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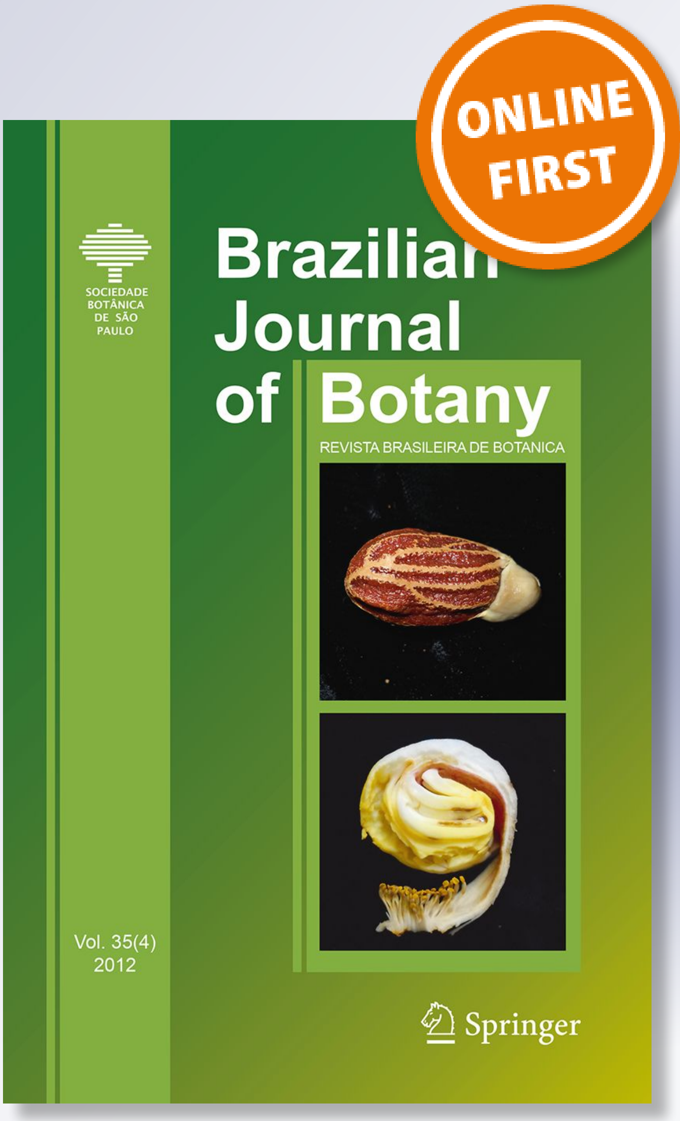

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ECOLOGY AND BIOGEOGRAPHY

Composition and vegetation structure in a system of coastal dunes of the "de la Plata" river, Uruguay: a comparison with Legrand's descriptions (1959)

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Abstract Forestation in dune systems blocks the transport of sand, making possible the extension of agriculture or urban development into coastal areas. This process, which has been taking place for a century on the Uruguayan shore, has affected the landscape and the composition and structure of plant communities. In this study, we describe the composition and structure of vegetation stands of a dune system at the seaside resort "El Pinar," Canelones, Uruguay. In addition, we compare it with a previous survey published by Legrand in Anales del Museo de Historia Natural 6:73, 1959. We recorded 76 species; with Asteraceae, Poaceae, Cyperaceae, and Apiaceae the most represented families. A cluster analysis was used to identify main groups of plant associations. This analysis defined seven groups. The group associated with the foredunes environment exhibits the lowest richness, with indicative species typical of extreme psammophilic environments. Five groups occur in interdune depressions associated with humid sites. The last group was defined in the fixed dunes environment. The species composition similarity was low in comparison with Legrand′s (1959) survey; furthermore we found a greater presence of non-native species. We associate this change with the presence of *Acacia longifolia*, a species with an extremely high invasive potential, considered an ecosystem transformer. Our proposal is the development of an investigation program to assess the effectiveness and challenges of potential management practices. We also suggest applying the tactic of eradication of *A. longifolia* on the fixed dunes, through different practices of management (e.g., manual control operations, biologic control agents, and the use of fire).

Keywords *Acacia longifolia* · Alien species · Floristic vegetation groups · Forestation · Human pressure

E. Castiñeira Latorre · E. da Costa
Centro Universitario de Rivera, Universidad de la República, Ituzaingó 667, Rivera, Uruguay

E. Castiñeira Latorre (✉)
Licenciada en Ciencias Biológicas, Facultad de Ciencias, Universidad de la República, Rivera, Uruguay
e-mail: elencasti@gmail.com

C. Fagúndez
Sección Ecología Terrestre, Facultad de Ciencias, Universidad de la República, Iguá 4225, C.P. 11400 Montevideo, Uruguay
e-mail: fagundezce@gmail.com

A. Canavero
Center for Advanced Studies in Ecology & Biodiversity (CASEB), Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile
e-mail: acanaver@gmail.com

Introduction

Coastal areas around the world are being altered as a consequence of various uses related to an increase in urban development, industrialization, and development of tourism and recreation. The expansion of agricultural and urban areas on coastal systems of dunes has being facilitated by forestation, disrupting sand transportation (Avis and Lubke 1996; Bate and Ferguson 1996; Gadgil and Ede 1998; Kutiel et al. 2004; Carruthers et al. 2011; Kull et al. 2011). These practices have effects at biotic and abiotic levels—plant formations, physical and chemical soil components, and geomorphic changes (Kutiel et al. 2004; Marchante et al. 2008, 2009; Kim and Yu 2009). However, in order to understand the present state of an ecosystem is necessary to know its previous status before modifications—e.g., the

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costal dunes of Lake Michigan (Arbogast et al. 2002), southern Israeli coastal dunes (Kutiel et al. 2004) and the Southern Baltic coast (Peyrat et al. 2009). Knowledge about the historical land use allows us to develop an understanding of dune ecology and generates tools for future conservation of this ecosystem and its functions (Antrop 2005; Foster 2006; Rhemtulla and Mladenoff 2007).

At the beginning of the 20th century, the global economically driven mindset resulted in a tendency to introduce alien species with the goal of expanding and improving agro-productive and urban areas (Carruthers et al. 2011; Kull et al. 2011). As in the well-reported introduction of *Acacia longifolia* (Andrews) Willd in Portugal (see Marchante et al. 2008, 2009, 2010, 2011b; Kull et al. 2011), a similar forestry program was performed on the Uruguayan coast introducing this Australian acacia (Delfino and Masciadri 2005; Gutiérrez and Panario 2005; Alonso Paz and Bassagoda 2006). This species consolidates sand dunes, prevents erosion, fertilizes the soil, and provides wind protection for forestation with *Pinus* spp. (Kull et al. 2011). This mindset of "national development" of the 1900s differs from the "sustainable development" of the 1980s and onwards, with the incorporation of concerns about negative impacts of alien and invasive species on the environment (Carruthers et al. 2011).

Acacia longifolia is one of the most successful and prolific invasive species globally, producing landscape modifications and ecosystem changes, and affecting the composition and structure of native vegetation including the loss of biodiversity (Marchante et al. 2010, 2011b, Morris et al. 2011). All of these patterns of change and replacement of native species by invasive exotic species have been reported in the coastal ecosystems of Uruguay (Chebataroff 1952; Legrand 1959; Delfino and Masciadri 2005; Alonso Paz and Bassagoda 2006). Currently, there is a growing interest in the restoration of these modified coastal systems through the elaboration of management programs (Suding 2011). A description of the present spatial patterns of vegetation, in contrast with knowledge of their past status, can be useful for detecting the impacts of human modifications (e.g., introduction of alien species) and contributing to the goals of conservation (Levin 1992; van der Meulen and Salman 1996; Forst 2009).

Legrand's work (1959)—a pioneering description of the floristic composition of the coastal area of "de la Plata" River extending from the eastern border of Montevideo to the Pando stream, Canelones, Uruguay—with botanical records obtained in 1934 allowed us to accomplish a comparison of plant associations with the present state of the ecosystem. These pioneering studies for the area described vegetation communities that develop in extensive fields of dunes, now converted into streets, roads, and housing. Those environments were reduced from 8 km to just 200 m from the shoreline today. Despite the extreme changes observed, you can find primary dunes with an herbaceous stratum composed of *Panicum racemosum* (P. Beauv.), *Senecio crassiflorus* (Poir.) DC. and *Spartina ciliata* Brongn, interdunes depressions with permanent and semi permanent presence of water where you can identify patches of 0.50–2 m high composed of species like *Eryngium pandanifolium* Cham. & Schltdl., *Hydrocotyle bonariensis* Lam., *Juncus* sp. L., *Mikania* sp. Willd., *Paspalum pumilum* Ness, *Polygonum acuminatum* Kunth, *Schoenoplectus californicus* (C.A. Mey.) Soják, *Typha dominguensis* Pers. and *Typha latifolia* L., and a zone of fixed dunes with a 0.50 m high herbaceous stratum of *Achyrocline satureioides* and *Androtrichum trigynum* (Spreng.) H. Pfeiff. that grows mixed with an arboreal stratum of *A. longifolia*.

The aim of this study is to describe the present composition and structure of the vegetation stands and their association with a series of environments—foredunes, interdune depressions, and fixed dunes—registered in a system of coastal dunes at the seaside resort "El Pinar," Canelones, Uruguay. We also compare our data with those presented in Legrand′s pioneering descriptions of this flora. This study allows us to reflect upon the effects of the introduction of *A. longifolia* and the processes that operated on the Uruguayan coastal ecosystem given their known characteristics before their urbanization. This knowledge can be useful in generating management strategies for restoration.

Material and methods

Study area

Uruguay is located in the southeast of South America (30°35′S, 53°58′W) with a surface of 176,215 km^2 and approximately 670 km of coast line (Chebataroff 1973). It is included in the phytogeographic unit Pampeana Province, which is a transition zone between Paranaense Province and the Atlantic forest (Cabrera and Willink 1973; Brussa and Grela 2007). The climate is temperate and rainy, with irregular precipitation all year round and with a mean yearly temperature of 17.5° C. The Uruguayan territory is "Cfa" according to Koeppen's climatic classification (Bidegain and Caffera 1997). The study area occupies a surface of 125,560 m^2 on the seashore of "de la Plata" River in the seaside resort "El Pinar," Canelones, Uruguay (34°48′S, 55°54′W) (Figs. 1, 2). It comprises a coastal system of transgressive dunes originated by variations in the sea level during the Holocene (Panario and Piñeiro 1997; Cavallotto et al. 2004, 2005). The beach has white and fine sands with a non-continuous fore dune which shows erosive forms (Gutiérrez and Panario 2005). The "Carrasco" stream constitutes the western limit of the study area and toward the east the "Pando" stream, both with great extensions of wetlands (Fig. 1).

Plant survey

The sampling sites were assigned using an aerial photograph of the study area (taken on 2001 by the "Servicio de Sensores Remotos Aeroespaciales" of Uruguayan Air Force). We determined three environment types in the study area: foredunes, interdune depressions, and fixed dunes (Fig. 2). After an entitation carried out by visual inspection of the whole study area we considered nine vegetation stands (according to the dominant species, e.g., *Acacia* stand; or according to a combination of floristic characteristics and the availability of water, e.g., psammophilic grassland): AS = *Acacia* stand, ES = *Eryngium* stand, HPS = hydrophilic pasture stand, PGS = psammophilic grassland stand, PPS = psammophilic pasture stand, PSS = psammophilic steppe stand, SS = *Schoenoplectus* stand, ThS = *Thelypteris* stand, and TyS = *Typha* stand. 22 transects (sample units) were placed in the previously chosen vegetation stands: three in AS, two in ES, three in HPS, two in PGS, one in PPS, two in PSS, three in SS, one in ThS, and five in TyS; each transect was located randomly within each vegetation stand (Fig. 2). In order to survey the species composition we performed a point-survey (0.5 mm diameter needle) over a transect in each vegetation stand, registering the species in contact with ten needles (each separated by 2 m) per transect (Brown 1954; Kent and Coker 1994). Species were determined in the field and in the laboratory using taxonomic keys (Rosengurtt et al. 1970; Lombardo 1982, 1983, 1984; Alonso Paz 1997; Izaguirre and Beyhaut 2003a, b) and consulting national collections (MVJB-"Jardín Botánico de Montevideo," MVFA-"Facultad de Agronomía, UDELAR, Montevideo") (Table 1). We deposited vouchers of reference at the national collection MVJB-"Jardín Botánico de Montevideo." The scientific names of the species list present in this work and that of Legrand's work follow Instituto de Botánica Darwinion (2011), Royal Botanic Gardens (2011) and W3TROPICOS (2009). In order to compare the composition of present-day vegetation at the study area with observations accomplished by Legrand, we used zones defined by him at "Cantón C" (the "Canton C" is a larger area than the study area but it includes it) where zones I and II are comparable to foredunes, zone III to interdune depressions, and zone IV to fixed dunes. Legrand used occasional surveys during 20 years to describe the floristic characteristics of the study area (see Legrand 1959).To

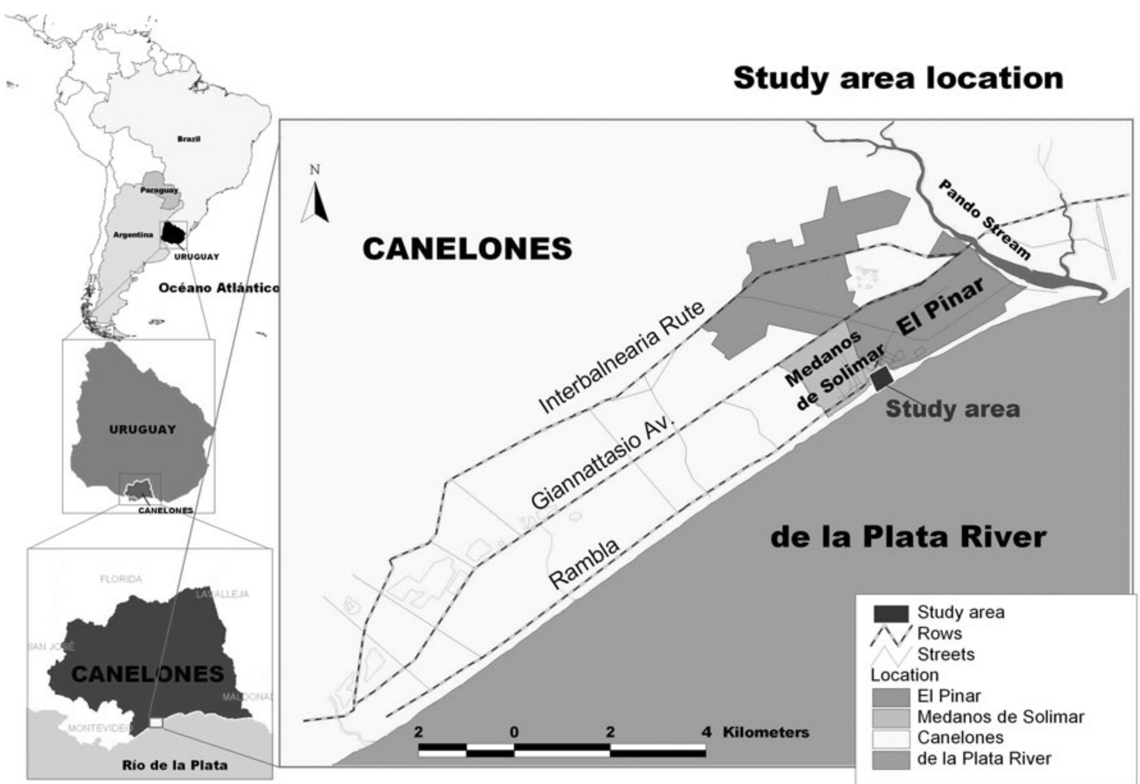

Fig. 1 Map of Uruguay showing the location of the study area at "El Pinar," Canelones, Uruguay

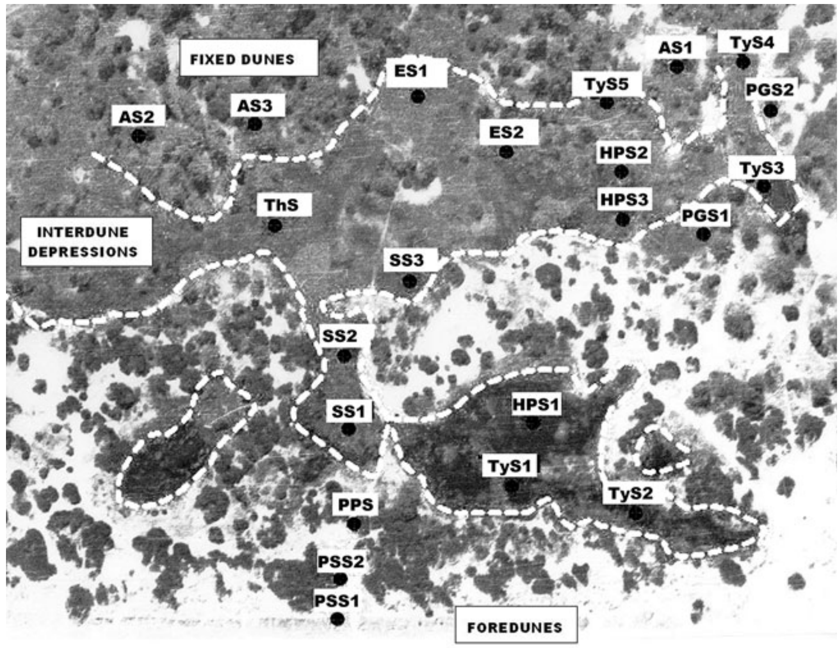

Fig. 2 Aerial photo of the study area (year 2001) at the seaside resort "El Pinar," Canelones, Uruguay. (292 × 430 m parallel to the coastal shore, 34°48′38.6″S, 55°54′39.4″W; 34°48′46.4″S, 55°54′32.9″W; 34°48′54.2″S, 55°54′47.0″W; 34°48′46.6″S, 55°54′53.3″W). We indicate the three environments (fixed dunes, interdune depressions, and foredunes), the sampling sites and the vegetation stands. *AS Acacia* stand, *ES Eryngium* stand, *HPS* hydrophilic pasture stand, *PGS* psammophilic grassland stand, *PPS* psammophilic pasture stand, *PSS* psammophilic steppe stand, *SS Schoenoplectus* stand, *ThS Thelypteris* stand, and *TyS Typha* stand

determine the status of conservation of species we used the data base of the "IUCN Red List of Threatened Species" (IUCN 2009), a local classification generated at the "Laboratorio de Botánica, Facultad de Agronomía, Universidad de la República, Uruguay" (Marchesi et al. 2008), and the species conservation priority report for Uruguay conceived by a group of experts for the SNAP (National System of Protected Areas) (Alonso Paz et al. 2009). Data were collected in three field works between the months of January and March 2009.

Statistical analysis

We developed an agglomerative cluster analysis using the Jaccard index as a distance metric and the Ward's method as the fusion algorithm. We incorporated an indicator species analysis (ISA) to detect the most informative level of cluster and indicative species of each group (Dufrene and Legendre 1997). The species indicator value ($IV_{kj} = RA_{kj} \times RF_{kj} \times 100$, where IV_{kj} is the indicator value for the species *j* in group *k*, RA_{kj} is the relative abundance of species *j* in group *k*, and RF_{kj} is the relative frequency of species *j* in group *k*.) combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence in a particular group (Dufrene and Legendre 1997). In each group it varies between 0 % (no indication) and 100 % (perfect indication) (Table 1). Statistical significance of the IV was tested using a Monte Carlo permutation test (10,000 replication) (McCune and Mefford 1999). The most informative level of the cluster was assigned calculating the maximum value of the sum of the IV of each species greater than 70 % (McGeoch et al. 2002; Gautreau and Lezama 2009). ISA was run on PC-ORD program (McCune and Mefford 1999). We used the software PAST. v. 1.24 to estimate the rarefaction curves for each plant group (Magurran 1988; Gotelli and Graves 1996; Hammer et al. 2001). We used the richness estimator Chao 2 computed with log-linear 95 % confidence intervals (Chao 1987) to estimate the species richness of total sample with the program estimates 8.2 (Colwell 2006). We also calculated the Jaccard Index to evaluate the degree of similarity between the species list of our study with that of Legrand (1959) [*J* = (shared species)/(exclusive species of Legrand study + exclusive species of current study + shared species)], and to evaluate the degree of similarity between the species of the three principal different environments observed in the study area (foredunes vs. zone I + II of Legrand; interdunes depressions vs. zone III of Legrand; fixed dunes vs. zone IV of Legrand) [*J* = (shared species)/(exclusive species of Legrand′s zone + exclusive species of the environment types of current study + shared species)]. Since Legrand used occasional surveys along 20 years to describe the floristic characteristics of the study area (see Legrand 1959), to make his survey comparable with our data, not only do we included the transect survey in this analysis but we also included species registered off of transects. This exception was made only for the calculation of the Jaccard Index to compare the Legrand′s survey with data presented in this study.

Table 1 List of species, family, vegetation stands where it was registered (*AS Acacia* stand, *ES Eryngium* stand, *HPS* hydrophilic pasture stand, *PGS* psammophilic grassland stand, *PPS* psammophilic pasture stand, *PSS* psammophilic steppe stand, *SS Schoenoplectus* stand, *ThS Thelypteris* stand, and *TyS Typha* stand), and the indicator value (IV) are shown between brackets and outside of the brackets is the number of the groups, 1 to 7, of the agglomerative analysis that the species is the indicator of (only taxa with significant values, $P < 0.05$)

Species		Vegetation stands	PS		PP	SU			HP			TyU					EU		ThU	PG		AU			IV
		Transects Family	1	2	1	1	2	3	1	2	3	1	2	3	4	5	1	2	1	1	2	1	2	3	
Carpobrotus edulis (L.) N.E. Br.	*	Aizoaceae																							
Sagittaria montevidensis Cham. & Schltdl.		Alismataceae																							
Centella asiatica (L.) Urb.	*	Apiaceae																				1			
Eryngium pandanifolium Cham. & Schltdl.		Apiaceae				1											10	10							5 (97.2)
Eryngium serra Cham. & Schltdl.		Apiaceae																							
Hydrocotyle bonariensis Lam.		Apiaceae					2		5		1	3	1	3				1		1	3				3 (54.8)
Achyrocline satureioides (Lam.) DC.		Asteraceae																			1	1		2	7 (60)
Baccharis articulata (Lam.) Pers.		Asteraceae												1											
Baccharis dracunculifolia DC.		Asteraceae																						1	
Baccharis gnaphalioides Spreng.		Asteraceae																							
Baccharis spicata (Lam.) Baill.		Asteraceae																		2	1				
Baccharis trimera (Less.) DC.		Asteraceae																					5		
Chevreulia sarmentosa (Pers.) S.F. Blake		Asteraceae																							
Cirsium sp. Mill.	*	Asteraceae																							
Conyza bonariensis (L.) Cronquist		Asteraceae												1											
Enhydra sessilis (Sw.) DC.		Asteraceae											1												
Eupatorium buniifolium Hook. Arn.		Asteraceae																							
Eupatorium tremulum Hook. & Arn.		Asteraceae																							
Gamochaeta coarctata Cabrera		Asteraceae																							
Hypochoeris radicata L.	*	Asteraceae																							
Mikania micrantha Kunth		Asteraceae														5	1								
Mikania sp. Willd.		Asteraceae						2	6				1	9											3 (90.9)
Pluchea sagittalis (Lam.) Cabrera		Asteraceae					1					2	1	1	2	1	9								
Pterocaulon lorentzii Malme		Asteraceae																							
Senecio crassiflorus (Poir.) DC.		Asteraceae	2	1																					1 (66.7)
Senecio selloi (Spreng.) DC.		Asteraceae																							
Sonchus asper (L.) Hill	*	Asteraceae																							
Androtrichum trigynum (Spreng.) H. Pfeiff.		Cyperaceae				1				1	1				6					9	9	9		3	7 (54.9)
Carex riparia Curtis		Cyperaceae					7												6						
Eleocharis sellowiana Kunth		Cyperaceae																							
Eleocharis sp. R. Br.		Cyperaceae							1						2			1							
Schoenoplectus californicus (C.A. Mey.) Soják		Cyperaceae				1	4	10																	2 (75)
Scirpus giganteus Kunth		Cyperaceae							1		3							1			1				
Scirpus olneyi A. Gray		Cyperaceae				4																			
Eriocaulon sp. L.		Eriocaulaceae								2															

Table 1 continued

Species		Vegetation stands	PS		PP	SU			HP			TyU					EU		ThU	PG		AU			IV
		Transects Family	1	2	1	1	2	3	1	2	3	1	2	3	4	5	1	2	1	1	2	1	2	3	
Acacia longifolia (Andrews) Willd.	*	Fabaceae																			1	9	10	9	7 (80)
Myriophyllum aquaticum (Vell.) Verdc.		Haloragaceae				1																			
Juncus maritimus Lam.		Juncaceae																							
Juncus sp. L.		Juncaceae								4	2				1										4 (92.3)
Hyptis floribunda Briq. Ex Micheli		Lamiaceae																							
Eugenia uniflora L.		Myrtaceae																							
Ludwigia hookeri (Micheli) H. Hara		Onagraceae																7	2						
Ludwigia peploides (Kunth) P.H. Raven		Onagraceae																							
Oenothera affinis Cambess.		Onagraceae																							
Pinus maritima Mill.	*	Pinaceae																				1	1		
Plantago sp. L.		Plantaginaceae																							
Andropogon arenarius Hack.		Poaceae																			1				
Andropogon sp. L.		Poaceae																				1			
Chascolytrum subaristatum (Lam.) Desv.		Poaceae																							
Cortaderia selloana (Schult. & Schult. f.) Asch. & Graebn.		Poaceae													1		1						1		
Cynodon dactylon (L.) Pers.	*	Poaceae											1									1			
Panicum schwackeanum Mez		Poaceae						3				1						7							
Panicum racemosum (P. Beauv.) Spreng.		Poaceae	6	1	4																				1 (100)
Paspalum notatum Flüggé		Poaceae																		6					
Paspalum pumilum Ness		Poaceae							6	9	9				4						1	2			4 (66.2)
Spartina ciliata Brongn.		Poaceae	3	7																1					1 (62.9)
Sporobolus indicus (L.) R. Br.		Poaceae			7																	1	1		
Polygala leptocaulis Torr. & A. Gray		Polygalaceae																							
Polygonum acuminatum Kunth		Polygalaceae				5	6	7	4			9							6						2 (58.5)
Polygonum punctatum Elliott		Polygalaceae																							
Rhynchospora sp. Vahl.		Potamogetonaceae								1						1	3								
Margyricarpus pinnatus (Lam.) Kuntze		Rosaceae			1																				
Cephalanthus glabratus (Spreng.) K. Schum.		Rubiaceae											1												
Richardia brasiliensis Gomes		Rubiaceae																							
Salvinia auriculata Aubl.		Salviniaceae											8												
Dodonaea viscosa Jacq.		Sapindaceae																					1	4	
Agalinis communis (Cham. & Schltdl.) D'Arcy		Scrophulariaceae										1													
Bacopa monnieri (L.) Wettst.		Scrophulariaceae						1																	
Solanum americanum Mill		Solanaceae																							
Solanum sisymbrifolium Lam.		Solanaceae											1												
Sphagnum sp. (Herb Linn)		Sphagnaceae																							

Table 1 continued

Species	Vegetation stands	PS		PP	SU			HP			TyU					EU		ThU	PG		AU			IV
	Transects Family	1	2	1	1	2	3	1	2	3	1	2	3	4	5	1	2	1	1	2	1	2	3	
Thelypteris rivularioides (Fée) Abbiatti	Thelypteridaceae																	20						
Typha dominguensis Pers.	Typhaceae										10	10		8	10	1		1						6 (92.7)
Typha latifolia L.	Typhaceae												10											
Cissus striata Ruiz & Pav.	Vitaceae																							

The scientific names follow Instituto de Botánica Darwinion (2011), Royal Botanic Gardens (2011) and W3TROPICOS (2009)

* Nonnative species

Results

We registered the presence of 75 species from 27 families (Table 1). The families with the greatest number of species were Asteraceae ($S = 21$), Poaceae ($S = 11$), Cyperaceae ($S = 7$), and Apiaceae ($S = 4$) (Fig. 3). Of 75 species, 50 were registered with point sampling and 25 observed occasionally outside of the transects. Estimates of total expected species diversity of plants at 22 sites (with the point-survey) predicted that nearly 23 additional species are still remaining to be found in addition to the 50 already recorded (Chao 2 ± 1 SD; 73.2 ± 14.3) (Fig. 4). Considering the species recorded in the study area ($S = 75$), we are close to the expected richness predicted by the estimation analysis. From the 80 species registered by Legrand (1959) (for the same study area), 64 species were absent in our samples (Table 2). In contrast, we registered 59 species not registered by Legrand and we share 16 species (Table 2). The Jaccard index ($J = 0.16$) confirms a low degree of similarity between both species lists.

The agglomerative classification analysis and the sum of significant IV jointly define seven groups for the plant association (Fig. 5). These were grouped in three higher groups that are associated with the following environments: foredunes, interdune depressions, and fixed dunes (Fig. 2). Group 1, Psammophilic steppe stands and Psammophilic pasture stand (PSS1, PSS2, PPS) (Fig. 2). This is an herbaceous stratum that grows on fine sands on foredunes. The indicative species is *P. racemosum* (P. Beauv.) Spreng. (IV = 100), but other species presented high IV: *S. crassiflorus* (Poir.) DC. (IV = 66.7) and *S. ciliata* Brongn. (IV = 62.9) (Table 1). This group presented the lowest observed richness (S = 5). This group is located in areas equivalent to zone I and II in Legrand's work (1959) where the most abundant species were *P. racemosum* and *S. crassiflorus* (Table 2). The degree of similarity between the species of the foredunes (present data) versus zone I + II of Legrand report a low degree of similarity ($J = 0.19$).

Group 2, *Schoenoplectus* stand and *Thelypteris* stand (SS1, SS2, SS3, ThS) (Fig. 2). This is an herbaceous stratum 2-meters high over a peaty ground flooded permanently or semipermanently located in the interdune depressions. The indicative species is *S. californicus* (C.A. Mey.) Soják (IV = 75) followed by *P. acuminatum* Kunth (IV = 58.5) (Table 1). This group presented an observed richness of $S = 17$. Group 3, Hydrophilic pasture stand and *Typha* stand (HPS1, TyS3) (Fig. 2). This is a dense pasture located in the interdune depressions. The *Typha*-stand of *T. latifolia* L. grows in the lowest zone of the study area. The indicative species is *Mikania* sp. Wild. (IV = 90.9) (Table 1) followed by *H. bonariensis* Lam. (IV = 54.8) (Table 1). This group presented an observed richness of

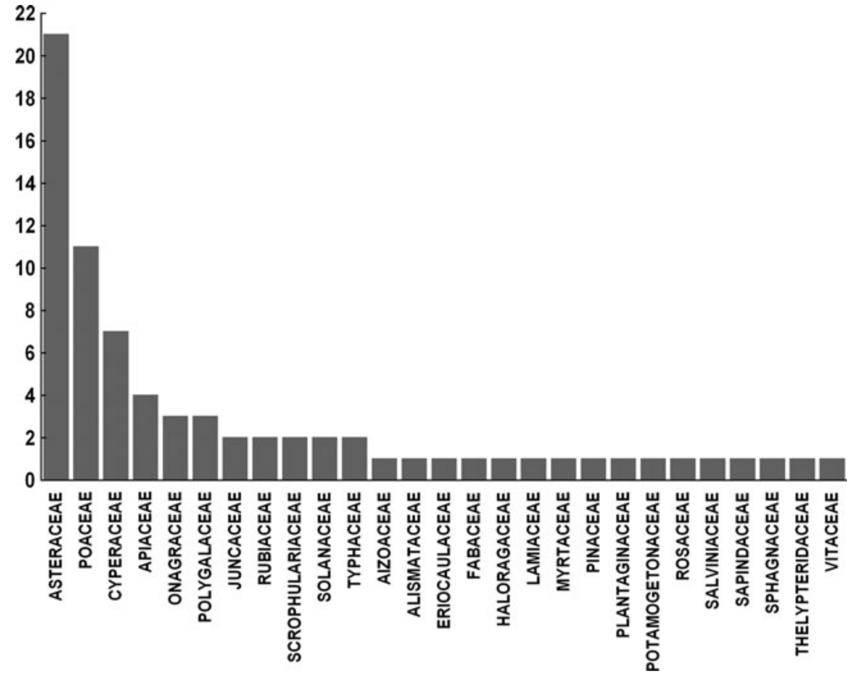

Fig. 3 Frequencies diagram: number of species per family registered in the study area

$S = 10$. Group 4, Hydrophilic pasture stands (HPS2, HPS3) (Fig. 2). This is a dense pasture located in the interdune depressions which only reaches 0.5-meters in height. The indicative species is *Juncus* sp. L. (IV = 92.3) followed by *P. pumilum* Ness (IV = 66.2) (Table 1). This group presented an observed richness of $S = 7$. Group 5, *Eryngium* stands (ES1, ES2) (Fig. 2). It is an herbaceous stratum continuum of 1.5-meters in height that grows in a semipermanent flooded area located in the interdune depressions. The indicative species is *E. pandanifolium* Cham. & Schltdl. (IV = 97.6) (Table 1). This group presented an observed richness of $S = 12$. Group 6, *Typha* stands (TyS1, TyS2, TyS4, TyS5) (Fig. 2). It is a gramineous stratum continuum of 2 m in height that grows in a permanent flooded area located in the interdune depressions. The indicative species is *T. dominguensis* Pers. (IV = 92.7) (Table 1). This group presented the highest observed richness ($S = 19$). Groups 2–6 are located in humid areas equivalent to zone III in Legrand's work where the most abundant species were: *Cyperus prolixus* Kunth, *Juncus microcephalus* Kunth, *Leiothrix arechavaletae* (Körn.) Ruhland, *Lycopodiella alopecuroides* (L.) Cranfill, *Scleria distans* Poir., *Typha domingensis* and *Xyris jupicai* Rich (Table 2). The comparison between interdunes depressions (present data) versus zone III of Legrand also report a low degree of similarity ($J = 0.22$).

Group 7, *Acacias* stands and psammophilic grassland stands (PGS1, PGS2, AS1, AS2, AS3) (Fig. 2). It is a 0.50 m high herbaceous stratum that grows on fixed dunes mixed with an arboreal stratum of *A. longifolia*. The indicative species is *A. longifolia* (IV = 80.0) followed by *A. satureioides* (Lam.) DC. (IV = 60.0) and *A. trigynum* (Spreng.) H. Pfeiff. (IV = 54.9) (Table 1). This group had the same values of observed richness as group 6. This group is located in areas equivalent to zone IV in Legrand′s work (1959) where the most abundant species were *A. satureioides, Andropogon selloanus* (Hack.) Hack., *Noticastrum diffusum* (Pers.) Cabrera, *Dichanthelium sabulorum* (Lam.) Gould & C.A. Clark, *Eragrostis bahiensis* Roem. & Schult., *Eragrostis trichocolea* Arechav., *Gamochaeta stachydifolium* (Lam.) Cabrera, *Helianthemum brasiliense* (Lam.) Pers., *H. bonariensis* Lam., *P. racemosum* (P. Beauv.) Spreng., *S. crassiflorus* (Poir.) DC., and *Sisyrinchium vaginatum* Spreng. (Table 2). The

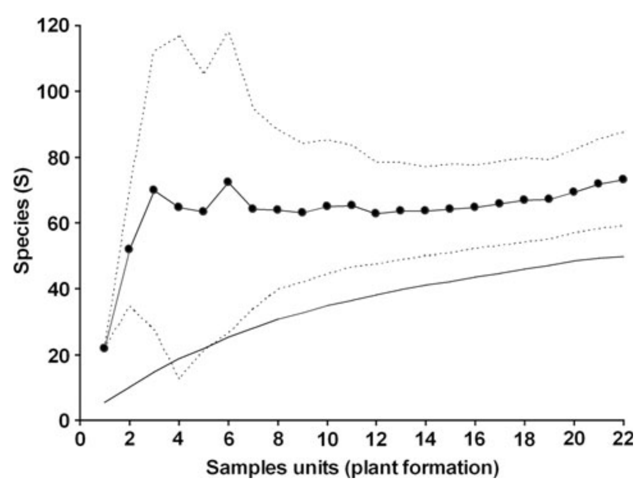

Fig. 4 Measure of species richness (*lower continuous curve*), performance of diversity estimator Chao 2 (*continuous curve with dots*) and its standard deviation (*dotted curves*) for the 22 samples of vegetation stands. Data from Estimates using 1,000 replications

Table 2 Legrand's (1959) list of species for the study area

Species	Family	Zone		Abundance category
Iresine portulacoides (A. St.-Hil.) Moq.	Amaranthaceae	I	+	Sparse
Eryngium pandanifolium Cham. & Schltdl.	Apiaceae	III		nc
Hydrocotyle bonariensis Lam.	Apiaceae	I, II, III, IV		Abundant
Acanthospermum australe (Loefl.) Kuntze	Asteraceae	IV	+	Frequent
Achyrocline satureioides (Lam.) DC.	Asteraceae	IV		Abundant
Baccharis genistifolia DC.	Asteraceae	IV	+	Frequent
Baccharis gnaphalioides Spreng.	Asteraceae	IV		Frequent
Baccharis microcephala Baker	Asteraceae	III, IV	+	nc
Baccharis rufescens Spreng.	Asteraceae	IV	+	Frequent
Baccharis spicata (Lam.) Baill.	Asteraceae	III		nc
Berroa gnaphalioides (Less.) Beauverd	Asteraceae	IV	+	Frequent
Conyza blakei (Cabrera) Cabrera	Asteraceae	II	+	nc
Conyza sp. Less.	Asteraceae	III, IV	+	nc
Gamochaeta calviceps (Fernald) Cabrera	Asteraceae	II	+	nc
Gamochaeta falcata (Lam.) Cabrera	Asteraceae	II	+	nc
Gamochaeta stachydifolium (Lam.) Cabrera	Asteraceae	I, II, IV	+	Abundant
Pluchea sagittalis (Lam.) Cabrera	Asteraceae	III		nc
Senecio crassiflorus (Poir.) DC.	Asteraceae	II, IV		Very frequent
Cakile maritima Scop.	Brassicaceae	I	*+	Sparse
Calycera crassifolia (Miers) Hicken	Calyceraceae	I, II	+	Abundant
Pratia hederacea (Cham.) G. Don	Campanulaceae	III	+	Abundant
Helianthemum brasiliense (Lam.) Pers.	Cistaceae	IV	+	Abundant
Noticastrum diffusum (Pers.) Cabrera .	Compositae	IV	+	Abundant
Calystegia soldanella (L.) Roem. & Schult.	Convolvulaceae	I	+	Rare
Androtrichum trigynum (Spreng.) H. Pfeiff.	Cyperaceae	III		Abundant
Cyperus prolixus Kunth	Cyperaceae	III	+	Abundant
Cyperus reflexus Vahl	Cyperaceae	III	+	nc
Cyperus rigens J. Presl & C. Presl	Cyperaceae	III, IV	+	nc
Eleocharis sp. R. Br.	Cyperaceae	III		nc
Kyllinga vaginata Lam.	Cyperaceae	III	+	nc
Rhynchospora brownii Roem. & Schult.	Cyperaceae	III	+	nc
Rhynchospora microcarpa Baldwin ex A. Gray	Cyperaceae	III	+	nc
Schoenoplectus californicus (C.A. Mey.) Soják	Cyperaceae	III		nc
Scleria distans Poir.	Cyperaceae	III	+	Abundant
Drosera brevifolia Pursh	Droseraceae	III	+	nc
Eriocaulon modestum Kunth	Eriocaulaceae	IV	+	nc
Leiothrix arechavaletae (Körn.) Ruhland	Eriocaulaceae	III	+	Abundant
Syngonanthus gracilis (Bong.) Ruhland	Eriocaulaceae	III	+	Sparse
Stylosanthes leiocarpa Vogel	Fabaceae	IV	+	Frequent
Laurembergia tetrandra (Schott ex Spreng.) Kanitz	Haloragaceae	III	+	nc
Sisyrinchium vaginatum Spreng.	Iridaceae	IV	+	Abundant
Juncus acutus L.	Juncaccea	III		nc
Juncus microcephalus Kunth	Juncaceae	III	+	Abundant
Juncus scirpoides Lam.	Juncaceae	III	+	nc
Juncus sp. L.	Juncaccea	III		nc
Utricularia gibba L.	Lentibulariaceae	III	+	nc
Utricularia tridentata Sylvén	Lentibulariaceae	III	+	nc
Lycopodiella alopecuroides (L.) Cranfill	Lycopodiaceae	III	+	Abundant

Table 2 continued

Species	Family	Zone		Abundance category
Lycopodiella caroliniana (L.) Pic. Serm.	Lycopodiaceae	III	+	Scarce
Oenothera mollissima L.	Onagraceae	II, IV	+	Frequent
Ludwigia hookeri (Micheli) H. Hara	Onagraceae	III		nc
Plantago brasiliensis Sims	Plantaginaceae	IV	+	Frequent
Andropogon selloanus (Hack.) Hack.	Poaceae	IV	+	Abundant
Chascolytrum erectum (Lam.) Desv.	Poaceae	IV	+	Frequent
Cortaderia selloana (Schult. & Schult. f.) Asch. & Graebn.	Poaceae	III		nc
Dichanthelium sabulorum (Lam.) Gould & C.A. Clark	Poaceae	IV	+	Abundant
Eragrostis bahiensis Schrad. ex Schult.	Poaceae	IV	+	Abundant
Eragrostis trichocolea Arechav.	Poaceae	IV	+	Abundant
Ischaemum minus J. Presl	Poaceae	III	+	nc
Panicum racemosum (P. Beauv.) Spreng.	Poaceae	I, II, IV		Abundant
Paspalum pumilum Nees	Poaceae	III		nc
Paspalum vaginatum Sw.	Poaceae	I	+	Rare
Piptochaetium panicoides (Lam.) E. Desv.	Poaceae	IV	+	Frequent
Poa lanuginosa Poir.	Poaceae	II, IV	+	Frequent
Poidium uniolae (Nees) Matthei	Poaceae	III	+	nc
Polypogon chilensis (Kunth) Pilg.	Poaceae	III	+	nc
Schizachyrium condensatum (Kunth) Nees	Poaceae	III	+	nc
Spartina ciliata Brongn.	Poaceae	I, II		Scarce
Polygala cyparissias A. St.-Hil. & Moq.	Polygalaceae	II, IV	+	Frequent
Polygala tenuis DC.	Polygalaceae	III	+	nc
Rumex cuneifolius Campd.	Polygalaceae	II	+	nc
Anagallis filiformis Cham. & Schltdl.	Primulaceae	III	+	nc
Margyricarpus pinnatus (Lam.) Kuntze	Rosaceae	II, IV		nc
Mitracarpus megapotamicus (Spreng.) Kuntze	Rubiaceae	IV	+	nc
Richardia brasiliensis Gomes	Rubiaceae	IV	+	nc
Dodonaea viscosa Jacq.	Sapindaceae	IV		nc
Bacopa monnieri (L.) Wettst.	Scrophulariaceae	III		nc
Scoparia montevidensis (Spreng.) R.E. Fr.	Scrophulariaceae	IV	+	Frequent
Typha domingensis Pers.	Typhaceae	III		Abundant
Xyris jupicai Rich.	Xyridaceae	III	+	Abundant

Zone (I, II, III and IV) and abundance category correspond to Legrand′s observations. The scientific names follow Instituto de Botánica Darwinion (2011), Royal Botanic Gardens (2011) and (W^{3}TROPICOS 2009)

nc not categorized by Legrand, sparse, frequent, very frequent, and abundant, + exclusive species of Legrand′s survey, * non-native species

lowest similarity is reported for the comparison of the fixed dunes (present data) versus zone IV of Legrand ($J = 0.08$).

Rarefaction curves showed that group 1 (psammophilic steppe stands and psammophilic pasture stand in foredunes) had the lowest observed and expected richness (Fig. 6). Interdune depressions had a wide range of richness values (Fig. 6). Group 4 (hydrophilic pasture stands) had the lowest richness, followed by group 3 (hydrophilic pasture stand and *Typha* stand of *T. latifolia*) (Fig. 6). Group 5 (*Eryngium* stand) had a higher richness than group 3 and, although it has a lower observed richness than group 2 (*Schoenoplectus* stands and *Thelypteris* stand), they did not differ significantly in their expected richness (Fig. 6). Group 6 (*Typha* stands of *T. dominguensis*) showed the highest observed richness of all groups of the interdune depressions and had similar values with group 7 (Fig. 6).

None of the species registered at the study area, in ours and Legrand's survey, has been evaluated and included at the "IUCN Red List of Threatened Species" (IUCN 2009), at local or global level. However, local evaluations using IUCN criteria (see Marchesi et al. 2008; Alonso Paz et al. 2009) considered *Eriocaulon modestum* Kunth, *Anagallis filiformis* Cham. & Schltdl. and *Syngonanthus gracilis* (Bong.) Ruhland as species with restricted distributions and in a retraction process by the action of human impact, and *Laurembergia tetrandra* (Schott) Kanitz a species in a

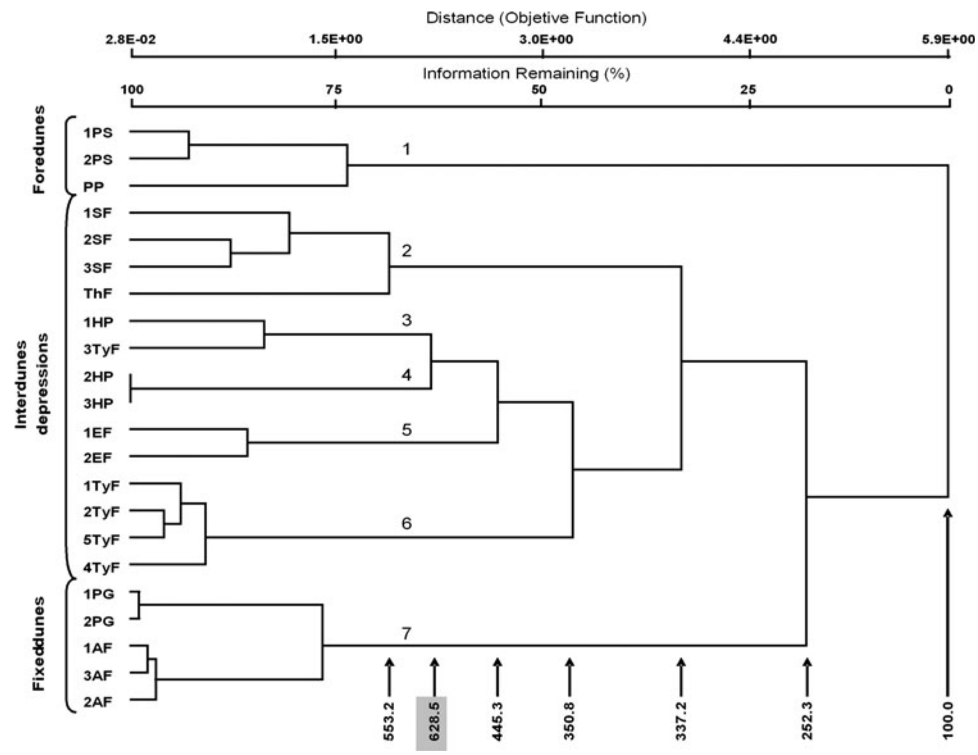

Fig. 5 Cluster analysis of the plant associations based on Jaccard′s distance and Ward′s method

retraction process with a socioeconomic value. All these species were registered in Legrand′s survey. We report here *Eleocharis sellowiana* Kunth, which is a species in a retraction process due to human impacts, and *Paspalum notatum* Flüggé, a species that has a restricted distribution but high socioeconomic value (Alonso Paz et al. 2009). We also reported the following non-native species: *Carpobrotus edulis* (L.) N.E. Br., *Centella asiatica* (L.) Urb., *Cirsium* sp. Mill, *Hypochoeris radicata* L., *Sonchus asper (L.) Hill*, *A. longifolia*, *Pinus maritima* Mill., *Cynodon dactylon* (L.) Pers. (Table 1). Legrand (1959) registered *Cakile maritima* Scop. as the only non-native species (Table 2).

Discussion

The global tendency of the introduction of Australian acacias to fix dune systems at the beginning of the 20th century, with the goal of expanding and improving agro-productive and urban areas, was also imposed in Uruguayan coastal ecosystems (Carruthers et al. 2011; Kull et al. 2011). The study area at the shore of the "de la Plata" River in the seaside resort "El Pinar," Canelones, Uruguay, corresponds to a relic dune system of a larger ecosystem that was modified with the introduction of *A. longifolia* and *Pinus spp*. for urban development (Legrand 1959; Gutiérrez and Panario 2005). This ecosystem management has produced large landscape modifications, affecting the soil, fire regimes, water availability, and the composition, structure, and dynamics of native vegetation in our study area, as has been reported in other studied dunes systems (Marchante et al. 2010, 2011b; Morris et al. 2011).

Representativeness of families of plant species at the study area agrees with the research of Delfino and Masciadri (2005) for the oceanic Uruguayan seashore, where Asteraceae and Poaceae were the prevailing families. Fontana (2005), at "Bahía Blanca," Buenos Aires, Argentina, found these two families to be the most abundant, but with Poaceae more common than Asteraceae. When comparing the description of plant species composition of each environment (i.e., foredunes, interdune depressions, and fixed dunes) written by Legrand (1959) with our results, we found similar indicator species. Legrand recognized this species as indicative based on their experience and by not using a statistical index like the indicator value (Dufrene and Legendre 1997). In spite of this similarity in the indicator species, one major result from the historical perspective is the low similarity of species composition between the present and past communities. Recognizing the causes behind this pattern is a major concern for ecological science and in particular for restoration ecology (Suding 2011).

In this sense, the existence of local evaluations of conservation status of species (see Marchesi et al. 2008; Alonso Paz et al. 2009), allowed us to verify that some species registered by Legrand had conservation problems and disappeared from the study area. Nevertheless, the magnitude of this change is due to the loss of these

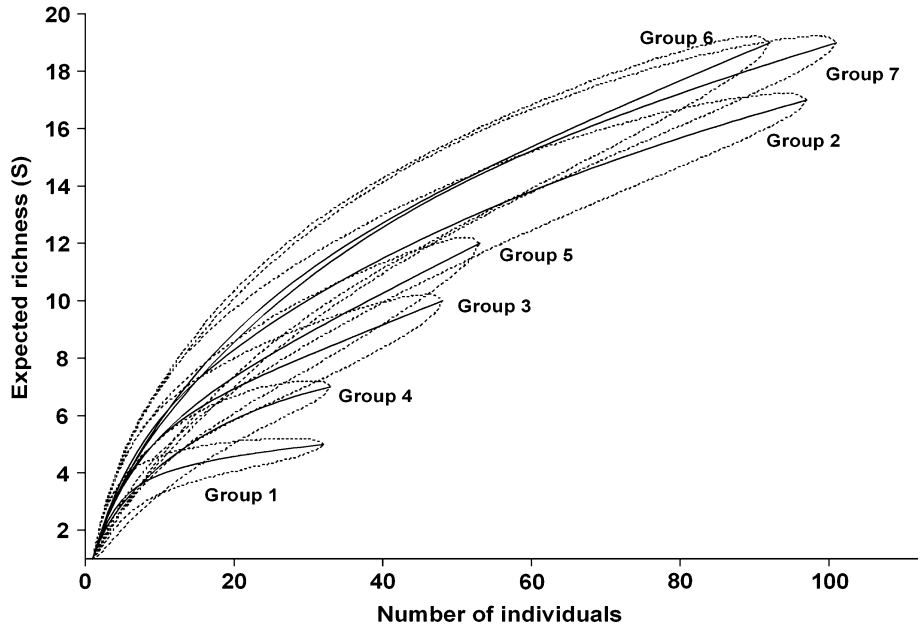

Fig. 6 Rarefaction curves showing mean expected richness and 95 % confidence intervals for each of the seven groups of the cluster analysis

threatened species. We observed a great change in the floristic composition and vegetation structure in less than 100 years in this system of coastal dunes, accompanied by the presence of non-native and in some cases invasive species (*C. edulis*, *C. asiatica*, *Cirsium* sp., *H. radicata*, *S. asper*, *A. longifolia*, *P. maritima*, *C. dactylon*). The agglomerative cluster analysis allowed us to identify seven plant groups which were associated with three coastal environments: foredunes, interdune depressions, and fixed dunes. The foredunes harbor communities of pioneer psammophilic plants (Hesp 2002). In this extreme environment, the action of the wind triggers mechanical and physiological effects in vegetation (e.g., abrasive effect, increase of transpiration rate, homeostatic changes) leading to a reduced number of species becoming established (Herrmann et al. 2008; Judd et al. 2008). As it was reported by Cordazzo and Seeliger (1993) for the Atlantic coast of "Río Grande do Sul," Brazil and by Fontana (2005) for "Bahía Blanca," Buenos Aires, Argentina, the least diverse plant association was located in the foredunes, where *P. racemosum*, *S. crassiflorus*, and *S. ciliata* were indicators of this psammophilic extreme environment. These species have special importance for conservation of dune systems because they contribute to the regeneration of foredunes after storms (Cordazzo and Davy 1999; Hesp 2002). From a conservation perspective, we witnessed an extreme retraction of a shore environment, because Legrand (1959) described that this plant association extended for 200 m from the beginning of the foredunes (i.e., zone I and II) and currently it only reaches about 20 m.

Behind foredunes we found interdune depressions. Here, the outcrop of the water table generates a moisture increase leaving the ground permanently or semi-permanently flooded. At interdune depressions wind and abrasive effects of transportation of sand decrease, hydrophilic plant associations become established and the specific diversity as well as the number of plant groups increases (Cordazzo and Seeliger 1993; Fontana 2005). The indicative species are the highest emergent herbs adapted to flooded environments: *E. pandanifolium*, *S. californicus*, *Juncus* sp. and *T. dominguensis* (Grace and Wetzel 1981; Grace 1989; Newman et al. 1996; Costa et al. 2003; Calviño and Martínez 2007). *Mikania* sp. was abundant in humid environments climbing on stems of *T. latifolia* (Lombardo 1983). *L. arechavaletae* is a perennial grass considered endemic for Uruguay with records from the Departments of Montevideo and Rivera. This species has been observed and categorized as "abundant" by Legrand (1959); however it has not been reported at the present study.

One of the most diverse environments was the fixed dunes where the indicator species were common in coastal dunes: *A. satureioides*, *A. trigynum* and an alien species *A. longifolia* (Legrand 1959; Lombardo 1983, 1984). This environment presents the lowest similarity between present and past. We associate this striking change with the presence of *A. longifolia*, as has been noted in several other places (e.g., Marchante et al. 2008, 2009, 2010, 2011b; Morris et al. 2011). This species presents ecophysiological traits associated to the resources acquisition that confers competitive advantages over native species (e.g., initial high relative growth rates, N_2 fixing symbioses and the development of ectomycorhitic symbiosis), and generates modifications in the composition of nitrogen and carbon, nutrients cycling, and in microbial soil processes (Smith and Read 2008; Morris et al. 2011). *A. longifolia* is considered a species with an extremely high invasive potential and an ecosystem transformer species (sensu Richardson et al. 2000; Marchante et al. 2008, see also Table 1 in Wilson et al. 2011). When it appears it modifies the community composition, species richness, and soil ecology (Marchante et al. 2008, 2009; Marchante 2011; Echeverría et al. 2009; Wilson et al. 2011). In terms of the environmental change, the *Acacia* stands can be interpreted as the psammophilic grassland stands invaded and modified by *A. longifolia* which gives a colonization opportunity to other non-native species (*C. asiatica* (L.) Urb., *C. dactylon* (L.) Pers.) (Marchante et al. 2011b).

In this context of extreme change of coastal plant communities, we consider the necessity of implementation of management plans for the restoration at least for the fixed dunes of the costal ecosystems of Canelones, Uruguay. Now we have a theoretical and empirical framework generated by the experience of almost 200 years of introduction of Australian acacias in many ecosystems around the world (see special issue: "human-mediated introductions of Australian acacias—a global experiment in biogeography", Diversity and Distribution 2011). This knowledge has led to the proposal of a set of management strategies for *A. longifolia* (van Wilgen et al. 2011; Wilson et al. 2011). Given the scarcity of local knowledge about the naturalization, invasion, and effects on native communities of *A. longifolia* in Uruguay, we encourage the development of an investigation program to assess the effectiveness and challenges of the potential management practices.

To achieve the greatest benefit with the management strategy, we suggest prioritizing the fixed dunes as the spatial areas of action. The population of *A. longifolia* in this environment has a low socioeconomic value [in this area it has not been considered a timber resource like in other places such as South Africa (see van Wilgen et al. 2011; Wilson et al. 2011) and it has invaded a low area. Although the species is invasive in all dune systems of the Uruguayan coast, we consider that the area invaded the study area is low due it being confined to a narrow strip of relict dunes. In this scenario, van Wilgen et al. (2011) suggest applying the tactic of eradication including a combination of different practices of management (see Fig. 3 in van Wilgen et al. 2011): manual control operations, biologic control agents [e.g., bud-galling wasp *Trichilogaster acaciaelongifoliae* (Hymenoptera: Pteromalidae) and seed-feeding weevil *Melanterius ventralis* (Coleoptera: Curculionidae)] and the use of fire. These management practices will have effects on the seed bank, buds, juvenile, and adult plants (Le Maitre et al. 2011, Marchante et al. 2010, 2011a, b, c, Wilson et al. 2011).

Despite the importance of the conservation of coastal environments, this area has been impacted for a century by human activities, primarily recreation and urbanization. In Uruguay, as in many other coastal areas around the world, plantations, dune fixation, and high human pressure have produced important modifications in the health of coastal dunes. The historical knowledge compared with the present status of the coastal ecosystems has allowed us to understand and disentangle causes and processes behind the ecological change. In consequence, we encourage progress in the design of a management program to control the *A. longifolia* invasion and the restoration of Uruguayan coastal dune systems.

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