ORIGINAL RESEARCH

Small Mammals Along SW-Atlantic Marshes: Diversity Correlates with Inland Habitats but Abundance Correlates with Marsh Characteristics

Alejandro D. Canepuccia · Jesús Pascual ·
Laura M. Biondi · Oscar O. Iribarne

Abstract Tidal marshes are narrow wetlands distributed worldwide between the ocean and a variety of inland-habitats. The high diversity of interacting terrestrial habitats may influence terrestrial species composition and abundance in marshes. We investigated if characteristics of small mammal assemblages inhabiting the South-West-Atlantic (SWA) marshes are influenced by marsh characteristics, or if they vary in relation to changes in the inland biogeographic context. Sampling at five-Spartina marshes across the SWA-coast showed that plant cover, richness and height (ANOVA analysis) and small mammal assemblages (PERMANOVA analysis) differed between habitats (marsh or inland) depending on the site. Generalized Linear Models (GLMs) showed that abundance of small mammals in marshes is related to vegetation cover and diversity. However, its richness was related to the richness of small mammal at the inland habitats. In fact, species present in each marsh were also recorded in adjacent inland habitats. Species composition differed among similar marshes surrounded by different landscapes, while those in the same landscape did not. Consequently, regional abundance of small mammals in SWA-marshes is consistent with ecological sorting of abundance ranges along environmental gradients (e.g., plant-cover and richness). In contrast, landscape composition and configuration strongly affect marsh small mammal species assemblages, even if the marsh-habitats are quite similar.

A. D. Canepuccia (✉) · J. Pascual · L. M. Biondi · O. O. Iribarne
Instituto de Investigaciones Marinas y Costeras (IIMyC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Mar Del Plata (UNMDP), CC 573 Correo Central, (7600), Mar del Plata, Argentina (B7600WAG)
e-mail: acanepuc@mdp.edu.ar
e-mail: acanepuccia@hotmail.com

Introduction

Understanding how the abundance and diversity of species changes in relation to the landscape context is important to identify the factors driving community structure and biodiversity patterns at regional scale (e.g., Andersen et al. 2012; Tscharntke et al. 2012). Tidal marshes are narrow coastal ecosystems occurring worldwide along low-energy coastlines in mid- to high-latitudes (Chapman 1977). These ecosystems are ecotones between terrestrial and marine environments, and can range from entirely marine to terrestrial environments across a few meters (Mitsch and Gosselink 1993). As production hotspots (e.g., Day et al. 1989; Mitsch and Gosselink 1993), tidal marshes provide habitat and food to many terrestrial vertebrates (Greenberg 2006; Greenberg and Maldonado 2006; Canepuccia et al. 2010) driving species turnover with the inland environment. However, given that the tidal marshes are exposed daily to tidal flooding, which may increase sediment salt accumulation and generate drastic changes in temperature (Adam 1993), these environments are physically harsh (e.g., Bertness and Hacker 1994; Greenberg 2006). Due to the adaptive challenge of animals attempting to colonize such habitats, marshes show a large number of quite distinctive species or subspecies (e.g., turtles: *Malaclemys terrapin terrapin*, snakes: *Nerodia clarkia clarkii*, birds: *Cistothorus palustris palustris*, shrews: *Sorex cinereus nigriculus*, and small mammals: *Microtus californicus paludicola*, Greenberg 2006; Greenberg and Maldonado 2006). Moreover, given their worldwide distribution, these relatively simple environments border diverse continental (hereafter inland) and marine habitats. The diversity of inland

habitats that border tidal marshes may act as biological filters (Woodward and Diament 1991; Tscharntke et al. 2012), changing the species composition among similar marshes. Thus, tidal marshes constitute interesting habitats to investigate the effects of different types of adjacent habitats on the abundance and diversity of marsh organisms.

Among terrestrial vertebrates, small mammals are common tidal-marsh inhabitants worldwide (North American: Greenberg 2006; England: Crain 2008; Gedan et al. 2009; South American: Canepuccia et al. 2008a; Canepuccia et al. 2010). Although common, only a few small mammal species are capable of living in these constraining environments (e.g., Greenberg and Maldonado 2006; Crain 2008; Canepuccia et al. 2008a), often including endangered and specialized species such as the salt marsh harvest mouse *Reithrodontomys raviventris* and the Florida salt marsh vole *Microtus pennsylvanicus dukecampbelli* (Greenberg 2006). This is not surprising given the high level of differentiation of tidal marsh taxa (Greenberg 2006), the restricted distribution of this habitat (Greenberg 2006; Valiela and Fox 2008), and the degradation of a large proportion of tidal marshes (Valiela and Fox 2008). However, the dynamics and diversity of small mammals in these environments are virtually unknown.

Some of the most extensive *Spartina* marshes of the South West Atlantic (SWA) coastline are found between the La Plata River (35° 13′ S) and the northern part of the Argentinean Patagonia (40° 50′ S; Isacch et al. 2006, Fig. 1). These *Spartina* marshes are distributed along a gradient of precipitation, decreasing from 1,200 mm in the north to 200 mm in the south (Isacch et al. 2006; Canepuccia et al. 2013). This gradient of precipitation may affect the abundance and distribution of small mammals (Stenseth et al. 2002; Canepuccia et al. 2008b; Canepuccia et al. 2010) by driving changes in salinity stress in marsh sediment and marsh vegetation structure (Canepuccia et al. 2010). In addition, the precipitation gradient may also influence the type of inland habitat that surrounds the *Spartina* marshes (Cabrera and Willink 1973). Consequently, these *Spartina* marshes may be adjacent to different inland habitats (Canepuccia et al. 2013; see Fig. 1). The northern marshes are limited by Pampa grassland, which is dominated by a grass steppe. Marshes located in the south are surrounded by different species of shrubs and halophytic grasses which are characteristic of the Monte landscape (Canepuccia et al. 2013). Thus, these relatively narrow and homogeneous *Spartina* marshes develop between one marine biogeographic province (Argentine province; Boschi 2000; Balech and Ehrlich 2008; Fig. 1) and two different inland

Fig. 1 Marshes sampled along the SW Atlantic coast. SC: San Clemente (36° 22′ S); MCH: Mar Chiquita (37° 32′ S); BB: Bahia Blanca (38° 43′ S); BA: Bahía Anegada (39° 48′ S); and BSA: Bahía San Antonio (40° 42′ S). SC and MCH are limited at the inland side by Pampas grasslands (*striped area*). BB, BA and BSA are limited at the inland side by Monte vegetation (*dotted area*). The coast between the arrows shows the area of development of tidal marshes dominated by *Spartina* spp. grasses. The dashed line indicates the geographic range of the Temperate Argentine Biogeographic Marine province. The isohyets for the study sites are gray lines with the rainfall values in millimeters obtained by averaging the period 1961 to 1990 (Argentinean National Weather Service, Servicio Meteo-rológico Nacional Argentino)
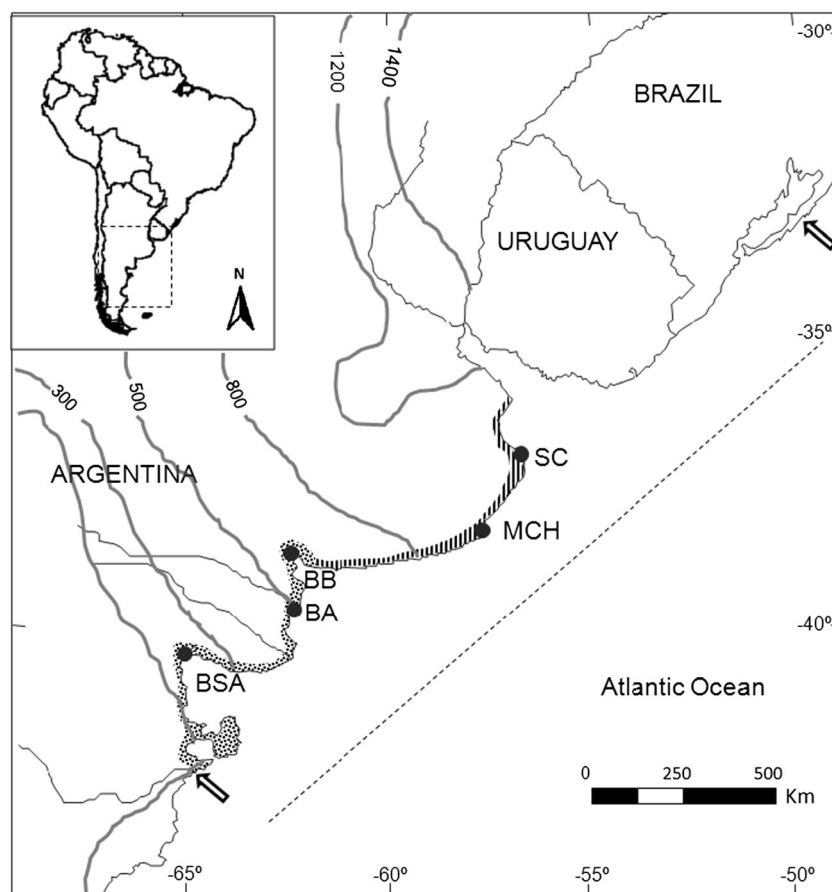
habitat types, which may affect the abundance and composition of small mammals in marshes.

Because of the high level of differentiation of tidal marsh taxa, and the restricted distribution of these habitats (Greenberg 2006), we could expect some quite distinctive species of small mammals from tidal marshes (Greenberg and Maldonado 2006), and their abundance being related to the habitat structure and floristic composition of marshes (Dalby 1975; Kravetz and Polop 1983; Eubanks et al. 2011). However, a contrasting scenario can be expected from a biogeographic perspective. Considering the narrowness of these habitats, it could be expected that the identities and abundance of these vertebrates are driven by the biogeographic changes in the outlying inland habitats (regional species pools of the matrix). In fact, the only information available show that species of small mammals inhabiting in a SWA marsh (Mar Chiquita coastal lagoon, 37° 45′ S), such as the Azara's grass mouse *Akodon azarae* and the yellow pygmy rice rat *Oligoryzomys flavescens*, are the same recorded in adjacent inland habitats (Canepuccia et al. 2008a, b). Thus, different tidal *Spartina*- marshes could have different species composition and abundance concordantly with species composition and abundance in adjacent inland habitats ('landscape-divergence hypothesis' Laurance et al. 2007; Tscharntke et al. 2012). Knowledge of the relationships between small mammal communities in tidal marshes and those in adjacent inland habitats is required to understand factors influencing community structure and diversity patterns at the landscape level. Here we test the hypothesis that landscape-type modulates local abundance and diversity of small mammals in tidal marshes. We describe general biogeographic patterns of small mammals in tidal *Spartina* marshes located along the SWA coastline, and explore (a) if small mammals are marsh-specific species or just represent a subset of species present in the adjacent inland habitat, and (b), whether small mammal abundance in these marshes is related with marsh characteristics (e.g., precipitation, marsh area, cover and plant species richness) or depends on the characteristics of adjacent inland habitats (e.g., abundance of small mammals, plant cover and plant species richness).

Methods

Study Sites

The study was carried out in five tidal marshes along the SWA coast, including some of the most extensive SWA *Spartina* marshes (Isacch et al. 2006). These marshes are extensive but discontinuous (Isacch et al. 2006). Sampling sites were: Mouth of La Plata River (San Clemente: SC, 36° 22′ S), Mar Chiquita coastal lagoon (MCH: 37° 45′ S), Bahía Blanca (BB: 38° 43′ S), Bahía Anegada (BA: 39° 48′S), and Bahía San Antonio (BSA: 40° 42′ S; Fig. 1).

Astronomical micro-tides in the north sites (SC=0.75 m, MCH=0.75 m) contrast with meso-macro tides that increases to the south sites (BB=2.44 m, BA=1.64 m, BSA=6.44 m, Isacch et al. 2006). These tidal marshes are similar in plant composition and topography, and marsh - inland borders topography is similar in shape (e.g., development and height). However, these marshes are adjacent to different inland habitats that represent several biogeographic provinces (see Cabrera and Willink 1973). The northern marshes (SC and MCH) are surrounded by the Pampas grasslands Biogeographic Province, characterized by herbaceous stratus which is dominated by the silver pampas grass *Cortaderia selloana* and the spiny rush *Juncus acutus*. These marshes are characterized by higher precipitation (SC=950 mm year^{-1}, MCH=920 mm year^{-1}, Canepuccia et al. 2013) than southern marshes and are subject to freshwater input from La Plata River estuary (caudal around 22,000 m^3 s^{-1}). Marshes in the middle portion of our study area received intermediate levels of precipitation (BB=645 mm year^{-1}, BA=500 mm year^{-1} Canepuccia et al. 2013), while the southernmost marsh received the lowest level of precipitation (BSA= 248 mm year^{-1}, Canepuccia et al. 2013). BB, BA and BSA marshes were adjacent to Monte Biogeographic Province on the landward side (Fig. 1), such as xeric bushes (e.g., *Atriplex lampa* and *Cyclolepis genistoides* and *Frankenia juniperoides*, Canepuccia et al. 2013).

Sampling of Small Mammal Species in Tidal Marshes and Inland Habitat

To evaluate if small mammal species in tidal marshes were influenced by adjacent inland habitats, we sampled small mammals in the *Spartina* marshes as well as in adjacent terrestrial environments. For each study site, we stratified our samples at three habitats: (a) the mid-marsh zone, which is frequently flooded by a monthly high tide; (b) the high-marsh zone, where flooding occurs only during extraordinary highest spring tides; and, (c) the adjacent inland or terrestrial habitats which are not flooded by tides. Both marsh zones [(a) and (b)] are dominated by *S. densiflora* followed by the perennial glasswort *Sarcocornia perennis* (Isacch et al. 2006). The inland habitats are dominated by different plant assemblages, depending on the biogeographic regions (see Study Area section). In the low-marsh zone (dominated by *S. alterniflora*) Sherman traps would be flooded twice a day by regular tides, which would likely result in the death of trapped animals. Consequently, though small mammals could use the low marsh habitat between flooding events, no sampling was undertaken in this zone. Sampling was conducted twice: once in May (early winter in the Southern hemisphere) when small mammal abundance is known to be high (e.g.,

Canepuccia et al. 2008b), and once in October (early spring) when small mammal abundance is known to be lower (e.g., Canepuccia et al. 2008b). These three habitats in the five localities were sampled in the same weather conditions (clear sky), and within the same week period. Sampling was conducted by mean of Sherman live traps ($8 \times 9 \times 23$ cm), effective for trapping small mammals (e.g., Nicolas and Colyn 2006). We placed 10 grids (2×2) of 4 traps at 3 m interval at each marsh zone and in adjacent inland habitats at each site (total of 600 traps for each sampling date). Grids were located at least 25 m apart as this distance was greater than the observed daily movement of small mammals in a similar marsh (Canepuccia 2005). Traps were baited with mixed bovine fat and rolled oats (following Canepuccia et al. 2008b) and checked after 24 h. For each captured individual, we determined species identity and released the animal at the point of capture. Given the low plant species richness and homogeneous composition of *Spartina* marshes (a small number of plant species with a broad geographic distribution, e.g., Mitsch and Gosselink 1993), and standardization of trapping technique (e.g., grids size, time efforts, marsh height and location) across study sites, we assumed a similar capture probability among marshes. Trapping results were then used to estimate small mammal species richness and relative abundance (e.g., Provensal et al. 1995; Hodara et al. 2000). To test for differences in small mammal composition along the geographical gradient, permutational analysis of variance (PERMANOVA) was conducted using PRIMER 6 software (Clarke and Gorley 2006). Bray–Curtis abundance similarity matrices (Clarke and Warwick 2001) were constructed to test the multivariate null hypothesis of no differences in small mammal assemblage composition (species presence and relative abundance) among groups. To account for undefined values caused by absence of data, a dummy species value of 1 was added in all samples (Anderson et al. 2008). Differences in small mammal species composition were tested between different habitats (middle marsh, high marsh and inland), and between marshes at the same habitat type (SC, MCH, BB, BA, BSA). To obtain P-values (P_{perm}), all PERMANOVA tests relied on 9,999 permutations following the unrestricted raw data permutation method, which is the most appropriate for one-way cases, providing a type I error close to α (Anderson et al. 2008). *Posteriori* pair-wise comparisons using 4,999 random permutations were performed when PERMANOVA tests were significant at the 0.05 level.

Relation Among Small Mammal Abundance in Marsh and Habitat Characteristics

To evaluate if small mammal abundance and diversity was related to the structure and floristic composition of tidal marshes, we sampled marsh plants before the first round of small mammal trapping. Ten plots (3 m side, and 10 m apart)

were established in the middle of each marsh level. At each plot we visually estimated plant cover, plant species richness, and measured plant height (height of one plant randomly chosen within each plot). In addition, the extension of each marsh was obtained from Canepuccia et al. (2013). We used Tukey tests after a two-way ANOVA (Zar, 1999) to test the H_0 of no differences in the cover, height, and richness of marsh plant species among habitats, and among marshes at the same habitat type. To evaluate the relationship between environmental predictor variables (marsh area, cover, richness and height of plants, and precipitations) and small mammal species richness and abundance for each habitat type, we used Generalized Linear Models (GLMs). A GLM is a statistical framework that allows for non-normal data to be analysed by using link functions and exponential family of functions (e.g., normal, Poisson or binomial distributions (Crawley 2007; Bolker et al. 2009). The predictor variables considered for the models were marsh area, precipitation and plant characteristics (cover, heights and diversity) for high and middle marsh habitats, and precipitation and plant characteristics for the inland habitat. Response variables (relative abundance and richness of small mammals) were converted to proportions of the total number of traps in each grid and the maximal number of different possible species, respectively. Binomial error structure and log-link function were chosen to perform these models. We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate support for models with all possible combinations of predictor variables, including a global model with all predictors and a null model without predictors. Model selection was based on Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). We used two measures to provide further insight into the amount of uncertainty in model selection. The first measure was the difference in AIC_c between the best approximating model and all the other models (Burnham and Anderson 2002), termed ΔAIC_c. In general, a ΔAIC_c score between 0 and 2 indicates substantial support for the model (Burnham and Anderson 2002). The second measure calibrates models to provide relative plausibility by normalizing each model on the basis of its ΔAIC_c value, termed "model weight" (Anderson and Burnham 1999; Burnham and Anderson 2002). To evaluate the support for predictor variables parameter likelihood were estimated (Burnham and Anderson 2002); predictor variables with good support will have high parameter likelihood values (near 1). Parameter estimates were calculated by the technique of model averaging (model-averaged inference) from AIC_c weights for all candidate models (Burnham and Anderson 1998). Unconditional variances of those candidate models were used to calculate standard errors. To supplement evidence of important effects with parameter likelihoods, we also assessed the degree to which the 95 % confidence intervals of parameter estimates overlapped zero. We calculated upper and lower confidence

limits by adding or subtracting 2×SE, respectively. All statistical analyses were carried out using R software, version 2.15.0 (R Development Core Team 2012).

Results

Sampling of Small Mammal Species in Tidal Marshes and Inland Habitats

A total of 5 species of small mammals were recorded across all sites. In each sampled site, species recorded in the marsh habitat were also recorded in adjacent inland habitats (Table S1). The assemblages of small mammals of northern sites adjacent to Pampas grasslands (SC and MCH) were characterized by *A. azarae*, *O. flavescens* and the red hocicudo *Oxymycterus rufus*. The assemblages of southern sites adjacent to Monte vegetation (BA and BSA) were characterized by Molina's grass mouse *Akodon molinae*, and the long-tailed pygmy rice rat *Oligoryzomys longicaudatus*. At the intermediate geographic site (BB), which is adjacent to the Monte Biogeographic Province but also near to Pampas grassland Biogeographic Province (see Fig. 1), we recorded species from both, Pampas grasslands province (i.e., *A. azarae* and *O. flavescens*) and Monte province (*A. molinae* and *O. longicaudatus*). As a result, the richness of small mammals was higher in BB, decreasing to the north and south (Table S1).

In winter, there was an interaction effect of site (P perm< 0.001) and habitat (P perm=0.01) on the specific small mammal richness (interaction effect, P perm=0.001, Table 1). Thus, the high marsh zone showed the highest species richness in the middle of our study area (BB) which declined toward southern sites (BA: P perm=0.01 and BSA: P perm< 0.001) and northern sites (SC: P perm=0.02). But at inland habitats, the northernmost site (SC) showed higher richness, which decreased towards southern sites (BB: P perm=0.05, BA: P perm=0.05, and BSA: P perm=0.001). In the middle marsh zone there were no differences in species richness among sites (P perm>0.05, Table 1).

In spring, species richness of small mammals varied among sites (P perm<0.001, Table 1), but not among habitats (P perm=0.07, Table 1). The inland northern sites (SC and MCH) showed higher species richness, which diminished towards southern sites (BB and BSA, P perm<0.001). Meanwhile at the marsh level there were no difference in species richness among sites (P perm<0.001, Table 1).

In winter, the relative abundances (hereafter abundances) of small mammals varied among habitats, depending on the sites (interaction effect, P perm=0.009, Table 1). Small mammal abundance in inland habitats decreased from SC toward the southern inland sites (BB, P perm=0.006; BA, P perm=

0.02, and BSA, P perm=0.001, Fig. 2a). The inland habitat at the northernmost site (SC) showed higher small mammal abundance than the adjacent marsh (high marsh, P perm= 0.004, and middle marsh P perm=0.001, Fig. 2a) while small mammal abundance in all other inland sites did not differ from their respective adjacent marsh habitats (P perm>0.05 for all comparison, Fig. 2a). At high marsh zones in the middle of our study area (i.e., BB), small mammal abundance was highest, decreasing toward the north (SC: P perm=0.02, Fig. 2a) and the south (BA: P perm=0.01, BSA: P perm= 0.001, Fig. 2a). There were no differences in small mammal abundance among sites in the middle marsh zone (P perm> 0.05, Fig. 2a).

In spring, small mammal abundances varied among sites (P perm<0.001, Table 1), but not between habitats (P perm= 0.06, Table 1). A *posteriori* pair wise comparison among the factor "site" within each level of the factor "habitat" showed that, at inland habitats, small mammal abundances were higher in northern sites (SC and MCH bordered by Pampas grassland), declining toward the southern ones (BB and BSA bordered by the Monte, P perm<0.05, Fig. 2b). There were no differences in small mammal abundance among sites at the high and middle marsh zones (P perm>0.05, Fig. 2b).

Relation Among Small Mammal Abundance in Marsh, and Habitat Characteristics

Environmental variables (height, cover and richness of plants) differed among sites (ANOVA p<0.05, Table 2). There was an interaction effect of sites and the habitat on plant cover when compared among marshes (interaction effect; P<0.05, Table 2). As a result, in central sites (MCH, BB and BA) plant cover was greater at the high-marsh zone. The inverse result was observed in the southernmost site (BSA), and no differences were observed in the northernmost site (SC, Tukey after two-way ANOVA, P>0.05, Fig. 3a; Table 2). At the high marsh zone, plant cover was greater in the intermediate geographic sites (BB and BA), with the lower cover values recorded in southern sites (BSA, Fig. 3a). There was also an interaction effect between sites and habitat on plant height (Fig. 3b, interaction effect, P<0.05, Table 2). In central sites (MCH, BB and BA) plant height was greater in the high-marsh zone, while in marshes from both geographical extremes (SC and BSA) plant height did not differ between habitats (tukey after two-way ANOVA, P<0.05, Fig. 3b; Table 2). In relation to plant richness, there was an effects of site (two-way ANOVA, P<0.05, Fig. 3b; Table 2), but not habitat (P>0.05, Fig. 3b; Table 2) on plant richness. As a result, in the central geographical site (BB), plant richness was higher than in northern and southern sites (P<0.05, Fig. 3c).

GLMs indicate that, during winter, marsh area and plant diversity were the stronger variables predicting small mammal abundance in the high-marsh zone (Table 3). This model

Table 1 Statistical summary of the PERMANOVA analyzing of effect of factor sites (see Fig. 1) and factor habitats (see Fig. 2) on the relative abundance of small mammal in marshes and inland habitat along SWA coast

		Factor	df	SS	MS	P, seudo-F	P(perm)	Unique perms
Relative abundances	Winter	Site (S)	4	7,176.9	1,794.2	6.0479	<0.001	9,949
		Habiat (H)	2	3,670.9	1,835.5	6.187	0.002	9,951
		SxH	8	6,195.3	774.41	2.6104	0.009	9,919
		Residuals	135	40,050	296.67			
		Total	149	57,093		0	0	0
	Spring	Site	3	4,354.8	1,451.6	5.9989	<0.001	9,954
		Habiat	2	1,320.5	660.26	2.7286	0.062	9,961
		SxH	6	2,195.2	365.87	1.512	0.171	9,932
		Residuals	108	26,134	241.98			
		Total	119	34,004		0	0	0
Species richness	Winter	Site	4	5,711.5	1,427.9	6.7531	<0.001	9,949
		Habiat	2	2,364	1,182	5.5902	0.003	9,954
		SxH	8	4,567.9	570.98	2.7004	0.008	9,937
		Residuals	135	28,544	211.44			
		Total	149	41,188		0	0	0
	Spring	Site	3	3,299.5	1,099.8	5.7522	0.001	9,961
		Habiat	2	1,007.8	503.89	2.6354	0.070	9,949
		SxH	6	1,761.9	293.64	1.5358	0.171	9,938
		Residuals	108	20,650	191.2			
		Total	119	26,719		0	0	0
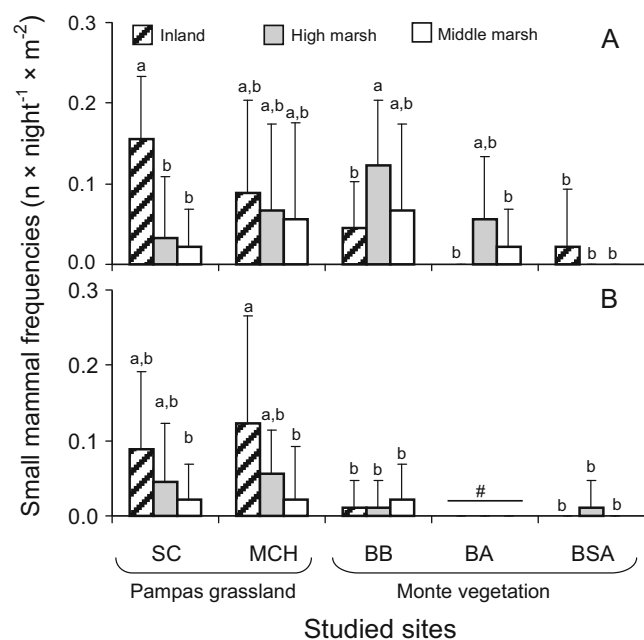
Fig. 2 Relative abundance of small mammals in two marsh heights (*middle* and *high*) and in its inland habitat, along five marshes of the SWA coast (see Fig. 1). (**a**) winter, and (**b**) spring. Here and thereafter bars represent mean values and vertical lines represent the standard deviation. Different letters indicate significant differences (*P*<0.05) by pair-wise comparisons using 9,999 random permutations when PERMANOVA tests were significant at the 0.05 level. (#) the sampling of small mammals was not possible due to great floods in this coastal area

accounted for 30 % of the variation in abundance and though there were other models with ∆AICc<2, which also included in plant cover, only marsh area and plant diversity showed high parameter likelihood (>0.80) and significant confidence intervals (without zero included, Table S2). These same variables showed a positive relationship with small mammal abundance. Regarding small mammal richness, the model with stronger support to this data included small mammal richness at inland habitat, as well as vegetation cover. This model accounted for 19 % of the variation in the response variable (Table S2). Small mammal richness at inland habitats and vegetation cover had a positive relationship with small mammal richness at the high-marsh zone, though only the former showed high parameter likelihood (0.91) and significant confidence intervals (Table S2).

At the middle marsh habitat, there was no significant relationship between any predictor and small mammal abundance and richness (Table 3a and b). In both cases, the null model was the one with the strongest support between all possible explanatory variable combinations (Table 3a and b).

For the inland habitat during winter, two models showed the highest support predicting small mammal abundance and richness; that is, cover and diversity of vegetation (Global model, 32 % of variance explained) for abundance data, and a single model with plant diversity (23 %) for small mammal richness (Table 3). Of the two predictor variables, only plant diversity showed importance as predictor variable for both

Table 2 Statistical summary of the two-way ANOVA analyzing of effect of factor sites (see Fig. 1) and factor habitats (see Fig. 1) on plant cover, plant heigh and plant richness in five marshes along SWA coast

|		SS	DF	MS	F	P
Plant cover	Site (S)	18,908.44	4.00	4,727.11	45.08	<0.01
	Habitat (H)	973.44	1.00	973.44	9.28	<0.01
	S x H	9,481.16	4.00	2,370.29	22.61	<0.01
	Error	9,436.60	90.00	104.85		
Plant height	Site (S)	63,134.56	4.00	15,783.64	147.15	<0.01
	Habitat (H)	1,040.06	1.00	1,040.06	9.70	<0.01
	S x H	2,492.95	4.00	623.24	5.81	<0.01
	Error	9,653.54	90.00	107.26		
Plant richness	Site (S)	11.76	4.00	2.94	10.89	<0.01
	Habitat (H)	0.81	1.00	0.81	3.00	0.09
	S x H	2.44	4.00	0.61	2.26	0.07
	Error	24.30	90.00	0.27		
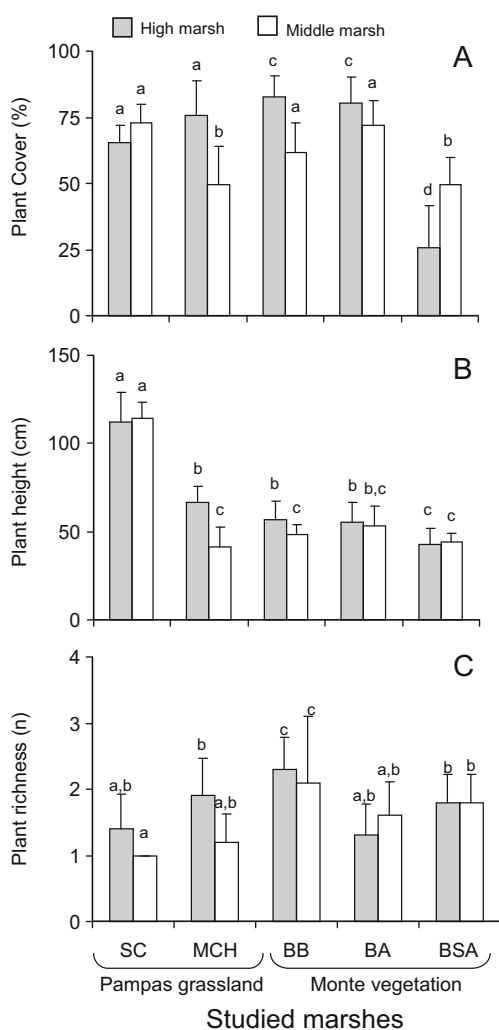
Fig. 3 Change in plant (**a**) cover, (**b**) height and (**c**) richness in relation to the changes in geographic regions, and marsh height along studied marshes. Different letters indicate differences ($p<0.05$) by Tukey test after two-way ANOVA (see Table 2)

small mammal abundance and richness, as it was reflected by the zero value exclusion in the confidence intervals for this variable (Table S2). Diversity of vegetation showed a negative relationship with both response variables, as indicated by the negative parameter estimates (Table S2).

During spring, for high and middle marsh zones, there were no significant support for the effect of any explicatory variables on the variation in small mammal abundance and richness (Table 4a, b). At inland habitats, only plant cover was an important predictor of small mammal abundance and richness, which was indicated by the high parameter likelihood values and confidence intervals excluding zero (Table S3).

Discussion

Our study carried out in five different sites along more than 1,400 km of the SWA coast shows that there are few species of small mammals in SWA marshes. While the abundance of small mammal are related on marsh characteristics (i.e., abundances increases with marsh area, plant cover and plant diversity), their richness and identity are related to the richness and identity of inland small mammals (i.e., the species in each marsh are the same recorded in adjacent inland habitats). Then, our results suggest that there are not marsh-specific small mammals in the SWA coast. These marshes may represent habitat of foraging and refuge for the inland small mammals, and that those small mammals responded to both local-habitat features and broader-scale characteristics of the habitat patch and surrounding landscape.

Small mammal species diversity in the studied marshes may be influenced by the diversity of small mammals in adjacent inland habitats. In marshes bordered by Pampas grasslands (north sites, SC and MCH) we recorded small mammal species that are typical of this habitat (e.g.,

Table 3 Generalized Linear Models explaining the variables relates to the small mammal abundance (**a**), and small mammal richness (**b**) in the three habitat types: inland (*Inl*), high marsh (*HM*) and middle marsh (*MM*), during winter period. Number of parameters (*K*) in each model included the intercept and each explanatory variable. Models with strong support are shown (i.e. $\Delta AIC_c < 3$). Global and Null models are also shown. Plant: *Pl*, height: *h*, cover: *cov*, diversity: *div*, frequencies of habitat use by small mammal: $F_{(h)}$, small mammal richness: Rich and AIC_c weight: $AIC_c w$

(A) Small mammal abundance

	Model	Explanatory variables	K	ΔAIC_c	$AIC_c w$	R^2
Inl	1_{Global}	Pl-cov+Pl-div	3	0.00	0.61	0.32
	2	Pl-div	2	0.98	0.37	0.26
	3_{Null}	–	1	14.91	0.00	–
HM	1	Area+Pl-div	3	0.00	0.25	0.30
	2	Area+Pl-cov+Pl-div	4	0.48	0.19	0.35
	3	Pl-cov+Pl-div	3	1.19	0.14	0.28
	4	Area+Pl-div+Inl-$F_{(h)}$.	4	1.66	0.11	0.32
	5	Area+Pl-cov+Pl-div+Inl-$F_{(h)}$.	5	1.91	0.10	0.37
	6	Area+Rain+Pl-div	4	2.09	0.09	0.31
	7	Pl-h+Area+Pl-div	4	2.36	0.08	0.30
	21_{Global}	Pl-h+Area+Pl-cov+Rain+Pl-div+Inl-$F_{(h)}$.	7	6.80	0.00	0.39
	24_{Null}	–	1	8.31	0.00	–
MM	1_{Null}	–	1	0	0.11	–
		Pl-div	2	0.70	0.08	0.06
		Area	2	1.10	0.07	0.05
		Pl-cov+Pl-div	3	1.73	0.05	0.11
		Area+Pl-div	3	1.81	0.05	0.11
		Pl-cov	2	1.84	0.05	0.02
		Pl-h	2	1.86	0.05	0.02
	64_{Global}	Pl-h+Area+Pl-cov+Rain+Pl-div+Inl-$F_{(h)}$.	7	11.88	0.00	0.16

(B) Small mammal richness

	Model	Explanatory variables	K	ΔAIC_c	$AIC_c w$	R^2
Inl	1	Pl-div	2	0.00	0.55	0.23
	2_{Global}	Pl-cov+Pl-div	3	0.77	0.37	0.26
	3_{Null}	–	1	6.87	0.02	–
HM	1	Pl-cov+Inl-Rich	3	0.00	0.17	0.19
	2	Inl-Rich	2	0.04	0.17	0.15
	3	Pl-h+Inl-Rich	3	1.27	0.09	0.16
	4	Pl-h+Pl-cov+Inl-Rich	4	1.40	0.08	0.22
	5	Pl-h+area+Inl-Rich	4	2.02	0.06	0.20
	6	Pl-cov+Rain+Inl-Rich	4	2.02	0.06	0.20
	7	Area+Inl-Rich	3	2.10	0.06	0.14
	13_{Null}	–	1	2.59	0.05	–
	57_{Global}	Pl-h+Area+Pl-cov+Rain+Pl-div+Inl-Rich	7	8.41	0.00	0.25
MM	1_{Null}	–	1	0	0.17	–
	2	Area	2	1.92	0.07	0.01
	3	HM-Rich	2	1.94	0.07	0.01
	4	Pl-div	2	2.05	0.06	0.01
	5	Pl-h	2	2.15	0.06	<0.01
	64_{Global}	Pl-h+Area+Pl-cov+Rain+Inl-Rich+Pl-div	7	13.97	0.00	0.07

O. rufus, *A. azarae* and *O. Flavescens*, Contreras and Alvarado 1968; Pardiñas et al. 2004; Canepuccia et al. 2008b). *A. azarae* and *O. rufus* are numerically and competitively dominant species in Pampas grassland (Reig 1965; Dalby 1975; Canepuccia et al. 2008b). Both species prefer habitat with high cover of grasses (Bonaventura et al. 1991; Dalby 1975; Mills et al. 1991), which likely provide them with better protection (Kincaid et al. 1983; Spencer and Cameron 1983). Despite the fact that both species inhabit inland sites, *O. rufus* was present only in the high-marsh zone, while *A. azarae* was present in both marsh zones. This spatial segregation may be due to the higher abundance of arthropods in the high-marsh zone (Canepuccia et al. 2009), which is an important food resource for *O. rufus* (Dalby 1975). *A. azarae*

Table 4 Generalized Linear Models explaining the variables affecting the small mammal abundance (**a**), and small mammal richness (**b**) in the three habitat types: inland (*Inl*), high marsh (*HM*) and middle marsh (*MM*), in spring period. Number of parameters (*K*) in each model included the intercept and each explanatory variable. Only models with strong support are shown (i.e. $\Delta AIC_c < 3$ or 2). If null and global models are not within the best models, they were also included at the end of each habitat's section. Plant: *Pl*, height: *h*, cover: *cov*, diversity: *div*, frequencies of habitat use by small mammal: $F_{(h)}$, small mammal richness: Rich and AIC_c weight: $AIC_c w$

(A) Small mammal abundance

	Model	Explanatory variables	K	ΔAIC_c	AIC_c w	R^2
INL	1	Pl-cov	2	0.00	0.71	0.19
	2	Pl-cov+Pl-div	3	2.43	0.21	0.19
	3 Null	–	1	5.10	0.06	–
HM	1	Rain	2	0.00	0.10	0.12
	2	Pl-h+Area	3	0.74	0.07	0.17
	3	Pl-h	2	1.49	0.05	0.08
	4	Pl-div	2	1.67	0.04	0.08
	5	Rain+Inl-F$_{(h)}$	3	1.77	0.04	0.14
	6	Rain+Pl-div	3	1.81	0.04	0.14
	8 Null	–	1	2.03	0.03	–
	63 Global	Pl-h+Area+Pl-cov+Rain+Pl-div+Inl-F$_{(h)}$	7	8.82	0.00	0.25
MM	1	Pl-h+Pl-div	3	0.00	0.21	0.44
	2	Pl-h+Pl-div+Inl-F$_{(h)}$	4	1.07	0.12	0.51
	3	Pl-h+Area+Pl-div	4	2.39	0.06	0.45
	4	Pl-h+Rain+Pl-div	4	2.47	0.06	0.45
	5	Pl-h+Pl-cov+Pl-div	4	2.47	0.06	0.45
	21 Null	–	1	5.89	0.01	–
	53 Global	Pl-h+Area+Pl-cov+Rain+Pl-div+Inl-F$_{(h)}$	7	10.40	0.00	0.52

(B) Small mammal richness

	Model	Explanatory variables	K	ΔAIC_c	AIC_c w	R^2
INL	1	Pl-cov	2	0.00	0.67	0.19
	2 Global	Pl-cov+Pl-div	3	2.29	0.22	0.20
	3 Null	–	1	5.02	0.06	–
HM	1	Rain	2	0.00	0.10	0.13
	2	Pl-h+Area	3	0.91	0.06	0.17
	3	Pl-h	2	1.45	0.05	0.08
	4	Pl-div	2	1.60	0.04	0.08
	5 Null	–	1	1.77	0.04	–
	6	Rain+Pl-div	3	1.87	0.04	0.06
	64 Global	Pl-h+Area+Pl-cov+Rain+Inl-Rich. + Pl-div	7	9.59	0.00	0.23
MM	1	Pl-h+Pl-div	3	0.00	0.11	0.36
	2	Pl-h+Inl.Rich+Pl-div	4	1.07	0.06	0.44
	3	Pl-div	2	1.32	0.06	0.16
	4	Inl-Rich+Pl-div	3	1.35	0.06	0.28
	5	Pl-cov	2	1.80	0.04	0.13
	6 Null	–	1	1.99	0.04	–
	64 Global	Pl-h+Area+Pl-cov+Rain+Inl-Rich. + Pl-div	7	10.07	0.00	0.47

also feed on insects; however, it has a broader diet and also incorporates plant leaves and seeds on its diet (Steinmann et al. 1997; Canepuccia et al. 2008a). Occasionally, we also recorded *O. flavescens*, which is a granivore / folivore (Bilenca et al. 1992) more related to hygrophilous and open vegetation (Reig 1965; Dalby 1975). In the southern marshes (BA and BSA), bordered by the xeric Monte vegetation, we recorded small mammal species (e.g., *A. molinae* and *O. longicaudatus*) that were typical of this habitat. These predominantly nocturnal and omnivorous species have been associated with dense plant cover in Monte vegetation (Campos et al. 2001; Tabeni and Ojeda 2003; Pardiñas et al. 2004).

The marsh located at the middle of our study range (BB) adjacent to Monte inland habitat showed the highest species richness (4 species). These marshes, although bordered by xeric Monte vegetation are close to the Pampas region (see Fig. 1). Here we recorded species representative of both landscapes (Pampas grassland: *A. azarae* and *O. flavescens*; and the Monte: *A. molinae*, and *O. longicaudatus*). Given the

proximity of the marsh to both inland habitats (Pampas grassland and Monte vegetation), it is possible that the inland habitat adjacent to the marsh at BB is an ecotone between these two inlands habitats. This biogeographic condition may increase the diversity and local habitat complexity (e.g., higher plant species richness). Similar patterns have been suggested from mangroves ecosystems, another ocean-inland ecotone dominated by trees, which develop in tropical and subtropical areas (e.g., Valiela et al. 2001). The richness of bird species in mangroves surrounded by structurally simple habitats is generally poorer than in those surrounded by complex ones (Mohd-Azlan and Lawes 2011). Similarly, the composition of small mammal species along *Spartina* marshes from SWA coast seems to be determined by the complexity of the inland adjacent matrix. Thus, there is a closer similarity between the small mammal species composition in marshes and their adjacent inland habitats than among marshes over several inland landscapes. Different surrounding environment (e.g., matrix habitat) may promote differences in species composition between sites (e.g., 'landscape-divergence hypothesis' Laurance et al. 2007; Tscharntke et al. 2012). For example, in the Brazilian Amazon, trees from forest fragments in different landscapes progressively tend to differ in species composition (Laurance et al. 2007). In our study area, different landscape contexts also seem to cause differences in composition of small mammal species between marshes; whereas those ones in similar landscapes do not. The abundance and occurrence of other vertebrates, such as tidal-marsh- birds in San Francisco Bay estuary were also related to landscape variables, such as the type of surrounding land use (Spautz et al. 2006). In US wetlands, the abundance of rice rats *Oryzomys palustris* are also affected by the proportion of upland grass cover adjacent to the wetland (Kruchek 2004; Eubanks et al. 2011). These results are also consistent with other studies in wetlands (Naugle et al. 1999) and shrub (Bolger et al. 1997) that show that landscapes, rather than individual patch habitats are associated with variation in bird distribution and abundance. This pattern suggests that landscape composition and configuration strongly affect marsh species pools. Thus, the characteristics of entire landscapes, rather than individual patches, must be quantified to assess their habitat suitability for small mammals inhabiting marshes.

At a regional scale, the abundance of small mammals decreased from the north-to-south in inland habitats. The SW Atlantic coastline develops along a precipitation gradient of increased aridity from the north to the south (see Isacch et al. 2006). From the inland perspective this precipitation gradient determines different inland landscapes, which are characterized by different plant coverage and structure (Canepuccia et al. 2013). In northern sites, Pampas grasslands are characterized by a dense grass cover (Cabrera and Willink 1973; Canepuccia et al. 2013). This is the area with the higher abundance of small mammals. Indeed, here the abundance of

small mammals was higher than in corresponding marsh habitats. Southward, paired with a decrease in precipitation there is a decrease in vegetation cover and a replacement of grass cover by xeric vegetation characterized by bushes and shrubs (Canepuccia et al. 2013). Plant cover (Dalby 1975; Kravetz and Polop 1983; Eubanks et al. 2011) and precipitation are important variables for small mammal populations (Jaksic et al. 1997; Jaksic 2001; Canepuccia et al. 2008a, b). Thus, given the low plant cover and the preponderant dry environments in southern sites (Cabrera and Willink 1973), the lower abundance of small mammals is not surprising. Indeed, where plant cover was higher in marshes (BB and BA), the abundance of small mammals increased. Higher plant cover is probably providing greater protection and food resources for small mammals (Kincaid et al. 1983; Spencer and Cameron 1983; Jaksic 2001). Also, the abundance of small mammals increased in relation to the marsh area. This pattern might be because greater marsh areas hold higher small mammal densities, or may also be because greater diversity of plants in larger marshes (e.g., BB, Canepuccia et al. 2013) results in an increase of potential niches for small mammals. As a consequence, the differential abundance of small mammals between the marsh and the adjacent inland habitats seems to vary in relation to the variation of the characteristics of both of these habitats along latitude.

Although there is a large number of quite distinctive species or subspecies of tidal marshes, most of them have been cited from the north hemisphere (see Greenberg and Maldonado 2006; Greenberg et al. 2006). The *Spartina* marsh along the SWA coast seems not to hold any "marsh-specific" small mammal species. In this area, both marsh and inland habitats are dominated by grassland vegetation. Even southern marshes surrounded by xeric shrubby have a very important grass component (Cabrera and Willink 1973; Canepuccia et al. 2013). Therefore, the lack of distinctive marsh species in SWA coast may be due to this low marsh-inland difference in vegetation structure, which contrasts with the observed pattern in north hemisphere, where coastal marshes, also dominated by grasses, are surrounded mainly by forests at the inland (Bailey 1995). This higher marsh-inland contrast could generate higher opportunities for species differentiation between both habitats than in the South Hemisphere counterpart, were the lower marsh-inland contrast reduce edge filter effects, thus providing greater connectivity between habitats.

In conclusion, there are no species of small mammals distinctive from the SWA marshes. These marshes were surprisingly open to colonization and establishment of inland small mammals, and marsh diversity does not appear to be tightly constrained by local features. Thus, there is a closer convergence between the small mammal species composition in marsh and its adjacent inland habitats than among marshes over different inland landscapes. However, the geographic pattern of abundance of small mammals in marshes is

consistent with an ecological sorting of abundance ranges throughout environmental gradients of productivity. Thereby, along SWA tidal-marshes, the abundance of small mammal is related to local habitat characteristics, while landscape composition strongly moderates its local biodiversity even if the habitats are quite similar.

References

Adam P (1993) Saltmarsh ecology. Cambridge Studies in Ecology. Cambridge University Press, Cambridge, UK

Andersen KM, Endara MJ, Turner BL, Bailing JW (2012) Trait-based community assembly of understory palms along a soil nutrient gradient in a lower montane tropical forest. Oecologia 168:519–531

Anderson DR, Burnham KP (1999) General strategies for the analysis of ringing data. Bird Study 46(Supplement):S261–S270

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+for PRIMER: Guide to software and statistical methods. PRIMER-E, Plymouth

Bailey RG (1995) Descriptions of the ecoregions of the United States, 2nd edn. Forest Service, Department of Agriculture, Washington

Balech E, Ehrlich MD (2008) Esquema biogeográfico del Mar Argentino. Revista de Investigación y Desarrollo Pesquero 19:45–75

Bertness MD, Hacker SD (1994) Physical stress and positive associations among marsh plants. Am Nat 142:718–724

Bilenca N, Kravetz FO, Zuleta GA (1992) Food habits of *Akodon azarae* and *Calomys laucha* (Cricetidae, Rodentia) in agroecosystems of central Argentina. Mammalia 56:371–383

Bolger DT, Scott TA, Rotenberry JT (1997) Breeding bird abundance in an urbanizing landscape in coastal southern California. Conserv Biol 11:406–421

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bonaventura SM, Piantanida MJ, Gurini L, Sánchez López MI (1991) Habitat selection in population of cricetine rodent in the region Delta (Argentina). Mammalia 55:339–354

Boschi EE (2000) Species of decapod crustaceans and their distribution in the american marine zoogeographic provinces. Revista de Investigacion y Desarrollo Pesquero 13:1–136

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, New York

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Cabrera AL, Willink A (1973) Biogeografía de America Latina, Serie de Biología, monografia n° 13. Washington, DC. Programa regional de Desarrollo Científico y Tecnológico, departamento de Asuntos Científicos, Organización de Estados Americanos, Washington

Campos C, Ojeda R, Monge S, Dacar M (2001) Utilization of food resources by small and medium-sized mammals in the monte desert biome, Argentina. Austral Ecol 26:142–149

Canepuccia AD (2005) Effect of rainfall increased of grassland community structure of Southeast pampas region Argentina. Doctoral Thesis, Universidad Nacional de Mar del Plata

Canepuccia AD, Fanjul MS, Fanjul ME, Botto F, Iribarne OO (2008a) The intertidal burrowing crab *Neohelice* (=*Chasmagnathus*) *granulata* positively affect rodents in South Western Atlantic salt marshes. Estuar Coasts 31:920–930

Canepuccia AD, Farias AA, Escalante AH, Iribarne OO, Novaro A, Isacch JP (2008b) Differential responses of marsh predators to rainfall-induced habitat loss. Can J Zool 86:407–418

Canepuccia AD, Cicchino A, Escalante AH, Novaro A, Isacch JP (2009) Differential responses of marsh arthropods to rainfall-induced habitat loss. Zool Stud 48:174–183

Canepuccia AD, Alberti J, Pascual J, Alvarez G, Cebrian J, Iribarne OO (2010) ENSO episodes modify plant/terrestrial-herbivore interactions in a southwestern Atlantic salt marsh. J Exp Mar Biol Ecol 396:42–47

Canepuccia AD, Pérez CF, Farina JL, Alemany D, Iribarne OO (2013) Dissimilarity in plant species diversity between salt marsh and neighbouring environments decreases as environmental harshness increases. Mar Ecol Prog Ser 494:135–148

Chapman VJ (1977) Wet coastal ecosystems. Ecosystems of the world, vol. 1. Elsevier Scientific, Amsterdam

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Clarke KR, Warwick RM (2001) Change in marine communities: An approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth

Contreras JR, Alvarado LJ (1968) Notas sobre los roedores cricétidos bonaerenses I *Oryzomys nigripes flavescens* en laguna Chasicó. Zoología Platense Investig Zoológicas y Paleontológicas 1:17–19

Crain CM (2008) Interactions between marsh plant species vary in direction and strength depending on environmental and consumer context. J Ecol 96:166–173

Crawley MJ (2007) The R Book. Wiley, New York

Dalby PL (1975) Biology of pampa rodents. Balcarce area, Argentina. Publications of the museum, Michigan state university. Biol Ser 5: 149–272

Day JW, Hall CAS Jr, Kemp WM, Yañez-Arancibia A (1989) Estuarine ecology. Wiley-Interscience, New York

Development Core Team R (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Available at: http://www.R-project.org

Eubanks BW, Hellgren EC, Nawrot JR, Bluett RD (2011) Habitat associations of the marsh rice rat (*Oryzomys palustris*) in freshwater wetlands of southern Illinois. J Mammal 92:552–560

Gedan KB, Crain CM, Bertness MD (2009) Small-mammal herbivore control of secondary succession in New England tidal marshes. Ecol 90:430–440

Greenberg RS (2006) Tidal marshes: home for the few and the highly selected. Stud Avian Biol 32:2–10

Greenberg RS, Maldonado JE (2006) Diversity and endemism in tidal marsh vertebrates. Stud Avian Biol 32:32–53

Greenberg RS, Maldonado JE, Droege S, Mcdonald MV (2006) Tidal marshes: a global perspective on the evolution and conservation of their terrestrial vertebrates. Biosci 56:675–685

Hodara K, Busch M, Kittlein MJ, Kravetz FO (2000) Density-dependent habitat selection between maize cropfields and their borders in two rodent species (*Akodon azarae* and *Calomys laucha*) of Pampean agroecosystems. Evol Ecol 14:571–593

Isacch JP, Costa CSB, Rodriguez-Gallego L, Conde D, Escapa M, Gagliardini DA, Iribarne OO (2006) Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. J Biogeogr 33:888–900

Jaksic FM (2001) Ecological effects of El Niño in terrestrial ecosystems of Western South America. Ecography 24:241–250

Jaksic FM, Silva SI, Meserve PL, Gutiérrez JR (1997) A long-term study of vertebrate predator responses to an El niño (ENSO) disturbance in western South America. Oikos 78:341–354

Kincaid WB, Cameron GN, Carnes BA (1983) Patterns of habitat utilization in sympatric rodents on the Texas coastal prairie. Ecol 64:1471–1480

Kravetz F, Polop J (1983) Comunidades de roedores en agoecosistemas del departamento de Río Cuarto, Córdoba. Ecosur 10:1–18

Kruchek BL (2004) Use of tidal marshland upland habitats by the marsh rice rat, (Oryzomys palustris). J Mammology 85:569–576

Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ewers R, Harms KE, Luizao RCC, Ribeiro JE (2007) Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. PLoS One 2:e1017

Mills JN, Ellis BA, Mckee KT, Maiztegui JI, Childs JE (1991) Habitat associations and relative densities of rodent populations in cultivated areas of central Argentina. J Mammal 72:470–479

Mitsch WJ, Gosselink JG (1993) Wetlands, 2nd edn. John Wiley and Sons, formerly Van Nostrand Reinhold, New York

Mohd-Azlan J, Lawes MJ (2011) The effect of the surrounding landscape matrix on mangrove bird community assembly in north Australia. Biol Conserv 144:2134–2141

Naugle DE, Higgins KF, Nusser SM, Johnson WC (1999) Scale-dependent habitat use in three species of prairie wetland birds. Landsc Ecol 14:267–276

Nicolas V, Colyn M (2006) Relative efficiency of three types of small mammal traps in an African rainforest. Belg J Zool 136:107–111

Pardiñas UFJ, Abba AM, Merino ML (2004) Micromamíferos (Didelphimorphia y Rodentia) del sudoeste de la provincia de Buenos Aires (Argentina): taxonomía y distribución. Mastozoología Neotropical 11:211–232

Provensal MC, Priotto JW, Steinmann A, Polop JJ (1995) Analysis of trap association among Argentina's wild cricetid species. Mastozoologia Neotropical 2:15–21

Reig OA (1965) Datos sobre la comunidad de pequeños mamíferos de la región costera del partido de General Pueyrredón y de los partidos limítrofes (prov. de Buenos Aires, Argentina). Physis 69:205–211

Spautz H, Nur N, Stralberg D, Chan Y (2006) Multiple-scale habitat relationships of tidal-marsh breeding birds in the San Francisco Bay Estuary. Stud Avian Biol 32:247–269

Spencer SR, Cameron GN (1983) Behavioral dominance and its relationship to habitat patch utilization by the hispid cotton rat (Sigmodon hispidus). Behav Ecol Sociobiol 13:27–36

Steinmann AR, Priotto JW, Provensal MC, Polop JJ (1997) Odor incidence in the capture of wild rodents in Argentina. Mastozoología Neotropical 4:17–24

Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. Sci 297:1292–1296

Tabeni S, Ojeda RA (2003) Assessing mammal responses to perturbations in temperate aridlands of Argentina. J Arid Environ 55:715–726

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87:661–685

Valiela I, Fox SE (2008) Managing coastal wetlands. Sci 319:290–291

Valiela I, Bowen JL, York JK (2001) Mangrove forests: one of the world's threatened major tropical environments. Biosci 51:807–815

Woodward FI, Diament AD (1991) Functional approaches to predicting the ecological effects of global change. Funct Ecol 5:202–212

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice-Hall, New York