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Original article

Patterns of woody plant invasion in an Argentinean coastal grassland

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A B S T R A C T

Coastal dune grasslands are fragile ecosystems that have historically been subjected to various types of uses and human activities. In Buenos Aires Province (Argentina), these areas are frequently afforested for urban and touristic development. The introduction and subsequent spread of exotic tree species is one of the main threats to conservation of natural grasslands as invasive trees strongly transform their structure and composition. The aim of this study was to identify patterns of woody plant invasion comparing plant communities and environmental variables between invaded and non-invaded areas surrounding the coastal village of Mar Azul, Argentina. Coastal grasslands in this area are being invaded by *Populus alba* (white poplar) and *Acacia longifolia* (coast wattle). The height of the saplings and the richness of the accompanying vegetation were evaluated in relation to the distance from the edge of the mature tree patches. Also, the cover, richness and diversity of all species in the invaded and non-invaded areas were measured, as well as soil pH, temperature and particle size. Negative correlations were found between the height of the saplings and distance to mature tree patches in all areas. The richness of the accompanying vegetation was negatively and positively correlated with the distance from the poplar and acacia area, respectively. The most abundant native species was *Cortaderia selloana*. Less cover, richness and diversity of native plant species and greater soil particle size were found in invaded areas, where the proportion of bare soil was higher. Also, a higher proportion of leaf litter in the invaded areas was registered. The results emphasize the invasive capacity of *P. alba* and *A. longifolia* advancing on the native communities and reducing their richness. Knowledge of the impact of invasive woody plants in coastal grasslands is important to design active management strategies for conservation purposes.

1. Introduction

Either intentionally or inadvertently, several species of different taxonomic and geographic origins have been relocated by man (Daehler, 2003), thus facilitating their dispersal across biogeographical barriers (D'Antonio and Vitousek, 1992; Vitousek et al., 1997; Figueroa et al., 2004). Once established in their new habitat, the exotic species can become widespread and modify the patterns of abundance and distribution of the native species (Figueroa et al., 2004). These invasive species may compete with native ones for space or food resources and affect ecosystems by altering (a) the resources available to other species, (b) the flow of energy or biomass across trophic levels, and/or (c) the natural disturbance regimes (Crooks, 2002).

Woody plant invasions are rapidly increasing in importance worldwide (see Richardson and Rejmánek, 2011 for a review). Transitions from grassland to woody systems can alter nitrogen dynamics (see Hellmann et al., 2011) and the balance of water and salt in the ecosystem (Jobbágy et al., 2008). Forests have higher transpiration capacity than grasslands because of their greater leaf surfaces, the roughness of the canopy and its deeper root systems. When higher transpiration occurs at the expense of consumption of groundwater, the establishment of trees on grasslands can cause salinization of soils and aquifers and jeopardize the sustainability of the forest system itself (Jobbágy et al., 2008). In such systems, most base cations are essential plant nutrients and play a key role balancing ecosystem acidity. Soil acidity in turn is a master control of soil fertility and affects many important biogeochemical processes, such as rock weathering and nitrification (Jobbágy and Jackson, 2003).

Natural grasslands are among the ecosystems that have been most disturbed by man (Hanna et al., 1995). The advance of exotic tree species as a result of invasion processes and direct plantation is one of the main threats to the conservation of natural grasslands

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and represents the introduction of a completely new life-form to the ecosystem (Richardson, 1998). Grasslands at the Argentinean Pampean plain have been subject of multiple transformations during the last two centuries, including exotic tree plantation and spread. Invasive trees have deeply transformed the structure and composition of native grasslands sometimes facilitating invasion by other exotic species (Zalba and Villamil, 2002). This process has reached a point where virtually all Pampean grasslands could no longer be restored naturally to their original state (Ghersa et al., 2002).

In Buenos Aires Province the last relicts of the Pampas's grasslands are restricted to habitats unsuitable for agriculture such as coastal dunes (Zalba and Villamil, 2002). Since the nineteenth century, these dune ecosystems have increasingly been subject of afforestation because of urbanization and coastal touristic development (Dadon, 2002). Afforestation has been carried out with the purposes of stabilizing dunes, reducing wind impacts, and increasing site attractiveness for tourists. Some of the most commonly used species for these purposes are *Acacia*, *Populus*, *Tamarix*, and *Pinus* and their dispersion now represents one of the main threats to dune conservation (Zalba and Villamil, 2002). Faggi and Dadon (2011) found that urbanization and touristic development are the main forces driving changes in plant composition along coastal dunes and beaches of Northern Argentina.

The objective of the present work was to evaluate patterns of dune grassland invasion by the woody exotic species *Populus alba* (white poplar) and *Acacia longifolia* (coast wattle), comparing plant communities and environmental variables in invaded and non-invaded areas.

2. Materials and methods

2.1. Study site and species

The study was conducted in a 5 km^2 coastal dune nearby Mar Azul village (37°20′S–57°02′W), Buenos Aires Province, Argentina (Fig. 1). The climate is humid temperate with a mean annual temperature of 14.0 °C. The average yearly precipitation is 930 mm mostly concentrated in winter (June to September). Soils are poorly developed and bear simple vegetal communities called "edaphic" since they are primarily controlled by soil, not climate (Cabrera, 1971).

The native plant community is a temperate grassland (Cabrera, 1971) now highly transformed (Vervoorst, 1967; Zalba and Villamil, 2002). There are stable populations of the invasive trees *P. alba* and *A. longifolia*, forming dense monospecific stands of large shrubs or small trees characteristic of an early stage of invasion. The distribution of poplar and coast wattle patches is quite heterogeneous. *P. alba* shows rapid growth and easy vegetative propagation by gemiferous roots. It also reproduces sexually but seedling survival and growth is highly dependent on soil moisture (González et al., 2010), which is low in sandy soils. *A. longifolia* is a leguminous N_2-fixing shrub that reaches up to 8 m height (Hellmann et al., 2011). It impacts hydrological and carbon cycling even in water-limited semi-arid ecosystems (Racher et al., 2011b) and has important effects on the catabolic diversity of soil microbial communities, which may have wider implications for nutrient cycling and ecosystem-level processes as well as the subsequently invasibility of the system (Marchante et al., 2008a). Acacias are often used to stabilize coastal dunes in different countries, subsequently spreading and invading considerable areas (Marchante et al., 2003; Fernández et al., 2006; Hellmann et al., 2011). *Populus* and *Acacia* are widespread woody invaders (five and thirty two invasive species respectively; Richardson and Rejmánek, 2011).

2.2. Plant surveys

Sampling was performed from spring 2009 to summer 2010. The study area was sub-divided into 4 strata: a) Mall: invaded by *P. alba*; b) Acacialaan: invaded by *Acacia longifolia*; c) Mixed: invaded by *P. alba* and *A. longifolia* and, d) Grassland: non-invaded grassland subdivided in 3 sub-strata; grassland adjacent to the Mall, the Acacialaan and the Mixed strata. Ten transects of variable length were located in each invaded area from the outer edge of the mature tree patches up to the last sapling or the presence of fences and paths. In the Grassland, thirty transects were distributed randomly, ten in each sub-stratum. Their length varied between 40 and 60 m, depending on the presence of paths. Sampling quadrats

Fig. 1. Study site, Mar Azul, Buenos Aires Province, Argentina.

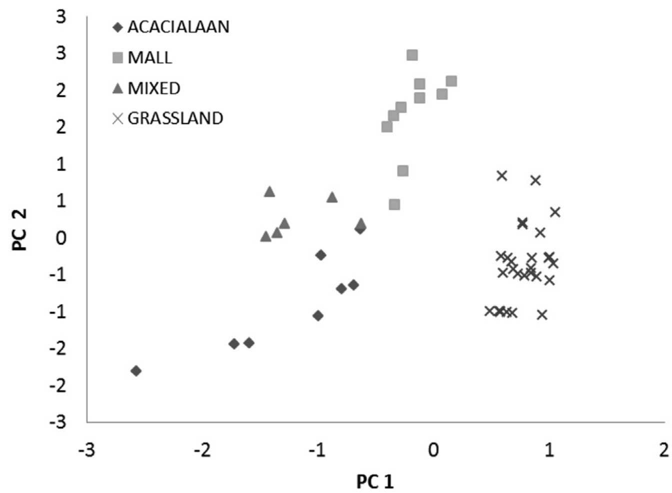

Fig. 2. Relationship between the first and second component of PCA analysis using a correlation matrix.

($4\ m^2$) (Klimeš, 2003) were placed every 2 m along the transects. In every quadrat, all plant species were identified at least to the genus level and their percent coverage estimated. Species richness and diversity (Shannon Weaver Index) were calculated for every quadrat (poplar and acacia were not included in the calculation). The cover of leaf litter and the percentage of bare soil (with no vegetation nor litter cover) were also estimated. In invaded areas, the height of the saplings and the richness of the accompanying vegetation related to the distance from the edge of the mature forest were registered. The density of *P. alba* in the Mall site was also recorded. Due to the bushy growth of *A. longifolia* and its great variability in sizes, only its coverage was registered.

2.3. Soil properties

Soil temperature at a depth of 10 cm was measured in each transect with a soil thermometer. Soil pH was measured using an Orion Research digital pHmeter 501 as follows: six samples were collected in each invaded stratum and six samples in each grassland sub-stratum (3 from the dune crest and 3 from the base of the dunes) with a cylindrical core (10 cm height and 12 cm diameter). Two measurements were taken from each sample: (a) in the soil paste saturated with distilled water (relation soil:water, 1:1) and, (b) in solution (relation soil:water, 1:2.5). Soil particle size was evaluated in the same samples used for pH determinations (mesh sizes: 1000, 500, 250 and 125 μm) and particle sizes were classified as coarse, medium, half-fine, fine and very fine sand.

2.4. Statistical analysis

R-commander free statistical software (R Core Team, 2012) was used in all analyses. Principal component analysis (PCA) was used to sort the measured variables (native and exotic species coverage and richness, coverage of *P. alba* and *A. longifolia*, leaf litter, bare soil and diversity) according to their importance. The variables were transformed to natural logarithm and PCA was performed using a correlation matrix. Pearson correlations were used to evaluate (a) the relationship between sapling height and distance from the edge of mature tree patches both in areas invaded by white poplar and coast wattle; and (b) the relationship between species richness and distance from the edge of mature tree patches at each stratum. Factorial ANOVA and Tukey tests were used to compare coverage, richness, diversity of accompanying vegetation, and soil variables between invaded and non-invaded environments. *T* test was used to analyze the most abundant species and soil particle size between invaded and non invaded areas.

Table 1
Factor-variable correlations of variables used in PCA analysis.

	PC 1	PC 2	PC 3
Native cover	0.90	−0.31	−0.12
Exotic cover	0.19	0.66	0.61
Exotic richness	0.39	0.70	0.44
Native richness	0.85	−0.06	0.03
Acacia cover	−0.80	−0.36	0.37
Poplar cover	−0.27	0.82	−0.24
Leaf litter	−0.74	−0.33	0.46
Bare soil	−0.52	0.64	−0.39
Diversity	0.822	−0.03	0.19

3. Results

The PCA analysis showed that the first three components accounted for 84.1% of the total variation in the data. The first component (PC1) explained 44.28% of the variance and was primarily related to cover and richness of native species, *Acacia* cover, leaf litter cover and diversity. The second component explained 26.36% of the variance and was primarily related to poplar cover, cover and richness of exotic species, and bare soil cover. PC1 was positively correlated with native plant cover as well as native species richness and diversity; and negatively correlated with *A. longifolia* and leaf litter coverage. PC2 was positively associated with the richness and cover of exotic species as well as *P. alba* and bare soil cover. The samples from the natural grassland are clearly separated from those of the three invaded areas along PC1 axis (Fig. 2; Table 1). The PC2 axis shows a relatively clear separation between samples of the Mall and the Acacialaan. Samples of the Mall stratum are displaced towards the positive extreme of PC2, and, thus, associated with higher values of richness and cover of exotic species. Acacialaan samples are associated with lower values of richness and cover of exotic species.

The maximum distance from the mature tree patches was 38.47 m for *P. alba* saplings (observed at the Mixed area) and 26.35 m for *A. longifolia* saplings (recorded at the Acacialaan).

Sapling height was negatively correlated with the distance to mature forest edge in the case of *P. alba* at the Mall and the Mixed sites. The height of *A. longifolia* saplings at the Acacialaan and the Mixed sites was not correlated with the distance from the mature forest (Fig. 3).

The total richness of accompanying species was negatively correlated with the distance from the mature tree patches at the Mall site ($n = 84$; $R = -0.31$; $t = -2.93$; $p < 0.05$). In contrast, the total richness of accompanying species at the Acacialaan and Mixed sites was positively correlated with the distance from the edge of the mature forest (Acacialaan: $n = 44$; $R = 0.52$; $t = 4.02$; $p < 0.05$; Mixed: $n = 44$; $R = 0.59$; $t = 4.80$; $p < 0.05$). Furthermore, the density of poplar saplings in the Mall stratum was negatively correlated with the distance from the edge of mature forest ($n = 124$; $R = -0.75$; $t = -12.06$; $p < 0.05$). This density varied from 1 to 21 individuals/m^2.

Native vegetation coverage of Acacialaan and Mixed strata differed significantly between invaded and non-invaded areas. The higher native species richness was registered in non-invaded areas (Table 2 and Table 3).

Thirty one species were registered in the whole study area, belonging to the following families: Apiaceae, Apocynaceae, Asteraceae, Cyperaceae, Fabaceae, Juncaceae, Onagraceae, Poaceae,

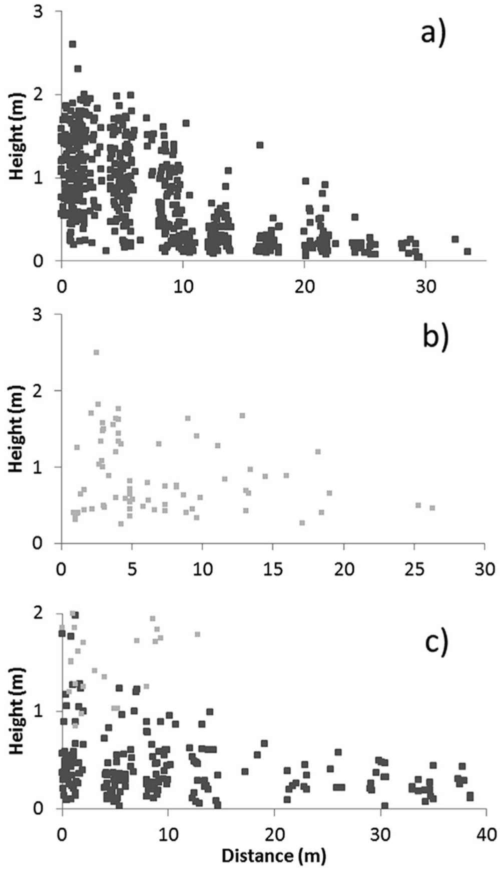

Fig. 3. Relationship between sapling height and distance from the mature tree patches. a) Mall area ($n = 603$; $R = -0.62$; $t = -19.62$; $p < 0.05$); b) Acacialaan area ($n = 77$; $R = -0.17$; $t = -1.57$; $p = 0.11$); c) Mixed area (*P. alba* (black squares): $n = 211$; $R = -0.36$; $t = -4.07$; $p < 0.05$; *A. longifolia* (grey squares): $n = 25$; $R = 0.21$; $t = 1.01$; $p = 0.31$). Pearson correlation ($\alpha = 0.05$).

Polygalaceae, Verbenaceae (Annex I). The percent cover of native and exotic species differed between invaded and non-invaded areas (Table 4), with higher cover of exotic species and lower cover of native ones at the invaded areas.

Diversity was always greater in grasslands relative to invaded areas (Table 5 and Fig. 4). Also some native and exotic species were only found in one stratum, although with low cover values. For example, the natives *Adesmia incana*, *Cyperus* sp. and *Conyza blakei* were only found in the grassland associated to the Mall stratum; *Baccharis notosergila* was only found in the grassland associated with the Acacialaan; and *Androtrichum triynum*, *Baccharis salicifolia* and *Polygala cyparissias* were only found in the grassland associated with the Mixed stratum.

The highest cover of leaf litter was registered in the Acacialaan (51.7% ± 2.03) while the highest percentage of bare soil was recorded in the Mixed (47.44% ± 2.03) and the Mall (29.41% ± 1.5) strata.

With regard to particle size, finer grain sizes were observed in non-invaded areas and coarser grain sizes in the invaded ones (Fig. 5).

Temperature values differed between native and invaded areas (initial temperature: 2.36 °C ± 0.41 – final temperature: 2.41 °C ± 0.42; initial temperature: 2.61 °C ± 0.38 – final temperature: 2.65 °C ± 0.36, respectively). Mean of pH values were almost one pH unit higher in Grassland than in the invaded areas (paste pH: 6.93 and 7.32; saturated pH: 6.92 and 7.58 respectively), but differences were not significant (Table 6).

Table 2
Results from two-way ANOVAs evaluating percent cover and richness of total native and exotic species in invaded and non-invaded areas (*P. alba* and *A. longifolia* not included).

	Natives				Exotics		
Source of variation	MS	*df*	*F*	*p*	MS	*F*	*p*
a. Cover							
Area	15.61	1	428.06	0.00	0.00	0.01	0.90
Stratum	1.10	2	30.12	0.00	0.05	3.57	0.02
Area × Stratum	5.78	2	157.66	0.00	0.33	21.23	0.00
Error	0.03	433			0.01		
b. Richness							
Area	532.52	1	241.61	0.00	0.02	0.07	0.78
Stratum	3.16	2	1.43	0.23	1.82	6.56	0.00
Area × Stratum	12.13	2	5.50	0.00	8.31	30.13	0.00
Error	2.2	434			0.27		

4. Discussion

P. alba and *A. longifolia* have deeply transformed the native grassland in the studied area. These invaders reduced total and native species coverage, richness and diversity. Clavijo et al. (2005) evaluated the effect of poplar planting on the structure, composition and diversity of native grasslands in the Flooding Pampas of Argentina. They found 42% lower plant cover, increased cover of exotic species and lower diversity under poplars. Costello et al. (2000) found a decrease in plant richness and diversity in Australian coastal grasslands invaded by *Acacia sophorae*. Rascher et al. (2011a) observed up to 50% reductions in species richness and diversity in Portuguese coastal dunes invaded by *A. longifolia*, and Hellmann et al. (2011) found that areas invaded by *A. longifolia* showed decreased plant biodiversity and severely altered soil properties.

The lower diversity found in invaded areas could be due to an interaction between height and coverage of the invaders, given that the impact of invasive species is often associated with their degree of dominance and space monopolization (Hejda et al., 2009). On the other hand, the high species diversity found in the different grasslands and the finding of certain species in one stratum and not in another could be associated with rates of species extinction and re-colonization (Yurkonis et al., 2005). The occurrence of different plant species in various strata contributes to the stability and resilience of the sand dune vegetation. The lower coverage of native species recorded in invaded areas could be due to the usually higher competitive ability of invasive species (Werner et al., 2010) and their phenotypic plasticity (Daehler, 2003). In addition, *A. longifolia* may be disrupting native flower visitation and fertilization by pollinators because of its massive flowering (Dietzsch et al., 2011).

The higher coverage of exotic species in the Mall respect to its adjacent Grassland could be because poplars are winter deciduous trees. This could favor cold-season species in the understory (Clavijo et al., 2005). Among all studied strata, the Mall seems to be the most suitable for exotic naturalized species such as *Dactylis glomerata* and *Melilotus albus*. This highlights the risk of introducing woody species in grassland relict areas, because even without causing an impact in itself, they could favor the arrival of alien plants that can also become invaders (Zalba and Villamil, 2002).

The height of invasive tree saplings is often related to the degree of progress of the invasion (Sarasola et al., 2006; Langdon et al., 2010). In the present study a negative relationship was found between the distance from the edge of mature tree patches and the height of the poplar saplings, which suggests that distal trees are

Table 3
Percent cover and richness of native and exotic species in invaded and non-invaded areas (*P. alba* and *A. longifolia* not included).[a]

		Natives		Exotics	
		Cv (%) ± sd	TR ± sd	Cv (%) ± sd	TR ± sd
Invaded areas	Mall	47.56 ± 27.27 b	2.77 ± 0.22 b	11.75 ± 15.79 a	0.27 ± 0.08 d
	Acacialaan	35.11 ± 22.30 b	2.64 ± 0.16 b	5.45 ± 10.50 ab	0.70 ± 0.16 a
	Mixed	21.96 ± 15.25 cb	2.33 ± 0.22 b	0.31 ± 1.60 b	0.04 ± 0.08 e
Non invaded areas	Mall	41.99 ± 11.62 b	4.51 ± 0.15 a	1.13 ± 4.88 b	0.15 ± 0.05 c
	Acacialaan	89.91 ± 18.02 a	4.85 ± 0.16 a	10.09 ± 18.02 a	0.47 ± 0.06 b
	Mixed	93.26 ± 11.55 a	5.34 ± 0.16 a	6.74 ± 11.55 a	0.36 ± 0.16 b

[a] Cv = cover vegetation, TR = total richness (species number), sd = standard deviation. Different letters indicate significant differences (Tukey test, $df = 133$; $p < 0.05$).

the younger ones. However, such a correlation was not found in the Acacialaan. This is probably due to the type of reproduction and seed dispersal of *Acacia* species, where seeds can fall to the ground, settle and develop in the vicinity of the adult, or be dispersed by animals or wind. This generates a patchy distribution of tree sizes throughout the environment. *A. longifolia* also produces a large number of seeds, which can remain viable in the ground for at least six years thereby providing a recruitment pool even if existing populations are cleared (Marchante et al., 2010).

Significant correlation between sapling height and distance from the mature tree patches in the Mall area could be due to the clonal expansion of *P. alba* via its gemiferous roots. Poplars also produce large amounts of wind- and water-dispersed, non-dormant, and short-lived tiny seeds that need bare, open, moist substrates to germinate and establish. In these sandy soils, however, drainage conditions are not compatible with *P. alba* seed germination or seedling establishment. The absence of fine soil particles prevents capillar movement and retention of water resulting in widespread seed mortality (González et al., 2010).

The negative relationship between the species richness and the distance to the edge of mature tree patches observed at the Mall may be due to an interaction between decreasing density of poplar saplings with increasing distance from the mature trees and increased grazing by horses and cows as poplar density decreases. Milton and Dean (2010) found that high densities of saplings limit the access of cattle and man to forest patches. Increased grazing due to low density of poplar seedlings might be leading to decreased plant species richness as distance from the mature trees increases. In the Acacialaan and Mixed strata there was high plant species richness far from the edge of the mature tree patches and no domestic animals were observed. So, the intensity of the invasion would be lower as distance from the mature trees increases and the accompanying plant species richness is higher (Yurkonis et al., 2005).

The coverage of leaf litter in the invaded areas was higher compared to non-invaded ones, being highest at the Acacialaan. Low coverage of native vegetation in tree-invaded areas is often associated with high coverage of leaf litter or bare soil (e.g. Clavijo et al., 2005). This could be caused by a combination of factors such as reduced incident light due to high coverage of invasive species (Iponga et al., 2010), or to the reduced water availability. For instance, *A. longifolia* and native species differ markedly in their functional traits and water use strategies. Native species typically have traits such as strong stomatal control, sclerophyllous leaves and/or seasonal changes in root/shoot ratio to minimize water loss and survive during drought periods. *A. longifolia*, in contrast, is a water spender, a feature that may promote its invasiveness by reducing the water available to native species even in water-limited environments (Rascher et al., 2011b). In addition, high leaf litter production and coverage may be preventing the growth of other plants, though this may not be the case with poplar afforestation (see Clavijo et al., 2005).

Plant invasions often strongly alter soil stability and sediment accumulation (Milton and Dean, 2010). Here we found that sand grains in invaded areas were coarser than in non-invaded ones, particularly in the Mall and Mixed strata. This is probably due to the higher proportion of bare soil found in the invaded areas. High proportions of bare soil are associated with low vegetation cover and, thus, high exposure to wind, which is expected to increase the transport of fine material in invaded areas. On the other hand, Milton and Dean (2010) showed that species like *Acacia karoo* have potential to hold soil and act as windbreaks in some circumstances. This could explain observed differences in bare soil cover and soil particle size between the Acacialaan and the Mall and Mixed strata.

The lack of significant differences in soil pH values between invaded and non-invaded dune areas is in agreement with the results obtained by other authors (Marchante et al., 2008a; Marchante et al., 2008b; Boyes et al., 2009; Ruiz Navarro et al., 2009: Hellmann et al., 2011). This includes the study of Boyes et al. (2009), who collected soil samples at different depths in

Table 4
Mean percent cover (±sd) of the most abundant species found at different strata.

	Mean ± SD	Mean ± SD			
Native	Mall	Grassland	*t*	*df*	*P*
Baccharis salicifolia	1.34 ± 6.86	8.86 ± 16.92a	−4.53	226	<0.01
Cortaderia selloana	18.06 ± 3.42	27.18 ± 3.41a	−2.13	226	0.03
Exotic					
Melilotus albus	3.08 ± 13.84	0.17 ± 1.27	2,12	225	0.03
Native	Acacialaan	Grassland			
Androtrichum tryginum	1.73 ± 3.81	7.85 ± 11.06[a]	−3.54	122	<0.01
Baccharis salicifolia	2.27 ± 7.11	6.35 ± 10.50[a]	−2.30	122	0.02
Cortaderia selloana	3.43 ± 10.37	18.32 ± 24.16[a]	−3.88	122	<0.01
Hydrocotyle bonariensis	2.91 ± 4.30	10.78 ± 7.93[a]	−6.10	122	<0.01
Solidago chilensis	2.23 ± 4.80	11.02 ± 13.97[a]	−4.04	122	<0.01
Bothriochloa laguroides	9.23 ± 7.79	3.45 ± 3.67[a]	3.85	122	<0.01
Exotic					
Dactylis glomerata	2.57 ± 7.08	0.29 ± 1.75[a]	2.72	122	<0.01
Melilotus albus	1.61 ± 4.46	7.74 ± 16.53[a]	−2.41	122	0.01
Native	Mixed	Grassland			
Adesmia incana	2.43 ± 5.60	0.49 ± 2.23[a]	2.86	132	<0.01
Bothriochloa laguroides	11.07 ± 7.51	5.61 ± 10.88[a]	2.99	132	<0.01
Hydrocotyle bonariensis	3.13 ± 3.66	11.41 ± 10.69[a]	−4.98	132	<0.01
Solidago chilensis	1.23 ± 3.75	8.27 ± 10.65[a]	−4.24	132	<0.01

[a] Shows differences between areas (t test, $\alpha = 0.05$).

Table 5
Results from two-way ANOVAs evaluating diversity of species in the Mall, Acacialaan and Mixed strata and their associated grassland.

Source of variation	MS	*df*	*F*	*p*
Area	17.51	1	104.19	0.00
Stratum	0.02	2	0.12	0.88
Area × Stratum	2.50	2	14.87	0.00
Error	0.16	430		

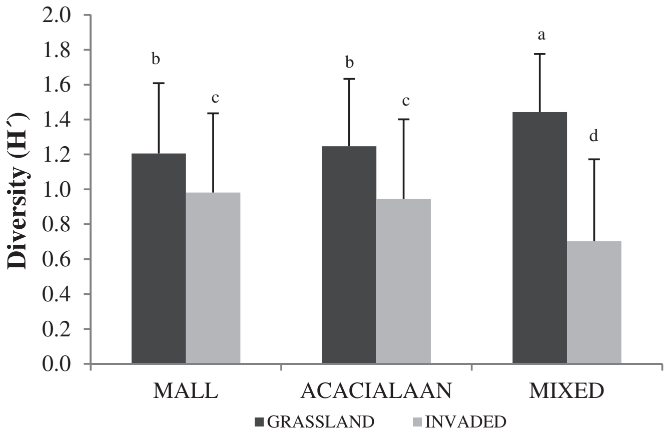

Fig. 4. Diversity of species (±sd) in the Mall ($n = 86$), Acacialaan ($n = 44$) and Mixed ($n = 44$) strata and their associated grassland (grassland adjacent to Mall: $n = 91$, grassland adjacent to Acacialaan: $n = 85$, grassland adjacent to Mixed: $n = 85$. Different letters showed significant differences (Tukey test, $df = 405$; $p < 0.05$).

sand dune areas invaded and non-invaded by *Acacia karoo*. However, differences in the availability of soil nutrients are likely (Boyes et al., 2009). Besides, although no statistical differences were found, one point in the pH scale might mean an increase or decrease in soil acidification by changing its chemical properties and thus altering the substrate for the normal development of the native flora. *Acacia* spp. have been shown to substantially alter soil nitrogen properties with long-lasting effects on soil N cycling (Hellmann et al., 2011) and soil microbial communities (Marchante et al., 2008a,b; Rodríguez Echeverría et al., 2009; Inderjit and van der Putten, 2010; Hellmann et al., 2011) even after stands of the invader have been cleared. This plant species increases its aboveground biomass in low nitrogen soils due to heavy nodulation resulting in symbiotic nitrogen fixation (Rodríguez Echeverría et al., 2009). Legumes can increase soil fertility through the decomposition of nitrogen-rich litter and the release of nitrogen from roots and nodules. Indeed, nitrogen enrichment is one of the mechanisms by which exotic legumes transform native communities (Rodríguez Echeverría et al., 2009) and have important implications on the long-term success of alien invader eradication (Marchante et al., 2008b) and the subsequent restoration of the indigenous flora at these sites.

The impact of invasive plants on plant communities can be complex, including changes in the interactions among species (such as competition and facilitation; Yang et al., 2009) as well as hydrology and soil stability (Milton and Dean, 2010). Woody invasive plants in the same sand dune areas are also affecting animal

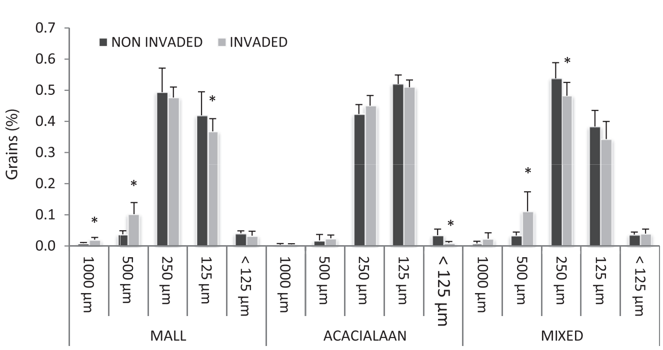

Fig. 5. Percentage of soil grain sizes in the four strata. Asterisks show significant differences between invaded and non-invaded areas (Tukey test, F (intercept coarse sand) = 62.64; F (intercept medium sand) = 103.89; F (half fine sand) = 3679.76, F (fine sand) = 2637.99, F (very fine sand) = 241.54; $df = 1$; $p < 0.01$).

Table 6
Results from two-way ANOVAs evaluating mean of initial/final temperature and mean of pH values between non invaded and the three invaded areas (Acacialaan, Mall and Mixed).

Source of variation	Initial temperature				Final temperature		
	MS	*df*	*F*	*p*	MS	*F*	*p*
a. Temperature							
Area	0.69	1	4.36	0.04	0.67	4.22	0.04
Stratum	0.12	2	0.75	0.47	0.09	0.58	0.56
Area × stratum	0.09	2	0.57	0.56	0.08	0.54	0.58
Error	0.15	48			0.16		
b. pH	Soil paste				Solution		
Area	0.12	1	0.46	0.50	0.03	0.27	0.60
Stratum	0.04	2	0.17	0.83	0.11	0.87	0.44
Area × stratum	0.31	2	1.15	0.34	0.12	0.93	0.41
Error	0.27	12			0.13		

communities by transforming habitats (Faggi et al., 2010; Alberio et al., 2011). Tree felling and livestock grazing could further enhance establishment of exotic species by creating disturbed sites (Sakai et al., 2001).

Based on the classification of Richardson et al. (2000), while *Populus* can be defined as an Invasive plant, *Acacia* would be a Transformer, which is an Invasive plant that changes the character, condition, form or nature of the ecosystem causing a more damaging invasion. Furthermore, Lamarque et al. (2011) concluded in their review that multiple factors simultaneously lead to the success of invasive tree species.

The problem of biological invasions requires an active management strategy including the prevention of new invasions and control or eradication of existing ones (Zalba and Villamil, 2002). It has been shown that after removal of a N_2-fixing invasive tree, it takes several years before soil nutrients and processes return to pre-invasion levels (Marchante et al., 2009). A thorough understanding of the factors driving the invasion and the changes in the biotic and abiotic components of the ecosystem can be used to direct control and restoration efforts (Le Maitre et al., 2011). Grassland relicts in Pampean coastal dunes are far from being protected from human influences. New important afforestation projects are underway due to urban and touristic development. If this continues the ecosystem will suffer profound changes that would be very difficult to revert. Controlling invasive alien plants is generally very costly and requires sustained investment over long periods of time, particularly when dealing with species that have very large and long-lived seed banks, like many acacias. Therefore, invaded areas should be managed before further ecosystem level changes take place (Marchante et al., 2009). Authorities need to implement policies, legislation and incentives in place to guide public and private investment in controlling invasive alien plant species and combine this with active or passive restoration as long as required (Le Maitre et al., 2011).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2013.09.003.

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