude as a result of constraining climatic conditions at higher altitudes (Daehler 2005). However, alien species may differ in their distribution along altitudinal gradients according to their biogeographical affinities and climatic tolerances (Arévalo *et al.* 2005; Daehler 2005), being highly successful whenever the new environment is similar to their native one (Mcdougall *et al.* 2005; Alexander *et al.* 2009).

At the local scale, habitat filtering may have an important effect on species richness and composition of roadside plant communities (Parendes & Jones 2000; Gelbard & Belnap 2003). In mountainous regions, road construction is accompanied by large-scale physical disturbances associated with cut and fill

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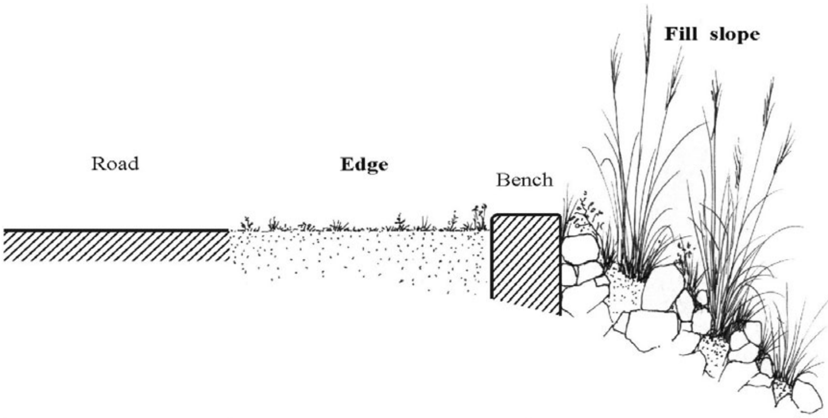

Roadside habitat / Characteristics	Edge	Fill slope
Topography (slope)	Flat (0°)	Pronunciated (>50°)
Vegetation structure	Short grasses and forbs	Tall grasses and shrubs
Vegetation cover	±	++
Substrate	Sandy	Rocky
Soil depth	++	+ (except sediment patches)
Soil moisture	+++	+ (except sediment patches)
Disturbance	High	Moderated
Nutrient level	+++	+ (except sediment patches)
Light availability	+++	++

Fig. 1. Sketch of typical roadway components showing the edge and fill slope habitats along an altitudinal gradient in the Córdoba mountains, central Argentina. ±, minimum factor intensity; +, low factor intensity; ++, intermediate factor intensity; +++, maximum factor intensity, not measured.

operations that drastically alter the landscape. Cut operations remove soil and rock from the hillside above the future road, which is then deposited on the down-slope area in fill operations (Rentch *et al.* 2005). The resulting roadsides comprise two types of habitat, edges and fill slopes, encompassing different characteristics (Fig. 1).

Climatic and habitat filtering, added to species specific traits related with dispersal and competitive abilities, may result in a variable set of native and alien species assemblages along an altitudinal gradient. The interplay of species richness among natives and aliens may be explained by the biotic resistance hypothesis (Tilman 1997), which assumes that a recipient community is resistant to invasion as a result of competition that stems from high local diversity and low niche vacancy. Up to now, this relationship has been rarely assessed in roadside communities along altitudinal gradients (but see Pauchard & Alaback 2004; Arévalo *et al.* 2005).

A number of exotic species, mainly of Eurasian origin, have spread in the lowlands surrounding the central Argentina mountains after the westward agricultural expansion that began in the Eastern Pampas at the end of the 19th century (Solbrig 1997; Tecco 2006; Tecco *et al.* 2006). Contrarily, and despite three centuries of heavy grazing, these mesic mountain grasslands show a limited number of alien plant taxa both in standing vegetation (Pucheta *et al.* 1998; Cantero *et al.* 1999, 2003) and in seed banks (Funes *et al.* 2003). Furthermore, the presence of exotic species in these mountain grasslands is restricted to patches subjected to disturbance, such as ploughed sites, abandoned fields and roadside habitats along the few routes connecting lowlands to highlands in the Córdoba Mountains (Tecco 2006).

In this study, we examine the variation in native and alien plant species richness and composition at two spatial scales defined by altitude and habitat type (edges and fill slopes), as well as the relationship between native and exotic species richness in roadside plant communities in montane grasslands of central Argentina.

We hypothesized that plant species richness is controlled at a regional scale by altitude, as a surrogate measure for several climatic factors. Then, we predicted a general decrease in the number of native and alien species with elevation, but an increase in the proportion of exotic species from higher latitudes of the Northern Hemisphere.

Second, we hypothesized that at the local scale plant species richness is controlled by differences in micro-

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site conditions and species interactions. Based on previous studies reporting higher exotic species richness in heavily disturbed habitats, we expected higher alien species numbers in edges. Finally, following the biotic resistance hypothesis (Tilman 1997), we predicted that alien species richness will decline with increasing native species richness.

METHODS

Study area

The study was conducted on roadsides along an altitudinal gradient from 1100 to 2200 m a.s.l. (31°32′27″S, 64°36′16″W – 31°36′38″S, 64°49′36″W) along National Route 20 in the Córdoba hills in central Argentina. This route is the arterial road from the lowlands to highlands in the Córdoba Mountains, connecting the eastern to the western lowlands, and is part of the projected 'Bi-oceanic Corridor' linking Chile to central Argentina. It was a consolidated gravel road until 10 years ago when it was paved, becoming a heavily transited two-way highway. Although other unpaved roads occur in these mountains, they are shorter and have low traffic pressure compared with National Route 20. Because only one route was used in this study, a spatial pseudo-replicated design (Hurlbert 1984) occurs; however, this is the only paved road within the region and, although we use inferential statistics, we limit the conclusions of our results to the studied road.

Two habitat types (edges and fill slopes) are clearly differentiated along the roadsides (Fig. 1). The edge habitat, immediately next to the road, is an almost flat 10–15 m wide strip comprising exogenous sandy material, compacted by vehicles and trampling. The contiguous habitat, which does not have any current disturbance, is fill derived from bedrock material extracted from the upper side of the road, and is rocky with very little soil (except patches filled with sediments) and has a steep slope (>50°). Benches at these habitats add stability to the slope. Vegetation in edges is mowed regularly, whereas fill slopes are not managed. Neither of these roadside habitats are planted or sown to fix soil or prevent erosion.

The climate of the region is temperate sub-humid with short cool summers and long cold winters. There are sharp differences in mean annual temperatures from 13.1°C at the lowest to 8°C at the highest altitude, and mean minimum temperatures range between 2.7°C and –2.0°C (Cabido *et al.* 1997). Mean annual rainfall varies from 786 mm at the lowest altitude to 979 mm at the highest and is concentrated mainly during the warmer season (November to March) (Cabido *et al.* 1997).

The vegetation of the study area belongs to the Sierra Chaco District of the Chaco Phytogeographical Province (Cabrera 1976). The natural vegetation is a mosaic of tall tussock grasslands and short grazing lawns. The physiognomy of the vegetation is similar along the gradient but the floristic composition changes, with the dominant species being replaced by morphologically equivalent taxa along the altitudinal gradient (Acosta *et al.* 1992).

Extensive grazing on natural grasslands has been the major productive activity and a source of disturbance for three centuries. Although most cities and towns are located below 1000 m a.s.l., there are isolated family houses at higher elevations. Tourism is important in the area, especially at higher altitudes where the National Park 'Quebrada del Condorito' is situated.

Vegetation sampling

Study sites were systematically located at 100 m altitude intervals from 1100–2200 m a.s.l. The distances between these study sites varied (5–10 km) depending on the slope and road course. At each study site we selected four plots, two for each roadside habitat (edge and fill slope). We sampled 45 plots (21 edge and 24 fill slope plots; three edge plots were missing as a result of difficulties in sampling walls with slopes >50°); this yielded 12 elevations × 2 habitat types × 2 sides of the road. Plots were 30 m × 10 m rectangles located on homogeneous vegetation stands and habitats, with the long axis parallel to the road. Plot size was chosen to maximize alpha diversity. In each plot, the cover/abundance of all the vascular plant species present was recorded on the Braun-Blanquet scale. Sampling was conducted mainly during the growing season (Southern Hemisphere summer), but extended until June 2002 to sample late annual species.

Species were classified according to their origin and distribution into Argentine native (including endemic species) and alien species. Alien refers to plant species that reproduce and sustain populations outside their native range without direct intervention by humans, although they are not necessarily expanding populations (*sensu* Richardson *et al.* 2000). Species classification and nomenclature followed Zuloaga *et al.* (1994) and Zuloaga and Morrone (1996, 1999). Life form of species was also recorded from this literature. Native species were further classified according to their biogeographical affinities and altitudinal ranges, as mentioned in the regional floras (Zuloaga *et al.* 1994; Zuloaga & Morrone 1996, 1999) and other publications containing distribution data (Cabido *et al.* 1997, 1998). We distinguished three chorological groups: (i) tropical and subtropical species, widely distributed in southern Brazil, Paraguay, Uruguay, and north-east Argentina; (ii) Austral-Antarctic and montane species, from the north-west Argentinian highlands and the Andean mountains; and (iii) widely distributed species, which have been recorded widely between 1100 and 2200 m a.s.l. Alien species were further classified by their indigenous distribution according to Parodi (1980), Arévalo *et al.* (2005) and Mcdougall *et al.* (2005), distinguishing four chorological groups: (i) European (non-Mediterranean)-Euroasiatic species; (ii) Mediterranean species; (iii) American-African species; and (iv) cosmopolitans, which have a wide geographic distribution.

Data analysis

Main trends in floristic variation of native and alien species at roadside habitats along the altitudinal gradient were analysed

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using Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980). Before performing the DCA ordination, the Braun-Blanquet cover-abundance values were transformed into the van der Maarel scale (van der Maarel 1979). Relationships between the two major axes of DCA and altitude were explored by means of Spearman correlation analyses. To determine whether some plant species were more likely to occur at one altitudinal level or roadside habitat than another, we contrasted species occurrence by altitudinal level and roadside habitat in an Indicator Species Analysis (Dufrene & Legendre 1997). This method combines information on species abundance and faithfulness of occurrence at a particular altitudinal level or roadside habitat, testing the null hypothesis that species have no indicator value.

We calculated richness and evenness (Shannon index/ln richness) at each sample plot using PC-ORD software (McCune & Mefford 1999). Two-way ANOVA was used to test the effects of altitude, roadside habitat and their interaction on native and alien species richness and evenness. We performed ordinary least-squares regression analyses to assess the relationships between altitude and species richness in the different plant groups (native, alien and the four chorological alien groups). For aliens, quadratic regression models offered the best fit and highest coefficients of determination. Correlations between the numbers of alien and native species were tested using Pearson's correlation coefficient. Alien species richness was log-transformed to achieve a normal distribution.

Basic statistical methods were implemented using the INFOSTAT statistical package (Di rienzo *et al.* 2000). Indicator Species analyses were carried out with PC-ORD software (McCune & Mefford 1999). Detrended Correspondence Analyses (DCA) were performed with CANOCO 4.5 (ter Braak & Šmilauer 2002).

RESULTS

General floristic patterns

We found a total of 271 plant species along the roadsides: 229 (84.5%) were native, including 38 (16.6%) endemic species; and 42 (15.5%) were alien. The best represented families were Asteraceae (66 natives, 12 aliens), Poaceae (53 natives, 8 aliens) and Fabaceae (11 natives, 5 aliens). Native species were dominated by annual and perennial forbs (60%) and grasses (24%), whereas only 16% were shrubs and sub-shrubs. Most of the alien species were annual or biennial forbs (45%) of European-Euroasiatic origin (48%), and all of them were ruderals. Of the 42 aliens, only three (8%) – *Cotoneaster* sp., *Rubus ulmifolius* and *Gleditsia triacanthos* – were woody species and these are known to be highly invasive in native plant communities (Zacharek 1990; Marco & Páez 2002; Daehler 2005; Williams *et al.* 2006).

Overall species richness averaged 40 species (35 native and 5 alien) per plot. Roadside communities showed a high evenness index (E > 0.89) with no dominance by a native or alien species. The percentage cover of alien species was rarely greater than 1% per plot although in a few quadrats the alien species *Eragrostis curvula*, *Hypochaeris radicata* and *Cynodon dactylon* reached a cover of 25–50%. Of the 42 alien species, 17 (40.5%) were observed in more than 5% of the quadrats along the elevation gradient. The most widely distributed alien species were the cosmopolitan forb *Taraxacum officinale* and the Eurasiatic forb *Rumex acetosella* (49% and 44% of the 45 plots, respectively). The woody invader *Cotoneaster* sp. was observed in eight (17.8%) plots, whereas *Rubus ulmifolius* and *Gleditsia triacanthos* were present in only one plot each (2.2%).

Variation in floristic composition

The most evident trend for native species was a gradual change in the floristic composition along the DCA axis 1 (Fig. 2a), which was significantly positively correlated with altitude ($r = 0.958$; $P < 0.01$). Sites below and above 1300 m a.s.l. were separated along this axis, suggesting that major floristic changes occurred at this altitude. The roadside habitats (edges and fill slopes) were separated along the second DCA axis. Alien species also partitioned out along the altitudinal gradient and between roadside habitats (Fig. 2b). DCA Axis 2 correlated significantly and positively with altitude ($r = 0.571$; $P < 0.01$), and roadside habitats were separated, although not clearly, along the first axis. Natives showed a gradual replacement from species with tropical or subtropical affinity at low elevations to Austral-Antarctic and montane species at high altitudes (DCA Axis 1; Fig. 3a). Conversely, for alien species there was no clear altitudinal replacement of chorological groups (DCA Axis 2; Fig. 3b).

In the Indicator Species Analyses, 50 species were statistically significantly ($P < 0.05$) associated with an altitudinal class (below and above 1300 m a.s.l.) and 47 species were significantly associated with one of the roadside habitats. Thirty native species, many of them with tropical or subtropical affinities, and six alien species (including four European-Euroasiatic species) were more likely to occur at lower altitudinal levels (below 1300 m a.s.l.); and 12 native, mostly Austral-Antarctic and montane, and two alien species (one cosmopolitan and one European-Euroasiatic) were indicators of sites above 1400 m a.s.l. (Table S1).

The numbers of species associated with edges (26 natives, 8 aliens) were higher than those associated with fill slopes (12 natives and only one alien) (Table S2). Although the species associated with edges were mainly annual or perennial forbs, most of the species associated with filled slopes were shrubs or sub-shrubs and perennial grasses. The only alien

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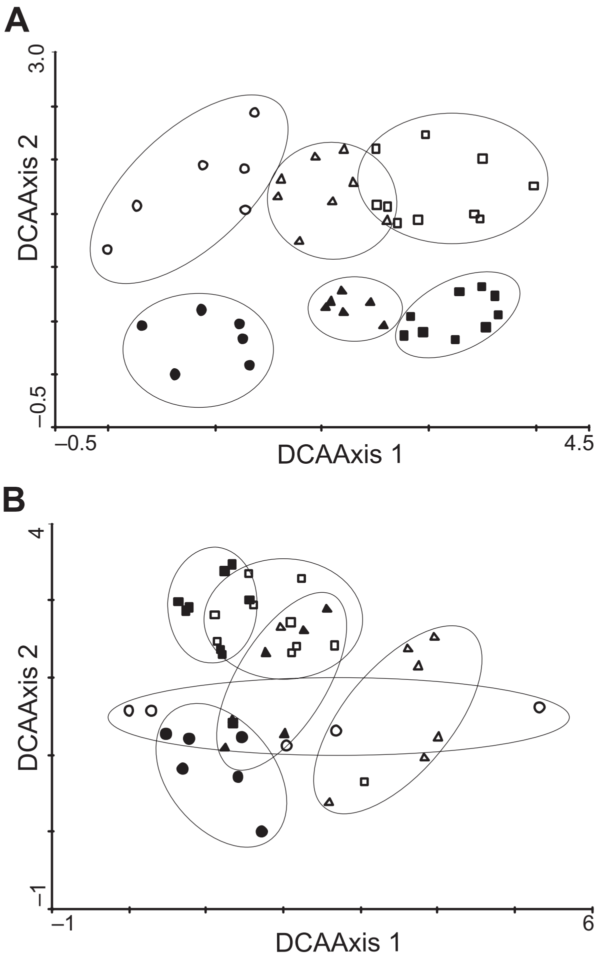

Fig. 2. Detrended Correspondence Analyses (DCA) of the 45 roadside plots according to (A) native and (B) alien plant species composition along an altitudinal gradient in the Córdoba mountains, central Argentina. Edges, filled symbols; fill slopes, empty symbols; circles, 1100–1300 m a.s.l.; triangles, 1400–1700 m a.s.l.; squares, 1800–2200 m a.s.l. Eigenvalues: (A): axis 1 = 0.511; axis 2 = 0.292; cumulative percentage variance: 20.6%; (B): axis 1 = 0.651; axis 2 = 0.430; cumulative percentage variance: 27.8%.

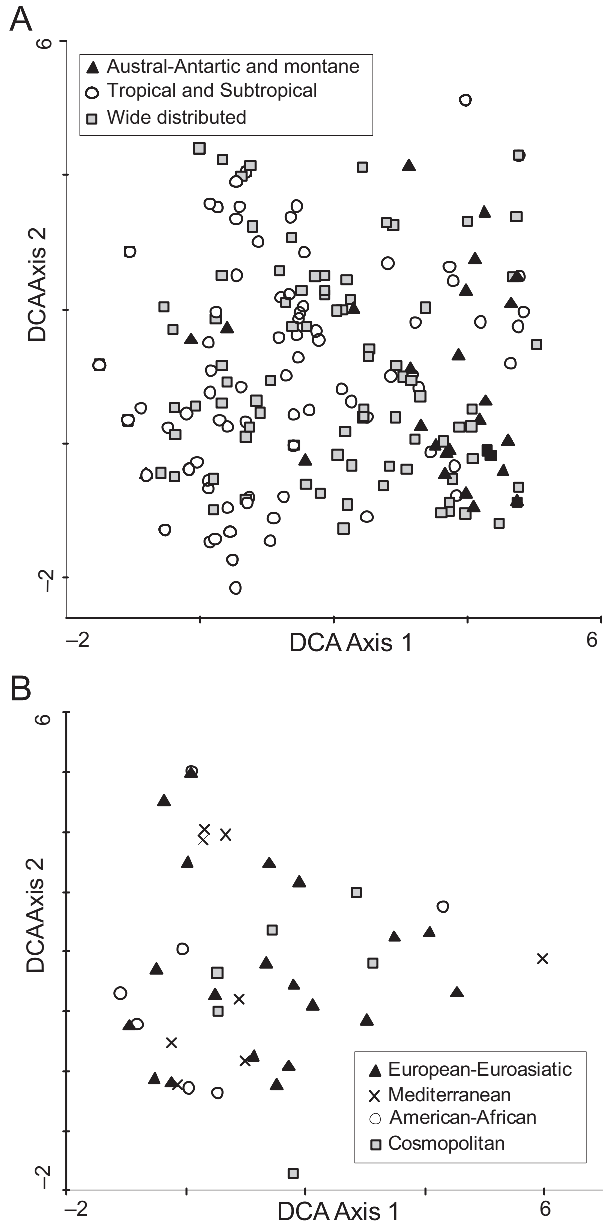

Fig. 3. Detrended Correspondence Analysis (DCA) of the (A) native and (B) alien species along an altitudinal gradient in the Córdoba mountains, central Argentina. Species are classified in chorological groups according to their biogeographical affinities. Eigenvalues: (A): axis 1 = 0.511; axis 2 = 0.292; cumulative percentage variance: 20.6%; (B): axis 1 = 0.651; axis 2 = 0.430; cumulative percentage variance: 27.8%.

species associated with fill slopes was the Asiatic shrub *Cotoneaster* sp.

Variation in species richness

There were significant effects of altitude on native ($F_{(11,23)} = 3.6$; $P < 0.005$) and alien ($F_{(11,21)} = 5.22$; $P < 0.001$) species richness, whereas evenness did not differ between elevations ($P > 0.05$). Native species richness was negatively correlated with altitude when both roadside habitats were pooled together ($R^2 = 0.101$; $P < 0.05$). Nevertheless, when both habitats were analysed separately, native species richness only significantly decreased with altitude in roadside edges ($R^2 = 0.2044$; $P < 0.05$, Fig. 4a). However, alien species richness showed a significant quadratic relationship with elevation, increasing at both ends of the altitudinal gradient (1100 and 2200 m a.s.l.) in the two habitat types, both together ($R^2 = 0.3519$; $P < 0.01$) and separately (edges: $R^2 = 0.5784$, $P < 0.01$; fill slopes: $R^2 = 0.2459$, $P < 0.05$; Fig. 4b). The species

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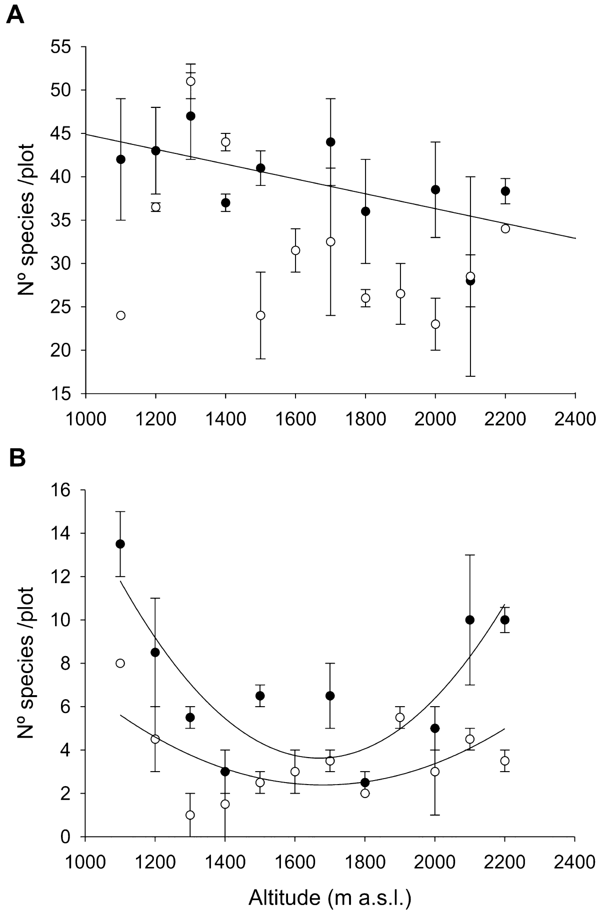

Fig. 4. Number of (A) native and (B) alien species in edge (filled circles) and fill slope habitats (empty circles) of roadsides along an altitudinal gradient in the Córdoba mountains, central Argentina. Data show the mean number (±SE) of species richness per plot (30 m × 10 m).

richness of European-Euroasiatic ($R^2 = 0.3768$; $P < 0.01$), Mediterranean ($R^2 = 0.2775$; $P < 0.01$) and American-African ($R^2 = 0.2025$; $P < 0.01$) showed a negative humped pattern similar to that revealed by total alien richness. Cosmopolitan species richness did not exhibit a significant relationship with elevation nor significant differences between altitudes ($P > 0.05$).

Native ($F_{(1,23)} = 13.28$; $P < 0.005$) and alien ($F_{(1,21)} = 28.54$; $P < 0.0001$) species richness, and evenness ($F_{(1,23)} = 52.56$; $P < 0.0001$) differed significantly between roadside habitats. Edges had a greater number of both native and alien species (Fig. 4) and were more even (data not shown) than fill slopes. No interaction effect between elevation and habitat was observed in any of the species groups ($P > 0.05$).

Native and alien species richness values were not significantly correlated when both roadside habitats were pooled together, or for roadside edges separately. However, native and alien richness showed a negative correlation for fill slopes ($r = -0.429$; $P < 0.05$).

DISCUSSION

General floristic patterns

The roadside vegetation studied in the mountains from central Argentina comprised a low number of alien species, mostly of European-Euroasiatic affinity. Although the proportion of exotic species was relatively low compared with a study from Chile (Pauchard & Alaback 2004), it was higher than those recorded off-roadsides in natural grassland communities (Pucheta *et al.* 1998; Cantero *et al.* 2003) and in the seed banks of the study area (Funes *et al.* 2003). A simple and obvious explanation for this pattern is that road construction severely disturbs natural communities (Christen & Matlack 2006), providing habitats more easily colonized by alien invasive species (Greenberg *et al.* 1997). Furthermore, imported road-building materials, vehicles and people all transport exotic plant seeds into roadside areas (Greenberg *et al.* 1997), increasing alien propagule pressure.

Role of altitude in species richness and composition

Altitude successfully explained the variation in species composition and differentially affected native and alien species richness at the studied roadsides. Floristic changes along the altitudinal gradient mainly reflected the replacement of native species according to their physiological tolerances. At lower elevations, roadsides were richer in tropical and subtropical species widely distributed in southern Brazil, Paraguay, Uruguay and north-east Argentina. Conversely, Austral-Antarctic and montane species from the north-west Argentinian highlands and the Andean mountains became conspicuous at higher altitudinal levels. The cross-over altitude between Andean and southern Brazilian taxa on roadside habitats (recorded in this study at 1300 m. altitude) differed from the transitional altitude reported for both chorotypes occurring in natural grasslands surrounding the roadsides off the study area (Cabido *et al.* 1998). In addition, the observed altitudinal distributions for some native species on roadsides were different from those expected based on their altitudinal distribution in natural grasslands (Cabido *et al.* 1998). This suggests that roadsides may function as vegetation corridors for native species, allowing many species from lower elevations to extend their ranges to higher altitudes, and vice versa.

As expected, native species richness decreased with altitude. However, surprisingly, and in contrast to results reported in previous studies (Pauchard & Alaback 2004; Arévalo *et al.* 2005; Daehler 2005;

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Mcdougall *et al.* 2005; Kalwij *et al.* 2008; Pauchard *et al.* 2009), alien species richness peaked at both extremes of the elevation gradient. Our data suggest that exotic plants may reach high-elevation environments, supporting previous records in other mountain ecosystems (Pauchard *et al.* 2009). This result partially agrees with a recent field experiment in mountain grasslands at the study area (Paiaro *et al.* 2007) where, after seed addition, elevation did not constrain and even favoured seedling recruitment of two alien species present at the studied roadsides, *Melilotus alba* and *Cirsium vulgare*.

The altitudinal pattern found for alien species richness along the studied roadsides was opposite to the humped-back curves for the number of native and alien species observed in subtropical oceanic islands, as response to stressful conditions at both extremes of the altitudinal gradient (Arévalo *et al.* 2005). Our findings for exotic richness are not easily explained. Contrary to expectation, alien species did not show a turnover of chorological groups along the altitudinal gradient. Moreover, alien species of Euroasiatic affinity were associated with elevations below 1300 m a.s.l. These results, and the restricted presence of the aggressive invaders *Cotoneaster* sp., *Rubus ulmifolius* and *Gleditsia triacanthos* along roadsides, suggest that alien species have not had enough time to reach their potential altitudinal ranges in these habitats, probably because this highway is a relatively new corridor. However, the lack of climatic restrictions for alien species also indicates they are likely to expand current distributions reaching their maximum altitudinal ranges in mountain grasslands of central Argentina.

Role of roadside habitats in species richness and composition

Edges and fill slopes were characterized by rather different assemblages of alien and native plant species. Although edges were dominated by annual or perennial forbs, shrubs, sub-shrubs and perennial grasses were associated with fill slopes. Furthermore, edge habitats were more even and richer in native and alien species than fill slopes, suggesting that these montane plant communities are not saturated with species. Our results disagree with those obtained by Rentch *et al.* (2005) in roadside plant communities in the USA, where no differences in species richness, evenness or composition were found between different highway habitats.

Variations in habitat characteristics between edges and fill slopes (Fig. 1) may mean that these communities have different susceptibility to plant species colonization. Considering that most aliens in roadsides were ruderals, the higher species richness and the association of alien and native forbs with edge habitats with high resource availability (deep soils, high light, soil moisture and nutrients) support the hypothesis of resource enrichment (Davis *et al.* 2000). Conversely, rocky substrates, with scarce soil and steep fill slopes and more unstable hydric and thermal conditions, may restrict the establishment and growth of pioneer plants (Gelbard & Harrison 2003; Rentch *et al.* 2005), but favour the presence of stress-tolerant ones, such as some shrubs that can deepen their roots into the crevices and fissures avoiding the unstable conditions referred to above.

The significant association showed by the aggressive alien shrub *Cotoneaster* sp. with fill slopes may represent a risk for the native grasslands of the Córdoba mountains, because this bird-dispersed shrub is a prolific seed producer capable of forming monospecific thickets altering and displacing native plant communities (Zacharek 1990), and is already spreading on the low Córdoba hills (Tecco 2006).

Relationship between native and alien species richness

We found a negative association between native and alien species richness in fill slopes and no significant relationship in edge habitats, suggesting different mechanisms driving native and alien species richness in the different roadside habitats. Our results disagree with previous studies on roadside communities along altitudinal gradients, where no relationship (Pauchard & Alaback 2004) and a positive one (Arévalo *et al.* 2005) were observed between native and alien species richness.

These complex interactions between aliens and natives within habitats with different disturbance and stress regimes can be explained by hypotheses of plant invasion, as a consequence of fluctuating resources, habitat filtering, and biotic and abiotic resistance (reviewed by Catford *et al.* 2009).

The lack of correlation between native and alien species richness on roadsides edges suggests that plant species richness is not controlled by species interactions in these habitats. This could reflect a low biotic resistance as a result of the absence of dominant native competitors and higher availability of unused resources in this habitat.

Although our findings for the fill slopes agree with the expectations of the diversity-resistance hypothesis (Tilman 1997), we cannot attribute them to competitive interactions between native and alien species. Alternatively, the abiotic stress and the availability of safe sites on this type of habitat might in turn control the presence of a particular arrangement of well adapted native and alien species.

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Concluding remarks

Our findings indicate that species richness and composition of both native and alien flora change along the altitudinal gradient and between roadside habitats, with some species occurring only at altitudes below or above 1300 m a.s.l. and at edges or fill slopes. For the first time, an inverse mid-domain altitudinal effect was found for alien species richness. In addition, this is one of the few studies to have demonstrated that both species richness and composition differed between roadside habitats and the only one where a negative relationship between native and alien species richness was found in one of such habitats. These results highlight the importance of altitude and roadside habitat as factors controlling regionally and locally, respectively, the species richness and composition of roadside communities in central Argentina. Although altitude acts as a filter for native plants, it does not constrain the establishment of alien species along the studied roadsides.

Floristic changes along the roadsides differed from patterns found by previous studies in adjacent natural grasslands, supporting the idea that roadsides may be functioning as plant species corridors. The relatively low number of alien species and the newness of the highway allow us to speculate that roadsides in central Argentina mountains are in the early stages of alien naturalization, operating as a novel species corridor. The lack of climatic restrictions for exotic species indicates that the influence of National Route 20 as a plant species corridor may increase with time, and especially after the implementation of the 'Bi-oceanic Corridor' linking very different ecosystem types, promoting the opportunities for alien species to expand their current distribution. Consequently, roadsides should be considered targets for local and regional management efforts to prevent and control plant invasions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Species indicator values (IV) for two altitudinal levels (below 1300 and above 1400 m a.s.l.) in the Córdoba mountains, central Argentina.

Table S2. Species indicator values (IV) for two roadside habitats (edge and fill slope) along an altitudinal gradient in the Córdoba mountains, central Argentina.

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