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Guests and gatecrashers in a New World's banquet: Old World plant species introduced from the Mediterranean Basin enriched the flora of grasslands and croplands in the Pampas of Argentina

Abstract

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Exchange of domesticated plants between Europe and the Americas has been a paramount episode of World History, which transformed agriculture and food habits at both sides of the Atlantic Ocean. However, many plant species have been inadvertently introduced mostly as contaminants of crop seeds, causing important changes in the flora. Here, we present a brief description of the floristic enrichment of the Pampa grasslands of Argentina due to the naturalisation of plant species from the Mediterranean Basin. Since the European colonisation in the 16th century, Old World plant species have been continuously introduced, intentionally or not, in the Pampas, especially during the expansion of agriculture in the late 19th century. Four botanical families comprised the highest numbers of species (*Asteraceae, Poaceae, Fabaceae,* and *Brassicaceae*), which have been recognised for having the largest contribution to the total number of alien species in local floras. Some families were only present in the Pampas by Mediterranean species occurring as weeds in croplands. The flora of the Pampas was also enriched with life-forms that were poorly represented in the pristine grasslands, such as species from *Fabaceae* and short-lived species vegetating during the cool season. Finally, seed trade from South America to Europa provided a vector for the dispersion of Neotropical and Pampean species naturalised in Mediterranean ecosystems. While the long term impact of alien naturalization in the evolutionary history of life-forms in the Pampas and the Mediterranean basin is difficult to elucidate, some naturalised Mediterranean plants are involved in providing ecosystem services in the intensively managed croplands in the Pampas or are seen as a threat to native flora.

Key words: aliens, arable weeds, biodiversity, invasions, non-natives, phytosociology, naturalisation.

Introduction

The development of Western agriculture and trade has been fostered historically by the exchange of domesticated plants between Europe and the Americas (Crosby 2003). This historical process, termed as the Columbian Exchange, has been a paramount episode of

World History that had important ecological and socioeconomic impacts at both sides of the Atlantic Ocean, especially concerning both agriculture and culinary traditions in the Western hemisphere. For instance, wheat, barley and flax were introduced in the Americas by the Spanish conquistadors, who also brought potatoes, maize and tomatoes to Europe. Moreover, plants native to Europe are recognised as highly invasive species worldwide for reason that are both historical and ecological (Pyšek 1998). Thus, propagules of many weedy and invasive plant species were also inadvertently transported by humans, for instance, as contaminants of crop seeds (Pyšek 1998; Mack & al. 2000). Some of these non-invited plants became weeds, whereas others invaded natural and disturbed habitats currently being more widespread than in their origin regions.

Pristine grasslands in the Rolling Pampa, the Pampa's region with the longest history of continuous cropping, have been almost entirely converted into intensively managed croplands. Grasslands were ploughed to sow annual crops (wheat, flax, and maize) and pastures (alfalfa, fescue, and ryegrass). Mediterranean species have been therefore introduced into the Pampas, intentionally or not, since the European colonisation in the 16th century. Many species have naturalised to the recipient environments, while some species become common as weedy plants in grasslands and croplands (Azara 1809; Darwin 1845; Hauman 1927; Söyrinki 1991). Thus, landscape transformation by human activities promoted the introduction and naturalisation of many exotic plant species, which nowadays constitute the major component of the weed flora (de la Fuente & al. 1999; Ghersa & León 1999; Poggio & al. 2004, 2010a). On the contrary, there are large areas still occupied by semi-natural grasslands in the Flooding Pampa, as soil quality and the recurrence of floods has limited land use to extensive rangeland grazing and prevented it from being replaced by crops. The long history of livestock grazing after European colonisation has promoted the introduction of exotic species, mainly those favoured by grazing: 74% of exotic species are annuals, 75% are forbs, while 85% of native species are perennials, and 79% of the grasses are native perennials (Perelman & al. 2001, 2007). Agriculture is restricted to well-drained soils which cover less than 20% of the area in the Flooding Pampa, while croplands occupy nearly the 60% of the area in the Rolling Pampa (Baldi & al. 2006).

Our aim is to develop a brief portrayal of the floristic enrichment of the Pampa grasslands of Argentina due to the introduction and naturalisation of plant species from the Mediterranean Basin. We first present a physiographic description and an historical account of both landscape transformations and land use changes in the Pampas of Argentina. We then describe the main floristic changes observed in Pampa grasslands and in the flora of both rangelands and croplands. We will focus our study on the Flooding and the Rolling Pampas. As aforementioned, the former region is covered by semi-natural grasslands mostly devoted to extensive cattle grazing, because soil quality and periodic flooding restrict farming to the scarce well-drained areas (León & al. 1984; Soriano & al. 1991), while intensively managed croplands predominate in the latter region (Hall & al. 1992). We highlight here that many Old Word plants, which are nowadays adventive in the Pampas, represents novel life-forms that were previously absent in the pristine grasslands. Interestingly, some naturalised plants are currently involved in sustaining ecosystem services in Pampean agro-ecosystems, such as thistles providing resources to flower visiting insects (Torretta & Poggio 2013).

The Pampas

The Pampas are a large grassland region in the central-eastern part of Argentina, in the southern cone of South America (Fig. 1). This region is a vast plain that spreads from the sea level, on its eastern limit with the Río de la Plata and the Atlantic Ocean, to up to c. 1200 m a.s.l. in the low sierras on the southwest. The northern limit is set by a xerophytic forest known as 'espinal', whereas the region is bounded westward by a shrub land named 'monte' (Cabrera 1976). Pristine vegetation corresponded to mesic tussock grasslands dominated by a rich mixture of C3 and C4 grass species (Parodi, 1930, 1947; Ghersa & León 1999; Burkart & al. 2011).

Climate and soils - Climate is temperate sub-humid in the northeast to dry sub-humid in the west and southwest. Winters are mild, whereas summers are warm and slightly dry (Burgos & Vidal 1951). Mean annual rainfall ranges from 1100 mm in the northeast to 600 mm in the south-west (Soriano & al. 1991). Temperature varies between the mean annual isotherms of 17ºC to the north and the 14ºC and 15ºC to the south (Soriano & al. 1991). Rainfall is relatively well distributed among seasons and incipient water deficit may occur during summers, though significant inter-annual variations are not uncommon (Hall & al. 1992). Snowfall is a rare event and frosts are not severe, frost-free period ranges between 180 and 260 days (Burgos & Vidal 1951). Soils are mainly Mollisols, characterised by their top horizon rich in organic matter, fertile and porous that determines the outstanding aptitude for agriculture (Soriano & al. 1991). Topography in the Rolling Pampas is gently undulated and crossed by shallow streams (Soriano & al. 1991). Conversely, the Flooding

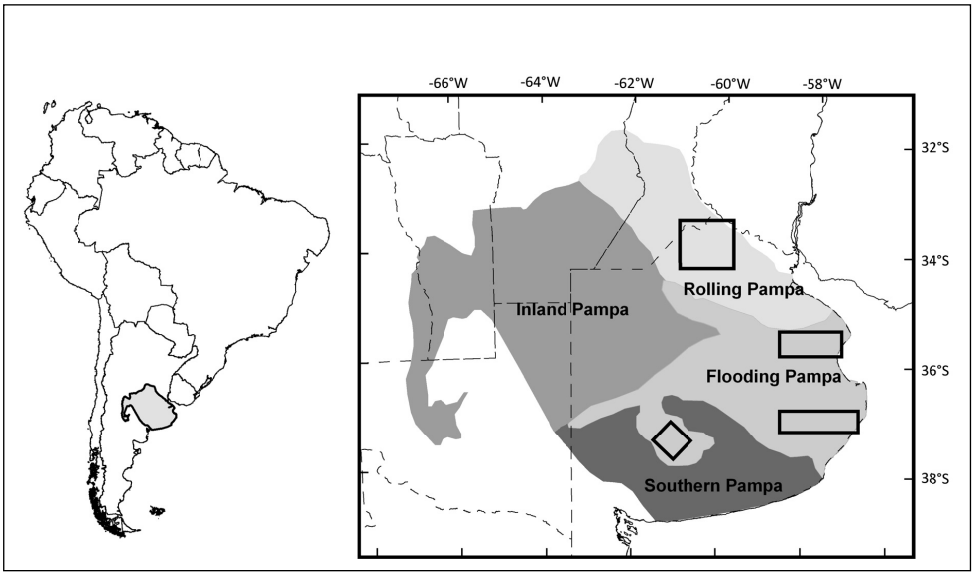

Fig. 1. The Pampas of Argentina with its four sub-regions. Squares indicates the study areas where phytosociological surveys in grasslands in the Flooding Pampa and in croplands in the Rolling Pampa were carried out.

Pampa, which was formed during an arid paleoclimatic period, has a minimal overall slope that has prevented the development of a hydrologic network in balance with their present humid conditions. Thus, groundwater remains near the soil surface for long periods in winter and spring (Paruelo & Sala 1990).

Historical land use changes - The Pampas of Argentina, thanks to their favourable climate and fertile soils, have become one of the most extensive and productive areas of agricultural commodities in the world. Extensive treeless grasslands and open, flat horizons characterised the Pampas when Spanish conquistadors arrived in the 16th century. European settlers introduced large domestic ungulates, such as cows and horses, which escaped, became feral and form large herds, because there were neither native ungulates in the Pampas as large as cows and horses nor large carnivores that could regulate their growing populations. South American megafauna, including ungulates and carnivores, became extinct in the Pampas during the Pleistocene (Soriano & al. 1991; Ortíz Jaureguizar & al. 1995). Early European towns and dwellings have been mainly concentrated in the Rolling Pampa, on a 200 km strip along the southern bank of the Río de la Plata. Rural populations considerably increased due to European immigration and the agricultural frontier was extended hundreds of kilometres to the west since late 1870's (Scobie 1964). Agriculture then rapidly expanded between 1880 and 1914. Grassland habitats were ploughed to sow row-crops, especially wheat. Landscapes were fragmented by intricate networks of railways and roads, which promoted the settlement of many towns and villages along them. Seeds from field crops and forage species were introduced during that period, mainly in alfalfa seeds imported from Western Europe (Poggio & al. 2010b). After several intervals of expansion and stagnation during the 20th century, agriculture has been increasingly intensified since the early 1970's, which was accelerated after the widespread inceptions of no-tillage and herbicide-tolerant, genetically modified soybean varieties during the 1990's.

Mediterranean plants enriched the flora diversity of grasslands and croplands in the Pampas

We listed a total of 94 Old World species originated from the Mediterranean basin (Table 1), after compiling phytosociological surveys in mesophytic grasslands in the Flooding Pampa (Perelman & al. 2001), and in croplands in the Rolling Pampa (de la Fuente & al. 1999; Poggio & al. 2004; R. J. C. León unpublished). Although both hydrophytic and halophytic grasslands cover larger areas than mesophytic grasslands in the Flooding Pampas, we focused on the latter grassland type because occur in depth, well-drained soils that are similar to cropland habitats in the Rolling Pampa. Seventy Mediterranean species were surveyed in mesophytic grasslands in the Flooding Pampa, which represents the 26.2% of the regional species richness (a total of 267 taxa including natives). Mesophytic grasslands are suitable for annual cropping because they are placed in positive topographic positions and well drained soils (Ghersa & al. 2007). Old World arable weeds surveyed in field crops in the Rolling Pampa totalised 50 taxa, which were 44.6% of the weed flora surveyed in this region (a total of 112 taxa including natives).

Seventeen botanical families were listed. *Asteraceae* (24 taxa) and *Poaceae* (20) comprised the highest numbers of species, followed by *Fabaceae* (14) and *Brassicaceae* (6)

Table 1. Latin binomial names and botanical families of species surveyed in grasslands and croplands in the Pampas. Species are classified according to their life-forms and growing seasons. Nomenclature follows Zuloaga & al. (2008). Values of constancy are grouped in classes[1].

				Grasslands[2]	Croplands	
					Cool-season[3]	Warm-season[4]
		Number of samples		202	74	102
Latin name	**Family**	**Life-form**	**Season**			
Lolium multiflorum Lam.	*Poaceae*	Annual grass	Cool	IV[1]	III	I
Medicago polymorpha L. var. *polymorpha*	*Fabaceae*	Annual forb	Cool	III	I	I
Ammi majus L.	*Apiaceae*	Annual forb	Cool	IV	I	I
Trifolium repens L.	*Fabaceae*	Perennial forb	Cool	I	II	I
Cynodon dactylon (L.) Pers. var. *dactylon*	*Poaceae*	Perennial grass	Warm	II	II	II
Taraxacum officinale G. Weber ex F.H. Wigg.	*Asteraceae*	Perennial forb	Cool	II	II	I
Capsella bursa-pastoris (L.) Medik.	*Brassicaceae*	Annual/Biennial forb	Cool	III	I	I
Anagallis arvensis L.	*Primulaceae*	Annual forb	Cool	I	I	I
Medicago sativa L.	*Fabaceae*	Perennial forb	Warm	I	I	I
Ammi visnaga (L.) Lam.	*Apiaceae*	Annual/Biennial forb	Cool		I	I
Brassica rapa L.	*Brassicaceae*	Annual/Biennial forb	Cool	I	I	I
Cirsium vulgare (Savi) Ten.	*Asteraceae*	Annual/Biennial forb	Cool	IV	III	
Carduus acanthoides L.	*Asteraceae*	Annual forb	Cool	III	IV	
Hypochaeris radicata L.	*Asteraceae*	Perennial forb	Cool	III	I	
Lactuca serriola L.	*Asteraceae*	Annual/Biennial forb	Cool	II	I	
Anthemis cotula L.	*Asteraceae*	Annual forb	Cool	I	I	
Poa annua L.	*Poaceae*	Annual grass	Cool	I	II	
Avena sativa L. var. *sativa*	*Poaceae*	Annual grass	Cool	I	I	
Sonchus asper (L.) Hill	*Asteraceae*	Annual/Biennial forb	Cool	I	I	
Melilotus albus Desr.	*Fabaceae*	Annual/Biennial forb	Cool	I	I	
Festuca arundinacea Schreb.	*Poaceae*	Perennial grass	Cool	I	I	

Table 1. continued.

Trifolium pratense L.	*Fabaceae*	Biennial/Perennial forb	Cool	I	I	
Medicago lupulina L.	*Fabaceae*	Annual/Biennial forb	Cool	II		I
Dactylis glomerata L.	*Poaceae*	Perennial grass	Cool	I		I
Cichorium intybus L.	*Asteraceae*	Annual/Biennial forb	Cool	I		I
Centaurium pulchellum (Sw.) Druce	*Geraniaceae*	Annual forb	Warm	IV		
Bromus hordeaceus L.	*Poaceae*	Annual grass	Cool	IV		
Cynara cardunculus L.	*Asteraceae*	Perennial forb	Cool	III		
Centaurea calcitrapa L.	*Asteraceae*	Annual forb	Cool	III		
Briza minor L.	*Poaceae*	Annual grass	Cool	III		
Carthamus lanatus L.	*Asteraceae*	Annual forb	Cool	III		
Silene gallica L.	*Caryophyllaceae*	Annual forb	Cool	III		
Gaudinia fragilis (L.) P. Beauv.	*Poaceae*	Annual grass	Cool	II		
Crepis setosa Hallier f.	*Asteraceae*	Annual forb	Cool	II		
Mentha pulegium L.	*Lamiaceae*	Perennial forb	Cool	II		
Leontodon saxatilis Lam.	*Asteraceae*	Perennial forb	Cool	I		
Bupleurum tenuissimum L.	*Apiaceae*	Annual forb	Warm	I		
Melilotus indicus (L.) All.	*Fabaceae*	Annual forb	Cool	I		
Trifolium dubium Sibth.	*Fabaceae*	Annual forb	Cool	I		
Phalaris coerulescens Desf.	*Poaceae*	Perennial grass	Cool	I		
Parapholis incurva (L.) C.E. Hubb.	*Poaceae*	Annual grass	Cool	I		
Geranium dissectum L.	*Geraniaceae*	Annual forb	Cool	I		
Centunculus minimus L.	*Primulaceae*	Annual forb	Cool	I		
Anthoxanthum odoratum L.	*Poaceae*	Perennial grass	Cool	I		
Trifolium fragiferum subsp. *bonanni* (C. Presl) Soják	*Fabaceae*	Perennial forb	Cool	I		
Lotus tenuis Waldst. & Kit. ex Willd.	*Fabaceae*	Perennial forb	Cool	I		
Echium plantagineum L.	*Boraginaceae*	Annual forb	Cool	II		
Carduus thoermeri Weinm.	*Asteraceae*	Annual forb	Cool	II		

Table 1. continued.

Carduus nutans L.	*Asteraceae*	Annual/Biennial forb	Cool	II		
Silybum marianum (L.) Gaertn.	*Asteraceae*	Annual forb	Cool	I		
Geranium molle L.	*Geraniaceae*	Annual forb	Cool	I		
Hordeum murinum subsp. *leporinum* (Link) Arcang.	*Poaceae*	Annual grass	Cool	I		
Medicago arabica (L.) Huds.	*Fabaceae*	Annual forb	Cool	I		
Sisymbrium officinale (L.) Scop.	*Brassicaceae*	Annual forb	Cool	I		
Rapistrum rugosum (L.) All.	*Brassicaceae*	Annual forb	Cool	I		
Picris echioides L.	*Asteraceae*	Annual forb	Cool	I		
Erodium cicutarium (L.) L'Hér. ex Aiton	*Geraniaceae*	Annual/Biennial forb	Cool	I		
Torilis nodosa (L.) Gaertn.	*Apiaceae*	Annual forb	Cool	I		
Leucanthemum vulgare Lam.	*Asteraceae*	Perennial forb	Cool	I		
Atriplex prostrata Boucher ex DC.	*Chenopodiaceae*	Annual forb	Warm	I		
Carduus pycnocephalus L.	*Asteraceae*	Annual/Biennial forb	Cool	I		
Centaurea melitensis L.	*Asteraceae*	Annual forb	Cool	I		
Foeniculum vulgare Mill.	*Apiaceae*	Perennial forb	Cool	I		
Marrubium vulgare L.	*Lamiaceae*	Perennial forb	Warm	I		
Phalaris canariensis L.	*Poaceae*	Annual grass	Cool	I		
Prunella vulgaris L.	*Lamiaceae*	Perennial forb	Cool	I		
Trifolium fragiferum L. subsp. *fragiferum*	*Fabaceae*	Perennial forb	Cool	I		
Centaurea solstitialis L.	*Asteraceae*	Annual/Biennial forb	Cool	I		
Melilotus officinalis (L.) Lam.	*Fabaceae*	Annual forb	Cool	I		
Digitaria sanguinalis (L.) Scop.	*Poaceae*	Annual grass	Warm	I	IV	V
Chenopodium album L.	*Chenopodiaceae*	Annual forb	Cool		IV	IV
Sonchus oleraceus L.	*Asteraceae*	Annual forb	Cool	I	III	II
Stellaria media (L.) Cirillo	*Caryophyllaceae*	Annual forb	Cool		III	III
Rumex crispus L.	*Polygonaceae*	Perennial forb	Cool		II	II
Veronica persica Poir.	*Plantaginaceae*	Annual forb	Cool		II	II

Table 1. continued.

Polygonum convolvulus L.	*Polygonaceae*	Annual forb	Cool		II	I
Lamium amplexicaule L.	*Lamiaceae*	Annual forb	Cool		II	I
Convolvulus arvensis L.	*Convolvulaceae*	Perennial vine	Warm		I	I
Matricaria recutita L.	*Asteraceae*	Annual forb	Cool		I	I
Raphanus sativus L.	*Brassicaceae*	Annual/Biennial forb	Cool		I	I
Vicia sativa L.	*Fabaceae*	Annual forb	Warm		I	I
Avena fatua L.	*Poaceae*	Annual grass	Cool		I	
Avena sterilis L.	*Poaceae*	Annual grass	Cool		I	
Fumaria agraria Lag.	*Fumariaceae*	Annual forb	Cool		I	
Senecio vulgaris L.	*Asteraceae*	Annual forb	Cool		I	
Urtica urens L.	*Urticaceae*	Annual forb	Cool		I	
Veronica arvensis L.	*Plantaginaceae*	Annual forb	Cool		I	
Veronica polita Fries.	*Plantaginaceae*	Annual forb	Cool		I	
Viola arvensis Murray.	*Violaceae*	Annual forb	Cool		I	
Viola odorata L.	*Violaceae*	Annual forb	Cool		I	
Eragrostis cilianensis (All.) Vignolo ex Janch.	*Poaceae*	Annual grass	Warm			I
Hirschfeldia incana (L.) Lagr.Foss.	*Brassicaceae*	Annual/Biennial forb	Cool			I
Setaria verticillata L. P. Beauv.	*Poaceae*	Annual grass	Warm			I
Setaria viridis (L.) P. Beauv.	*Poaceae*	Annual grass	Warm			I
		Number of species		70	43	30

[1.] Constancy classes. I: 0.1 – 20% (rare); II: 20.1 – 40% (low); III: 40.1 – 60% (intermediate); IV: 60.1 – 80% (moderately high); V: 80.1 – 100% (high); (Mueller-Dombois & Ellenberg, 1974).
[2.] Grassland data correspond to mesophytic grassland surveys published in Perelman & al. (2001).
[3.] Cool season crops, wheat and field pea, were published in Poggio & al. (2004).
[4.] Warm season crops are soybean and maize. Soybean data were published in de la Fuente & al. (1999), while maize data are unpublished (R.J. C. León).

(Table 2). These four families have been recognised for having the largest contribution to the total number of alien species in local floras worldwide (Pyšek 1998). Other families that are conspicuous in the Old World flora were represented by fewer species (*Apiaceae*: 5, *Lamiaceae*: 4, *Caryophyllaceae*: 2, and *Chenopodiaceae*: 2). Some families only occurred in either grasslands or croplands. Species from two families only occurred in grasslands (*Boraginaceae*, *Geraniaceae*), while six families were only surveyed in croplands (*Convolvulaceae*, *Fumariaceae*, *Plantaginaceae*, *Polygonaceae*, *Urticaceae*, *Violaceae*, Table 2). Many of these families are scarcely represented in the native flora of the Pampa grasslands (Cabrera & Zardini 1978). Conversely, species from *Papaveraceae* were not surveyed in either grasslands or croplands (Poggio & Mollard 2010), even though many species belonging to this family has been recognised as weeds and highly invasive plants (Pysek 1998; Weber & Gut 2005). For instance, *Papaver dubium* and *P. rhoeas* did not become widespread weeds in croplands as in Europe, even though both species were documented as casual in cereal crops in the Pampas in the early 20th century (Spegazzini 1905).

Asteraceae, which is recognised as a botanical family including many wind-dispersed species, have enriched the floras of grasslands and croplands in the Pampas (Table 1). Strong westerly winds, along with both the absence of trees and the flat topography that characterise the Pampas, would have promoted the spread of anemochorous species. Moreover, areas in agricultural landscapes that are not ploughed, such as grasslands, may

Table 2. Number of species listed for each botanical families in grasslands and croplands in the Pampas. Percentages are also shown for each family.

	Total		**Grasslands**		**Croplands**	
Family	**Taxa number**	**(%)**	**Taxa number**	**(%)**	**Taxa number**	**(%)**
Asteraceae	24	25.5	22	31.4	11	22.0
Poaceae	20	21.3	15	21.4	12	24.0
Fabaceae	14	14.9	13	18.6	7	14.0
Brassicaceae	6	6.4	4	5.7	4	8.0
Apiaceae	5	5.3	5	5.7	2	4.0
Lamiaceae	4	4.3	3	4.3	1	2.0
Chenopodiaceae	2	2.1	1	1.4	1	2.0
Caryophyllaceae	2	2.1	1	1.4	1	2.0
Primulaceae	2	2.1	2	2.9	1	2.0
Geraniaceae	4	4.3	4	5.7	-	-
Boraginaceae	1	1.1	1	1.4	-	-
Plantaginaceae	3	3.2	-	-	3	6.0
Polygonaceae	2	2.1	-	-	2	4.0
Violaceae	2	2.1	-	-	2	4.0
Fumariaceae	1	1.1	-	-	1	2.0
Urticaceae	1	1.1	-	-	1	2.0
Convolvulaceae	1	1.1	-	-	1	2.0
Total	94	100.0	70	100.0	50	100.0

function as sources of anemochorous weeds dispersed towards fields (Moyer & al. 1994). Regarding *Poaceae*, tussock perennial grasses were the prevalent life-form in the mesophytic grasslands, whose dominance was importantly reduced by grazing and trampling and the opportunistic planting of pastures with more palatable grasses and legumes of Mediterranean origin (Ghersa & al. 2007). Perennial grasses were thus introduced as forage crops in the Pampas during the agricultural expansion between 1880 and 1914 (*Cynodon dactylon*, *Festuca arundinaceae*, *Sorghum halepense*), but some of these species became conspicuous invasive plants few decades later of their introduction. Other annual forage grasses, such as ryegrass (*Lolium multiflorum*), already naturalised before agricultural expansion (Hernández 1884), have been continuously sown in pastures, albeit this species is also recognised as weed in cereal crops (Scursoni & al. 2014). Conversely, abundance of cool-season native grasses was undermined by cattle grazing because their greater sensitivity to grazing and trampling than Old World grasses (Chaneton & al. 1988; Longo & al. 2013). Species from *Fabaceae* are underrepresented in the native pampa grasslands in comparison to the European flora (Cabrera & Zardini 1978; Burkart & al. 2011). Most Old World species from this family have been deliberately introduced in the Pampas as forage plants to sown pastures, principally *Medicago sativa*, followed by *Trifolium repens* and *T. pratense*, and into a lesser extent *Lotus tenuis* and *Melilotus albus* (Table 1). Many other species, due to their seed sizes and shapes were highly similar to that of forage legumes, were inadvertently introduced as seed contaminants, mostly alfalfa seeds imported from Europe during the early period of agricultural expansion (Poggio & al. 2010b). All species from *Brassicaceae* were short-lived species growing during the cool season (Table 1). Species from this family usually have low constancy in both grasslands and croplands (Perelman & al. 2001; Poggio & al. 2004). *Brassicaceae* species were observed in early stages in post-agricultural fields (D'Angela & al. 1986; Tognetti & al. 2010).

Old World plant species occurring in grasslands and croplands in the Pampas are mostly short-lived forbs vegetating during the cool season (Fig. 2). Short-lived species are proportionally more numerous in croplands than in grasslands (80% vs. 71.6%, Fig. 2), including more forbs (*Chenopodium album*, *Polygonum convolvulus*, *Stellaria media*, *Sonchus oleraceus*, *Veronica persica*) than grasses (*Digitaria sanguinalis*, *L. multiflorum*, *Poa annua*). In addition, short-lived grasses growing during the cool season were numerous in grasslands (e.g. *Bromus hordeaceus*, *Briza minor*, *Gaudinia fragilis*, *L. multiflorum*). Life cycles of plants occurring in grasslands and croplands are thus reflecting the influence of environmental filtering on plant functional traits, which may favour or discriminate against the establishment of species having particular traits (Díaz & Cabido 2001). Annual ploughing creates highly unstable conditions within arable fields, where the occurrence of long-lived species is usually much lower than ephemeral species, which arrive to complete the growth cycle and reproduce early during the growing season and thus thrive to persist in fallows (i.e. the uncultivated period between two consecutive crops in rotation; a common practice to recover fertility in Pampas croplands before the inception of no-tillage practices). However, perennial species are also frequent in croplands when farming practices contribute to spread species having vegetative propagation, such as through rhizomes or sprouting roots (*Convolvulus arvensis*, *C. dactylon*, *Sorghum halepense*).

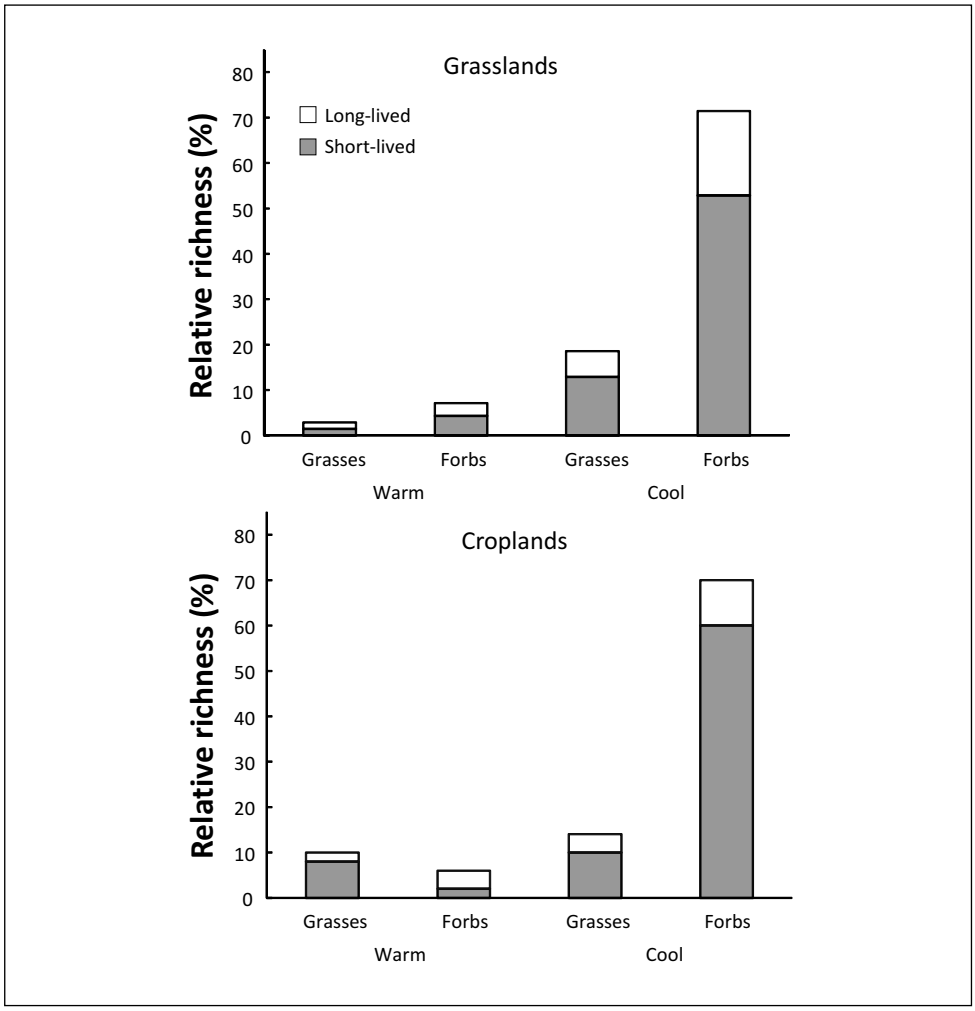

Fig. 2. Proportional contribution to the total species richness of different plant life-forms from Mediterranean flora occurring in grasslands and croplands in the Pampas. The bars show the percent number of grass and forb species (short- and long-lived) vegetating in either cool or warm growing seasons. Short-lived plants include annuals and annual-biennials, while long-lived plants include biennials, biennial-perennials and perennials.

Many Old World arable weeds naturalised in the Pampas have also found refuge in habitats other than grasslands and croplands. Hence, Old World species were also cited as inhabiting livestock handling facilities in ranches and farms (i.e., corrals, fencerows, water troughs, and reservoirs) create places where cattle is brought or spontaneously gather generating fertility spots and habitat for ruderal, nitrophyllous species, such as *Urtica urens*. Water troughs in extensive paddocks with high stocking rates also brought about over-

grazed spots where some ruderal species such as *Plantago lanceolata* and *Leontodon taraxacoides* may thrive (León & al. 1984; Sala & al. 1986). Overgrazing or heavy cattle trampling also increase the abundance of unpalatable ruderals, such as *Centaurea* sp.pl., which prosper along cattle paths. Other Old World species, usually found as weeds in croplands, were also found in less disturbed sites, such as fencerows, railway and roadside embankments, as well as in small woodlots surroundings abandoned rural settlements (locally named as "taperas"). In addition, the large introduction and planting of exotic trees for cattle shelter, surrounding dwellings and along roads, paved the way for the thriving of Mediterranean sciophytes or sciophyte-facultative species, for instance *Galium aparine*, *Viola arvensis*, *Malva parviflora*, *Marrubium vulgare*, and the Rhubarb-like leaved *Arctium minus*. Moreover, flowers of many Mediterranean weedy plants occurring in fields and along field margins, such as *Ammi majus*, *Brassica rapa*, *Carduus acanthoides*, *S. oleraceus*, and *T. repens*, are visited by insects, which provide ecosystem services for agriculture, such as pollination and biotic regulation of crop pests (Torretta & Poggio 2013).

Returning the kindness: Neotropical aliens naturalised in the Mediterranean Basin

The Pampas and Mediterranean floras not only share weeds native from the Mediterranean Basin, or alien in both regions, but also there is an extensive list of Neotropical species native from the plains of Argentina, Brazil, Paraguay and Uruguay that have become alien in Mediterranean ecosystems. The list includes many Asteraceae species, such as *Baccharis articulata* (Lam.) Pers., *Galinsoga parviflora* Cav., *Bidens pilosa* L., *Conyza bonariensis* (L.) Cronquist (= *Erigeron bonariensis* L.), *C. blakei* (Cabrera) Cabrera (= *E. blakei* Cabrera), *Senecio grisebachii* Baker and *Symphyotrichum squamatum* (Spreng.) G.L. Nesom (= *Aster squamatus* (Spreng.) Hieron.), which behave as synanthropic species as they proliferate in uncultivated fallows in Pampean croplands, or disturbed sites and became naturalised in Spain, Italy and France encroaching on similar habitats than those in the Pampas (Pignatti 1982; Celesti-Grapow & al. 2010; R. J. C. León personal observation). Perennial bunchgrasses from the tribe Stipeae that are also representative of Pampa grasslands, such as *Nassella neesiana* (Trin. & Rupr.) Barkworth, *N. trichotoma* (Nees) Hack. ex Arechav., and *Jarava brachychaeta* (Godr.) Peñailillo, are found as aliens in embankments and uncultivated croplands in northern Italy, Spain and France (Pignatti 1982; Euro+Med database, 2006). Some Neotropical Paniceae also found the way to became alien in Mediterranean countries: *Paspalum quadrifarium* Lam. (in Italy), *P. urvillei* Steud., *P. vaginatum* Sw., *P. notatum* Flüggé, and *P. distichum* L. With respect to rangelands, *Ambrosia tenuifolia* Spreng. and *Setaria parviflora* (Poir.) Kerguélen are increaser species which rapidly encroach on overgrazed Pampean grasslands, also managed to establish in disturbed lands in Spain, France and Italy.

As many of these species thrive in the Pampas the following question arises: Have the Pampas backfired and supplied Mediterranean countries with members of its own flora? The question is enticing as the Pampas were one of the major producers of crop and farm seeds (e.g. linseed, alfalfa), which have been traded and exported to European countries. These exported seed lots were known to be rich in arable weed seeds as contaminants (Poggio & al. 2010b). While the putative vector exists, the possibility that the current

Mediterranean genotypes have originated from Pampas accessions is difficult to corroborate because the above-mentioned species (and other not mentioned here) have a broad native range which encompasses different regions in South America. One exception is *Solanum bonaeriense* L., which has a narrower native range in the Pampas of Argentina and Uruguay. A detailed study of herbarium records of the Mediterranean specimens from the above-mentioned Pampean species may shed light into the probable origin and naturalization process of New World species naturalized in the Mediterranean.

Concluding remarks

Many plant species of Mediterranean origin are currently documented as adventive or naturalised species in the flora of the Pampean grasslands and croplands (Zuloaga & Morrone 1996, 1999). Four botanical families comprised the highest numbers of taxa (*Asteraceae, Poaceae, Fabaceae, and Brassicaceae*), which have been also recognised for having the largest contribution to the total number of alien species in local floras worldwide (Pysek 1998). The Pampas were enriched with species mostly found in croplands, which belong to a group of families widely known as arable weeds in the Old World, such as *Fumaria agraria*. Interestingly, species from *Papaveraceae* were absent in both grasslands and croplands, even though many species are widely recognised as weeds in European croplands, such as *P. dubium* and *P. rhoeas*. However, the introduction of Mediterranean species, intentionally or accidentally, have greatly contributed to increase the species diversity of the Pampean flora, as well as enriched with life-forms poorly represented in the pristine pampa grasslands.

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