



Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Distributional patterns in an insect community inhabiting a sandy beach of Uruguay

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ARTICLE INFO

Article history:

Accepted 2 May 2015

Available online xxx

Keywords:

sandy beach
insect community
temporal variation
zonation pattern
deconstruction
Uruguay

ABSTRACT

Most studies of sandy beach macrofauna have been restricted to semiterrestrial species and do not include insects when providing species richness and abundance estimates. Particularly, spatio-temporal patterns of community structure of the entomofauna inhabiting these ecosystems have been scarcely documented. This study assessed spatio-temporal distributional patterns of the night active entomofauna on a beach-dune system of Uruguay, including variations in species richness, abundance and diversity, and their relationship with environmental factors. A deconstructive taxonomic analysis was also performed, considering richness and abundance patterns separately for the most abundant insect Orders (Hymenoptera and Coleoptera) to better understand the factors which drive their patterns. We found clear temporal and across-shore patterns in the insect community inhabiting a land–ocean interface, which matched spatiotemporal variations in the environment. Abundance and species richness were highest in spring and summer, concurrently with high temperatures and low values of sediment moisture and compaction. Multivariate ordinations showed two well-defined species groups, which separated summer, autumn and spring samples from winter ones. Generalized Linear Models allowed us to describe a clear segregation in space of the most important orders of the insect community, with specific preferences for the terrestrial (Hymenoptera) and beach (Coleoptera) fringes. Hymenoptera preferred the dune zone, characterized by high elevation and low sand moisture and compaction levels, whereas Coleoptera preferred gentle slopes and fine and humid sands of the beach. Our results suggest that beach and dune ecosystems operate as two separate components in regard to their physical and biological features. The high values of species richness and abundance of insects reveal that this group has a more significant ecological role than that originally considered so far in sandy beach ecology.

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1. Introduction

Exposed ocean beaches are harsh and dynamic environments primarily controlled by waves, tides, and sediment type (McLachlan and Defeo, 2013). These physical factors operating over several spatial scales are the main drivers governing macrofauna biodiversity patterns on sandy beaches. Thus, global macrofaunal patterns can be reliably predicted on the basis of these distinctive physical features of the beach environment (Defeo and McLachlan, 2005, 2013). The benthic macrofauna of sandy beaches include representatives of many phyla, but crustaceans, molluscs and

polychaetes predominate, accounting for up 95% of marine species richness (McLachlan and Brown, 2006). On the other hand, insects are the most abundant terrestrial invertebrate group inhabiting coastal dunes and the supralittoral fringe of sandy shores, playing a key role in trophic webs (McLachlan and Brown, 2006). Recent deconstructive analyses based on taxonomy indicated that species richness of these four taxa increased from reflective (steep slopes, coarse sands) to dissipative (flat slopes, fine sands) beaches (Defeo and McLachlan, 2011; Barboza et al., 2012).

Most studies of sandy beach macrofauna have been restricted to marine and semiterrestrial species and do not include insects when providing species richness and abundance estimates (McLachlan and Brown, 2006). Indeed, studies describing terrestrial invertebrate communities of sandy beaches, including insects, have been relatively scarce (Giménez and Yannicelli, 2000; Colombini et al.,

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2002; Gauci et al., 2005; Costa et al., 2006; Fanini et al., 2009; Sivadas et al., 2012) or have been focused in only one insect group (Fallaci et al., 1997, 2002; Aloia et al., 1999; Fattorini and Carpaneto, 2001; Colombini et al., 2002, 2003, 2005; Chelazzi et al., 2005; Comor et al., 2008), and most of them are restricted to Mediterranean coasts. Especially, in sandy beach ecology, spatio-temporal patterns of species richness, abundance and distribution of the entomofauna belonging to both, the beach zone and the terrestrial dune ecosystem, have been mostly documented in the Adriatic coast (Chelazzi et al., 2005). These two distinct areas, along with the surf zone, comprise together a single geomorphic unit termed the Littoral Active Zone (LAZ, McGwynne and McLachlan, 1992; McLachlan and Brown, 2006). As the insect distribution extends landwards, abundance estimates are biased because sampling design commonly do not take into account the full across-shore distribution of the species, including the terrestrial dune ecosystem (Defeo and McLachlan, 2011).

Besides the need to assess spatial and temporal distributional patterns of the entomofauna in sandy beach, it is also important deconstruct these communities to discriminate patterns among distinct taxonomic groups that could respond differently to the environment, thus exhibiting contrasting patterns that would be obscured if only aggregate richness is considered (Marquet et al., 2004). By treating such species groups separately, a more complete understanding of the factors driving species richness patterns may emerge (Defeo and McLachlan, 2011). This is particularly important in temperate zones, where environmental seasonal changes tend to translate into temporal activity patterns in living organisms according to particular characteristics of the life cycle of the species. In this context, various macroclimatic and microclimatic changes and variation in the availability of food resources are important factors in triggering seasonal activity of insects (Wolda, 1988).

The aim of this paper was to assess spatial and temporal patterns of species richness, abundance and diversity of the entomofauna of the LAZ (the beach zone and the terrestrial dune ecosystem) on the dissipative beach Barra del Chuy (Uruguay), and the relationship between these ecological descriptors and environmental factors. This beach has the highest macrofauna richness (including insects) and it is the widest ocean one among all Uruguayan beaches (Barboza et al., 2012). Specifically, it is assessed whether within-year environmental changes translate into temporal differences in species richness, abundance, diversity and composition of insect community. Moreover, it is postulated that gradients in environmental factors throughout the beach-dune system generate across-shore variations in species richness and abundance of insects, which vary according to the group of species analysed.

2. Materials and methods

2.1. Study site and sampling design

The study was undertaken in Barra del Chuy (33° 45' S, 53° 27' W), a sandy beach on east coast of Uruguay (Department of Rocha). This is a wide (beach width ca 70 m) dissipative beach with fine to very fine (grain size = 0.20 mm) well-sorted sands, a gentle slope (2.7%), a wide surf zone and high macrofauna richness, total abundance and biomass (Defeo et al., 2001; Barboza et al., 2012). The active dunes are covered by a great abundance of the perennial herb *Panicum racemosum* (Poaceae) and some halophilous annual species such as *Blutaparon portulacoides* (Amaranthaceae), *Cakile maritima* (Brassicaceae) and *Calycera crassifolia* (Calyceaceae).

Environmental and biological samples were taken in nocturnal surveys carried out in 2012: summer (23/01–24/01), autumn (18/

04–19/04), winter (22/08–23/08) and spring (13/11–14/11). Insects were collected using pitfall traps as sampling units (SU) set along three transects perpendicular to the shoreline, spaced 8 m apart from each other (10 SU per transect). Nocturnal sampling with pitfalls is an effective method to achieve a good representation of the richness and abundance of insect species in sandy beaches (Gauci et al., 2005). Traps were set during new moon days and were kept active overnight, because it has been shown that most nocturnal insects are especially active during those days (see e.g. Nag and Nath, 1991). Pitfall traps were placed every 8 m from the swash zone to 40 m inland from the beginning of the active dune. Each trap consisted of a plastic cup (12 cm diameter and 12 cm depth) filled with 150 ml of a solution of propylene glycol (50%) with a few drops of detergent. Propylene glycol is an effective killing and preservative agent, odourless, non toxic to vertebrate and slow to evaporate (Aristophanous, 2010). In the laboratory, captured insects were sorted, counted and identified to the species or genus taxonomic level or morphospecies. Some insect groups were preserved dry and others were sorted in 70% ethanol and were deposited in the Entomological Collection of Facultad de Ciencias, Universidad de la República (Montevideo). As pitfall trapping is a standard method to catch epigeic arthropods (Chen et al., 2011), all the biological data analyses included only those insect groups with well-known epigeic habits.

Sand temperature, sand compaction and elevation were measured in correspondence to each pitfall trap (SU), together with sediment samples for determination of granulometric parameters, sand moisture, and sediment organic matter content. Sand compaction was measured using a piston pocket penetrometer and the elevation was estimated according to Emery (1961). Laboratory analysis of sediment statistics was made following Folk (1980). Estimation of mean particle size and sorting were made using the GRADISTAT v.6.0 software (Blott and Pye, 2001). A fraction of the sediment sample was oven dried at 80 °C for 24 h, weighted (± 0.001 g) and then burned at 460 °C for 4 h, and finally weighted again to estimate sediment moisture and organic matter content.

2.2. Statistical analyses

Between-season differences in the environmental variables were tested through one-way analyses of covariance (ANCOVA), using the distance from the dune as the covariate and season as the main factor, performing a Fisher's LSD test when significant differences were found. Non-metric multidimensional scaling (NMDS) based on Euclidean distance matrix of log transformed standardized environmental variables was used to create a two-dimensional (2D) ordination of the samples for each season. For NMDS overlays, measurements of physical parameters in each season were averaged for the three SU at same distance from the dune. Changes in environmental conditions across zones (dune and beach) were assessed by one-way Permutational Analysis of Variance (PERMANOVA; Anderson, 2001) included in the PRIMER 6.0 software package (Clarke and Gorley, 2006). One fixed factor (season) and 1000 permutations of residuals under a reduced model were considered in the design. To confirm that environmental differences between zones were due to location differences rather than to data dispersion, we used a permutational analysis of multivariate dispersions (PERMDISP; Anderson et al., 2006) included in the same software package. Abundance (mean values per transect) and species richness (number of species per transect) were used to compute the Shannon–Weiner species diversity index and Simpson's dominance index (Magurran, 1988), using the Diverse routine included in the PRIMER 6.0 software package (Clarke and Warwick, 1994).

Differences in abundance, species richness and diversity indices were also evaluated between seasons through a one-way ANCOVA, using the distance from the dune as the covariate and season as the main factor, performing a Fisher's LSD test when significant differences were found. In these analyses, abundance and species richness were expressed, respectively, as ind/pitfall and n° species/pitfall. Between-season similarity in species composition (abundance) was also analysed by NMDS, using root – root transformed data from each season and the Bray–Curtis similarity index. Species that contributed at least 2% of the total abundance were used. Then, a one-way PERMANOVA and PERMDISP were performed following the same approach as in environmental variables. Similarity percentages (SIMPER) were calculated to estimate the average contribution of each species to the similarity (typifying species) and dissimilarity (discriminating species) between zones. All these analyses were carried out using the PRIMER 6.0 software package (Clarke and Gorley, 2006).

Following the methodological approach used by Defeo and McLachlan (2011), we deconstructed the entomofauna found in Barra del Chuy to the Order level, to better understand the species richness and abundance patterns in relation to temporal and across-shore variations in the physical environment. The faunal categories considered in the deconstructive analyses were the orders Hymenoptera and Coleoptera, which were those with the highest number of individuals (see Results). Generalized linear models (GLMs, McCullagh and Nelder, 1989) were used to examine across-shore variations in species richness and abundance and the main physical variables, discriminated by Order (Coleoptera and Hymenoptera). Models were examined using Gaussian, Poisson and binomial error distributions. The Poisson distribution and a log-link function provided the best fit for species richness whereas the Gaussian error distribution and an identity link function best fit across-shore variations in abundance. Akaike's Information Criterion (AIC) was used to evaluate each model fit and parsimony. Residual plots were evaluated for violations of model assumptions. In order to conduct the analyses, the information provided by all SU taken in the four seasons of 2012 ($n = 120$) was considered.

3. Results

3.1. The environment

Among the six environmental variables recorded in the sampling site, only mean grain size did not show significant differences between seasons (Table 1, Supplementary Material Table S1). Sediment temperature was significantly higher in summer than in the other three seasons, and intermediate and similar values obtained in autumn and spring were significantly higher than in

winter. Sediment compaction was significantly lower in summer than in the other seasons. Organic matter was significantly higher in autumn and lowest in spring, reaching intermediate and similar values in summer and winter (Table 1). Moisture was lowest in summer and gradually increased during the following seasons, with significant differences found between summer and winter and spring. Elevation of the beach was significantly lower in winter than in the other three seasons (Table 1).

Across-shore variations in environmental variables are shown in Fig. 1. Sediment temperature did not show large variations, increasing slightly towards the dune in all seasons, excepting in winter (Fig. 1a). Sand compaction tended to increase seaward in all seasons (Fig. 1b). Grain size was coarsest in the dune in summer, autumn and spring, whereas in winter the coarsest grains were found at 32 m from the base of the dune (Fig. 1c). Sediment organic matter content and sand moisture increased towards the sea, but both decreased in winter in the station close to the sea (32 m, see Fig. 1a,b). Elevation showed the highest slope values from 8 to 24 m from the base of the dune to inland (Fig. 1f).

Ordination of environmental data (Fig. 2) showed that dune samples were clustered separately from beach ones in all seasons (stress values 0.01). Moreover, samples taken at the base of the dune (0 m) joined the beach group in all seasons except spring, demarcating a transition between zones. PERMANOVA revealed multivariate environmental differences between zones (global $F_{(1,38)} = 19.68, P \leq 0.05$), which were attributed to location differences rather than to dispersion differences (PERMDISP $F_{(1,38)} = 0.90, P \geq 0.05$). In all seasons, PERMANOVA revealed multivariate environmental differences between zones (Summer: $F_{(1,8)} = 8.66, P \leq 0.05$; Autumn: $F_{(1,8)} = 7.22, P \leq 0.05$; Winter: $F_{(1,8)} = 3.67, P \leq 0.05$; Spring: $F_{(1,8)} = 3.67, P \leq 0.05$). These differences were attributed to location differences rather than to dispersion differences (PERMDISP: Summer, $F_{(1,8)} = 0.25, P \geq 0.05$; Autumn, $F_{(1,8)} = 1.26, P \geq 0.05$; Winter, $F_{(1,8)} = 1.82, P \geq 0.05$; Spring, $F_{(1,8)} = 2.16, P \geq 0.05$).

3.2. Biodiversity patterns

A total of 2283 insects of 67 species belonging to 26 Families of 5 Orders were captured (Supplementary Material Table S2). The abundance per transect (mean \pm SE) was highest in summer (337 ± 55 ind/transect), intermediate in autumn (152 ± 38 ind/transect) and spring (184 ± 50 ind/transect), and was significantly lowest in winter (46 ± 11 ind/transect) (LSD, $P < 0.05$) (Table 3; Supplementary Material Fig. S1a). Species richness (number of species per transect) was significantly higher in spring (15 ± 1) and summer (13 ± 2), than in autumn (8 ± 1) and winter (8 ± 1) (LSD, $P < 0.05$) (Table 1; Supplementary Material Fig. S1b). Diversity (H')

Table 1

Summary of ANCOVA results and multiple comparisons (post-hoc LSD test) performed on environmental and biotic variables data recorded at Barra del Chuy beach. Distance from the sand dunes was used as the covariate and season as the main factor. Su = summer, A = autumn, W = winter, S = spring, ns = non-significant. *: $P < 0.05$.

	F	Su–A	Su–W	Su–S	A–W	A–S	W–S
Environmental variables							
Sand temperature (C°)	708.43*	<0.01	<0.01	<0.01	<0.01	ns	<0.01
Compaction (kg/cm ²)	7.45*	<0.01	<0.01	<0.01	ns	ns	ns
Mean grain size (μ m)	0.94	ns	ns	Ns	ns	ns	ns
Organic matter content (%)	10.62*	<0.01	ns	<0.05	<0.01	<0.01	<0.05
Sand moisture (%)	5.27*	ns	<0.01	<0.01	ns	ns	ns
Elevation (m)	0.92*	ns	<0.05	Ns	<0.01	ns	<0.05
Biotic variables							
Abundance (ind/transect)	7.06*	ns	<0.01	ns	0.02	ns	<0.01
Richness (species/transect)	9.20*	<0.01	<0.01	ns	ns	<0.01	<0.01
Diversity (H')	0.13	ns	ns	ns	ns	ns	ns
Dominance (D)	2.90*	ns	ns	ns	ns	0.02	0.04

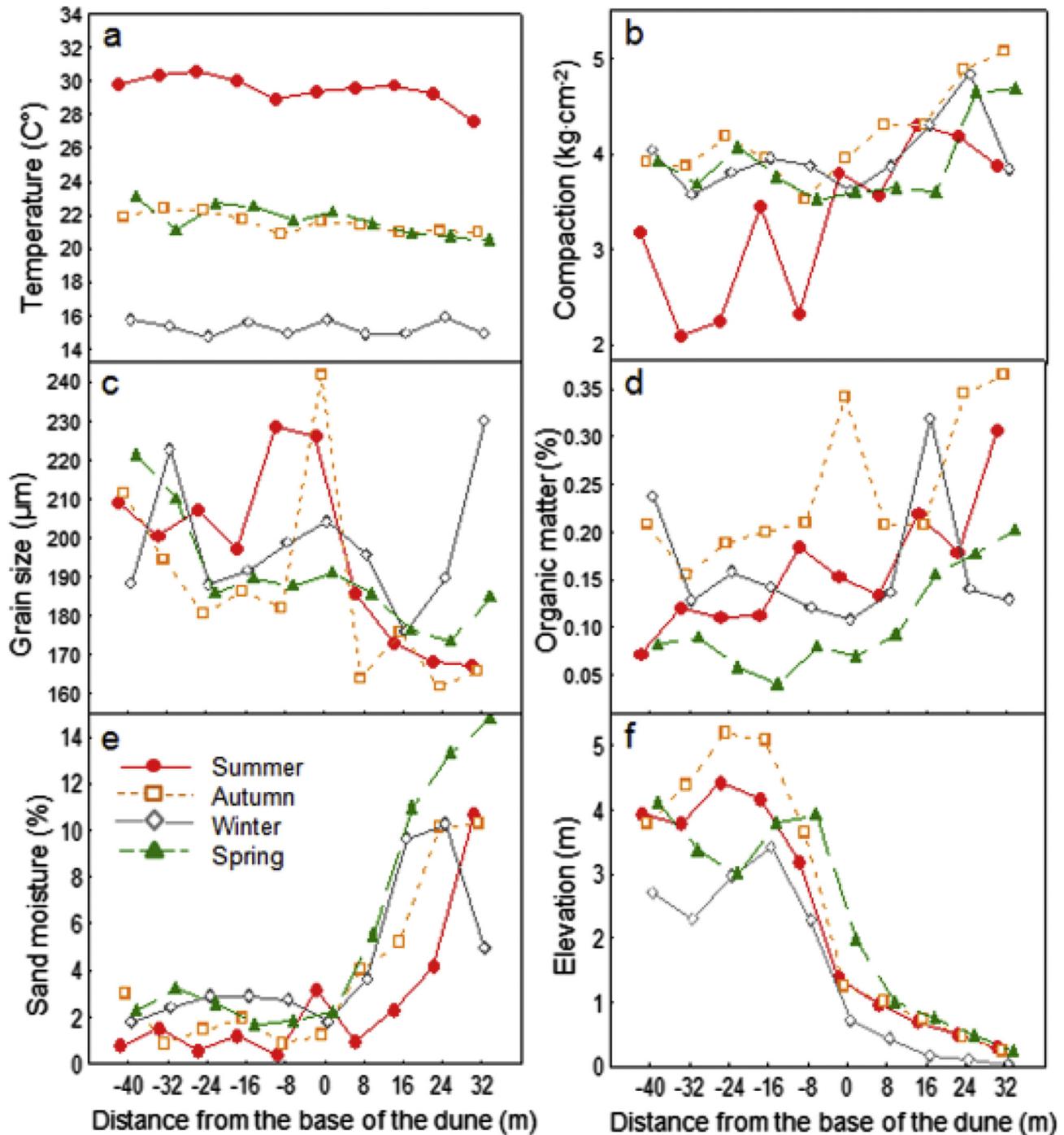


Fig. 1. Across-shore variations in environmental variables at Barra del Chuy beach for each season: (a) temperature, (b) compaction, (c) grain size, (d) organic matter, (e) sand moisture and (f) elevation. The zero value in the X axis indicates the base of the sand dunes, negative values indicate a landward direction and positive ones a downshore direction.

did not differ between seasons (LSD, $P > 0.05$), even though it tended to be higher in spring (Table 1). Dominance in spring (0.74 ± 0.03) was significantly higher than those found in autumn (0.57 ± 0.09) and winter (0.37 ± 0.07), reaching an intermediate value in summer (0.55 ± 0.03) (Table 1).

Concerning across-shore variations of community descriptors, abundance exhibited their highest values between 8 and 24 m from the base of the dune to inland (i.e., from -8 m to -24 m), decreasing towards both extremes in all seasons, except in spring. In this season, abundance showed a bimodal distribution pattern (Fig. 3a), with peaks located inland (-32 m) and at the beach

(16 m). Across-shore variations in species richness did not show the same pattern in all seasons (Fig. 3b). In summer, species richness increased from the intertidal to the dunes, reaching the highest values at -24 m (Fig. 3b). In autumn and winter, the highest species richness occurred at the base of the dunes (-8 m and 0 m, respectively), decreasing towards both extremes of the dune-sea gradient (Fig. 3b). In spring, species richness showed a more homogeneous across-shore distribution (Fig. 3b). In all seasons, diversity (H') showed the highest values at the dune, decreasing towards both extremes of the dune-sea axis, but tended to increase again near the intertidal fringe (Fig. 3c). Dominance exhibited

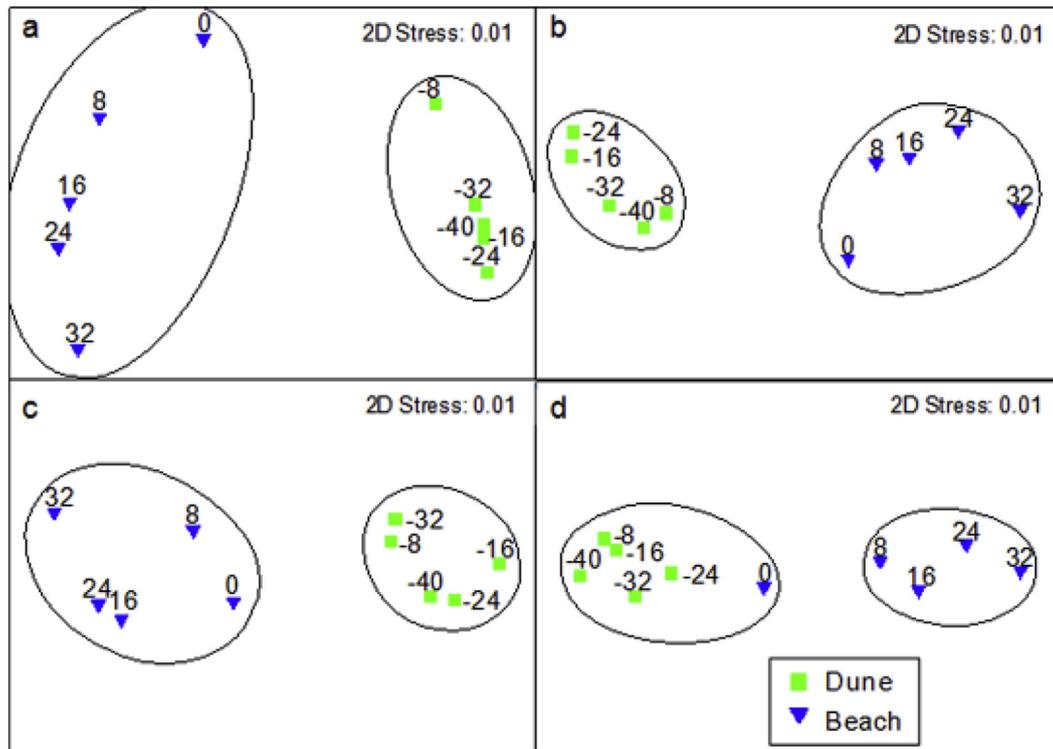


Fig. 2. NMDS configuration based on Euclidian distance matrix of root – root transformed environmental variables of each sampling level across Barra del Chuy beach. (a) summer, (b) autumn, (c) winter and (d) spring. Ellipses indicate a Euclidean distance = 10. The zero value indicates the base of the sand dunes, negative values (■) indicate a landward direction and positive ones (▼) a downshore direction.

similar and consistent patterns of variation during the four seasons, excepting for the peaks that occurred in the SU nearest to the intertidal fringe in autumn and at the base of the dunes (0–8 m) in winter (Fig. 3d).

NMDS ordinations of the insect community at Barra del Chuy beach showed well-defined similarity patterns, reflected in a very low stress value (0.06) that indicates a good and useful 2D representation of the groups. Summer, autumn and spring samples were clustered and clearly separated to those of winter within the 50% similarity boundary (Fig. 4). In agreement with these patterns,

Table 2

SIMPER analysis showing the contribution of insect community species to the average Bray–Curtis similarity (typifying species >10%) and the average Bray–Curtis dissimilarity (discriminating species >5%) between seasons at Barra del Chuy beach, Uruguay. Su = summer, A = autumn, W = winter, S = spring.

Typifying species	Summer	Autumn	Winter	Spring		
<i>Pheidole subarmata</i>	28.47	34.78	81.80	22.55		
<i>Dorymyrmex pyramica</i>	29.03	24.04		14.95		
Attini sp.		13.45				
<i>Phaleria testacea</i>	11.09	17.96		28.50		
<i>Labidura xanthopus</i>				11.09		
Average similarity	74.40	72.40	48.42	63.40		
Discriminating species	Su vs. A	Su vs. W	Su vs. S	A vs. W	A vs. S	W vs. S
<i>Pheidole subarmata</i>	22.00	17.26	17.97	17.95	13.52	7.58
<i>Dorymyrmex pyramica</i>	20.33	27.60	16.83	22.41		12.87
Attini sp.	5.54			11.70	6.64	
<i>Solenopsis richteri</i>	6.51					
<i>Megacephala cruciata</i>			6.36		9.04	7.38
<i>Phaleria testacea</i>		7.54	11.79	12.92	14.64	20.34
<i>Labidura xanthopus</i>	7.40	6.51			6.79	7.07
<i>Forelius</i> sp.	5.41					
Average dissimilarity	37.73	66.68	43.67	57.36	44.16	67.25

significant differences in the insect community composition were found among seasons (PERMANOVA $F_{(3,8)} = 4.44$, $P = 0.001$).

The SIMPER procedure identified species of Formicidae (Hymenoptera) as typifying species of the insect community at Barra del Chuy beach: *Pheidole subarmata* Mayr in all seasons, *Dorymyrmex pyramica* Roger in summer, autumn and spring, and Attini sp. in autumn (Table 2). Another typifying species were *Phaleria testacea* Say (Coleoptera: Tenebrionidae) in summer, autumn and spring, and *Labidura xanthopus* Stal (Dermaptera: Labiduridae) in spring. *P. subarmata*, *D. pyramica* and *P. testacea* also discriminated the communities in most seasons (Table 2). The species of Formicidae, *Solenopsis richteri* Buren and *Forelius* sp., discriminated between summer and autumn, and Attini sp. discriminated between autumn and the other seasons. *Megacephala cruciata* Brulle (Coleoptera: Carabidae) discriminated the insect community of spring from the remaining seasons and *L. xanthopus* discriminated warmer seasons (summer and spring) from colder seasons (autumn and winter) (Table 2).

3.3. Taxonomic deconstruction

The insect community included representatives of Hymenoptera (74%), Coleoptera (17%), Hemiptera (4%), Dermaptera (3%) and Diptera (2%). Within Hymenoptera, only Formicidae species were captured, whereas Tenebrionidae was the dominant family (80%) in Coleoptera, with only one species, *Phaleria testacea*. Taxonomic deconstruction based on Hymenoptera and Coleoptera showed that abundance (ind/pitfall) and species richness variations along the transverse axis of the beach exhibited opposite trends (Fig. 5): Formicidae was exclusively found in the dunes, while Coleoptera mainly occupied the beach zone. This pattern was consistent for all seasons, both for abundance (Supplementary Material Fig. S2) and species richness (Supplementary Material Fig. S3). In Coleoptera,

Table 3
Results for the generalized linear models (GLM) for species richness and abundance, discriminated by Order, using sand compaction (kg/cm²), grain size (mm), organic matter content (%), sand moisture (%) and elevation (m) as independent variables. For species richness, a Poisson distribution function and a log-link function was used, whereas abundance was modelled using a Gaussian distribution and an identity link function. Akaike Information Criterion (AIC) and likelihood ratio test (L. Ratio χ^2) are given for the best models fitted (in all cases $P < 0.001$). GLM coefficient estimates (mean and SE) derived from the best models are shown together with the Wald statistic. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = non-significant.

	Hymenoptera (Formicidae)				Coleoptera			
	Estimate	SE	Wald statistic	P	Estimate	SE	Wald statistic	P
Species richness	DF = 2; AIC = 236.39; L. Ratio $\chi^2 = 124.11$				DF = 4; AIC = 265.76; L. Ratio $\chi^2 = 61.33$			
Intercept	-0.4965	1.5217	0.1064	ns	9.9617	1.9493	26.1160	***
Compaction	-0.0537	0.1591	0.1139	ns	-0.7904	0.2193	12.9853	***
Grain size	5.7257	5.7889	0.9783	ns	-28.1743	7.7169	13.3296	***
Organic matter	-2.4718	1.4042	3.0987	ns	-6.6559	1.7295	14.8091	***
Moisture	-0.2806	0.0889	9.9438	***	0.0405	0.0312	1.6783	ns
Elevation	0.2956	0.0784	14.1806	***	-0.4648	0.0997	21.7246	***
Abundance	DF = 2; AIC = 1154.87; L. Ratio $\chi^2 = 32.40$				DF = 5; AIC = 799.94; L. Ratio $\chi^2 = 32.09$			
Intercept	78.536	45.5095	2.9781	ns	36.3694	10.1886	12.7421	***
Compaction	-17.467	5.9058	8.7473	**	-3.5706	1.3221	7.2931	**
Grain size	-105.978	162.442	0.4256	ns	-80.8345	36.3674	4.9405	*
Organic matter	22.634	38.7024	0.3420	ns	-21.0873	8.6646	5.9230	*
Moisture	0.720	1.0738	0.4490	ns	0.6079	0.2404	6.3936	*
Elevation	7.486	2.2479	11.0894	***	-1.2566	0.5032	6.2349	*

the maximum abundance and species richness shifted from the base of the dune toward the sea, from winter to summer (Supplementary Material Figs. S2, S3).

Different sets of environmental variables explained across-shore patterns of species richness and abundance in Formicidae and

Coleoptera (Table 3). In the former, the best GLM showed that species richness was significantly explained by across-shore variations in moisture and elevation, whereas these two variables together with compaction and grain size were the most significant predictors of spatial variations in species richness of Coleoptera in

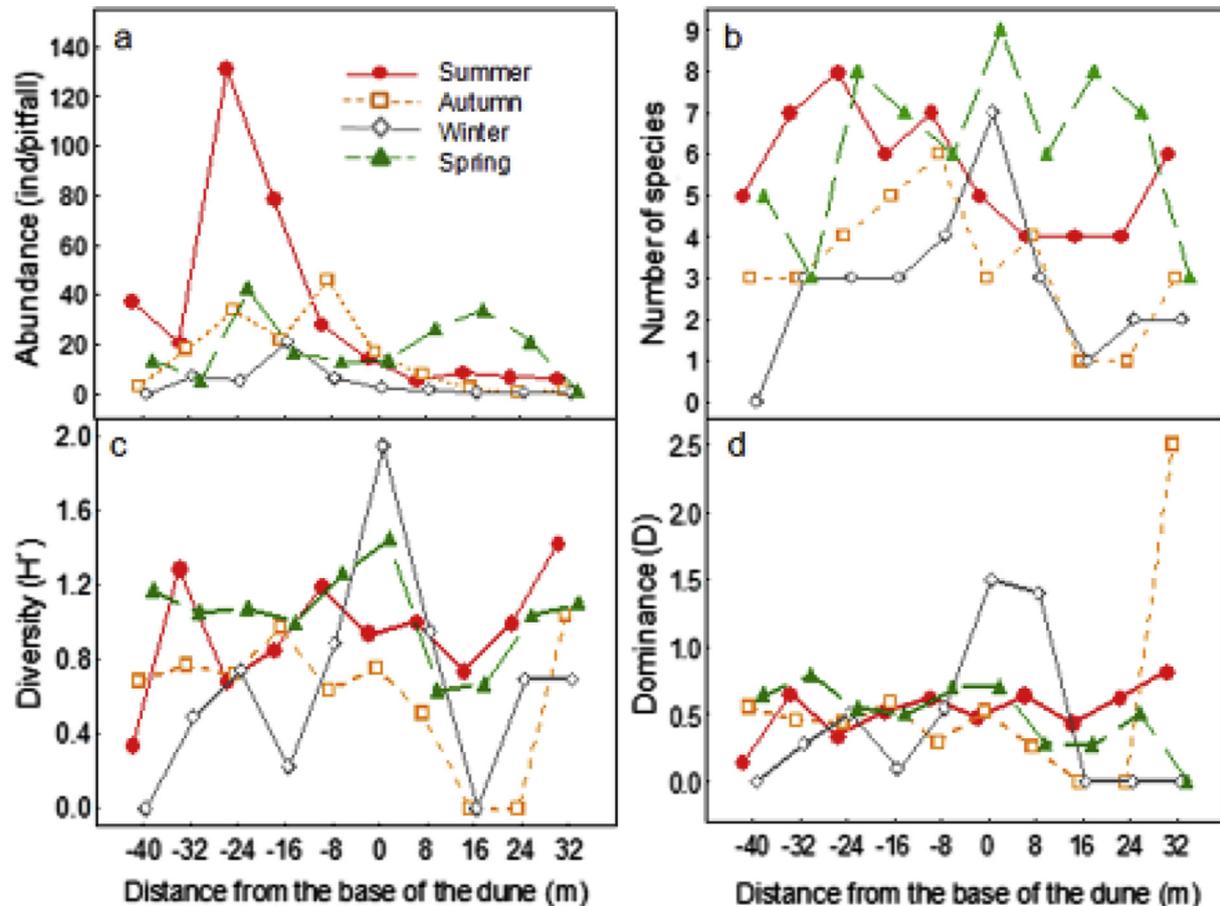


Fig. 3. Temporal across-shore variations of the insect community at Barra del Chuy beach in (a) abundance, (b) species richness, (c) diversity and (d) dominance. The zero value in the X axis indicates the base of the sand dunes, negative values indicate landward direction and positive ones a downshore direction.

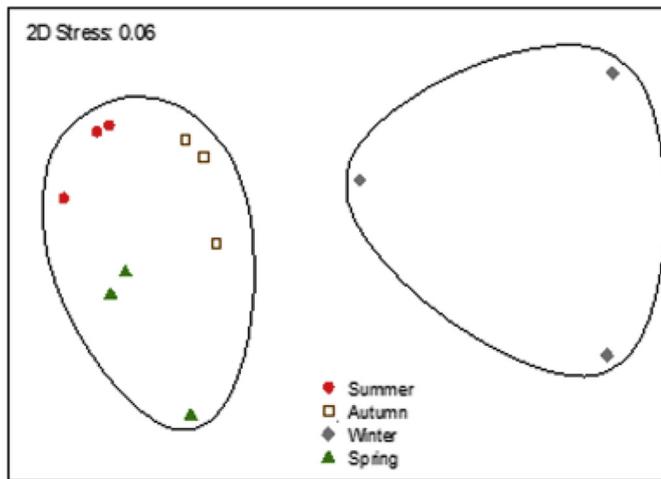


Fig. 4. NMDS configuration of temporal variations of the insect community at Barra del Chuy beach, based on the Bray–Curtis similarity index. Ellipses indicate the similarity percentage (50%) from cluster analysis. Only species that contributed >2% were included.

the dune-sea axis. The most striking differences between both groups relied on the significantly negative role of sand moisture for ants and the opposite trends observed in the role of elevation (positive for Formicidae and negative for Coleoptera). Concerning abundance, the same set of variables as in species richness plus sand moisture provided an accurate statistical description of zonation patterns in Coleoptera, whereas elevation and, in decreasing order, sand compaction, were significant explanatory

variables of spatial variations of abundance in Formicidae (Table 3). Following the same patterns as in species richness, the opposite trends observed in the role of elevation (positive for Hymenoptera and negative for Coleoptera) were of utmost importance in explaining the dissimilar across-shore pattern in abundance.

4. Discussion

This study showed clear temporal and across-shore patterns in the night-active insect community inhabiting a land–ocean interface, which matched spatiotemporal variations in the environment. Moreover, a clear segregation in space of the most important orders of the insect community was documented, with specific preferences for the terrestrial (Hymenoptera) and beach (Coleoptera) fringes of the LAZ of Barra del Chuy beach.

The orders found in this study and their relative abundances were consistent with those collected in different sandy beaches around the globe (Giménez and Yannicelli, 2000; Camus and Barahona, 2002; Colombini et al., 2002; Costa et al., 2006). Hymenoptera was represented specially by Formicidae, which constitutes one of the most conspicuous families inhabiting coastal dunes (Gianuca, 1998a; Martínez and Psuty, 2004; Costa et al., 2006). *Pheidole subarmata* and *Dorymyrmex pyramica* were the most important Formicidae species. *P. subarmata*, which is reported here for the first time for Uruguay, is one of the most abundant and wide-ranging species of New World *Pheidole*, occurring in a wide range of habitats and being a generalist forager (Wilson, 2003). *D. pyramica* is a predator–scavenger species that nests on littoral dunes (Fowler, 1993) although it is not exclusive of this habitat (Beck et al., 1967; Tizón and Quirán, 2009). Concerning Coleoptera, *Phaleria testacea* (Tenebrionidae) represented 80% of total beetles. *Phaleria* species also typify beach ecosystems (Fallaci et al., 2002). *Phaleria testacea* is a nocturnal and detritivorous species that inhabits the supralittoral fringe of American sandy beaches (Watrous and Triplehorn, 1982; Caldas and Almeida, 1985; Gianuca, 1998a). Another typifying species was the Neotropical earwig *Labidura xanthopus*, which is very similar to the cosmopolitan species *Labidura riparia* (Pallas), and could only be a form of this species (Brindle, 1971). *Labidura riparia* is a predator species that has been commonly recorded in sandy beaches in Southern Brazil (Gianuca, 1998b).

The night-active insect community at Barra del Chuy beach showed marked temporal patterns that followed variations in sand temperature, being reflected in a winter with low species richness and abundance, contrasting with the highest values found in summer and spring. Temperature is suspected to have a large effect on the activity of epigeal arthropods (Honek, 1988, 1997). In this study, Formicidae and Tenebrionidae represented 88% of the total catch and therefore were mainly responsible for the temporal fluctuations in abundance observed in the insect community. Positive correlations between temperature and total captures of both, ants and beetles, in temperate zones have been documented, reflecting parallel seasonal patterns in temperature and adults' emergence, foraging activity, and reproductive and diapauses periods (Whitford et al., 1981; Stevens et al., 1998; Fattorini and Carpaneto, 2001; Fallaci et al., 2002). Studies on Formicidae have shown that different species exhibit greater foraging activity in the summer months and lower in spring and autumn, being null in winter; its surface activity is closely associated with temperatures above 20 °C, with optimum temperatures around 30 °C and limiting temperatures below 15 °C (Whitford et al., 1981; Retana et al., 1992). The surface activity levels found in our study, reflected by the highest abundance recorded in summer, are consistent with temporal variations in sand temperature, according to the antecedents mentioned above. On the other hand, Tenebrionidae

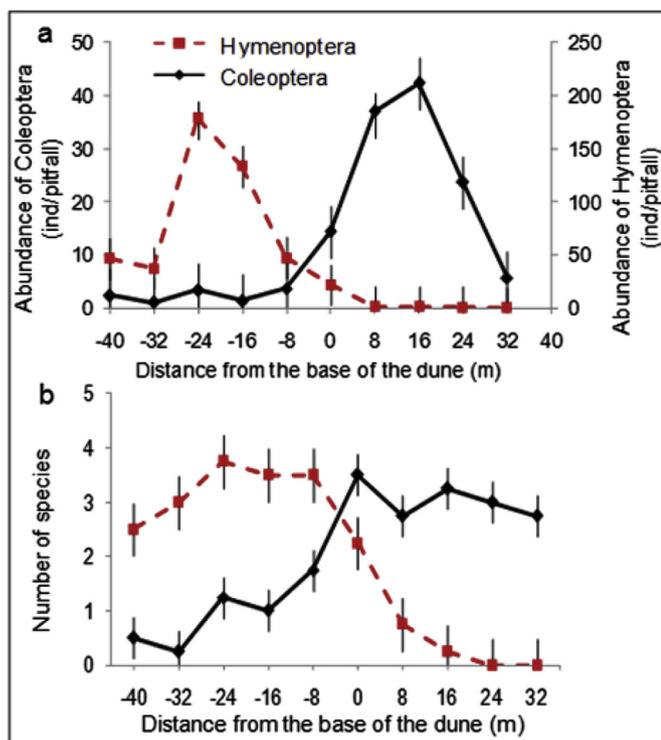


Fig. 5. Across-shore variations (mean \pm SE) in (a) abundance and (b) species richness of Hymenoptera (Formicidae) and Coleoptera at Barra del Chuy beach. The zero value in the X axis indicates the base of the sand dunes, negative values indicate landward direction and positive ones a downshore direction.

species, mostly adults, are particularly active on sandy beaches from spring to autumn (Fallaci et al., 2002; Chelazzi et al., 2005).

Taxonomic deconstruction of the community showed contrasting across-shore distribution patterns of Formicidae (Hymenoptera) and Coleoptera in both, abundance and species richness. While Formicidae mostly inhabited the sand dunes, Coleoptera predominated on the beach zone, because of the different responsive patterns to across-shore environmental gradients. Ants preferred those beach fringes characterized by high elevation and low sand moisture and compaction levels (see Table 3), which, together with low organic matter content, are typical of sand dune environments (Sykes and Wilson, 1991). Morrison (2003) has shown that ant abundance and species richness are positively correlated with drier substrates and dune vegetation cover. In particular, the presence of nests of *Dorymyrmex pyramica* (one of the ants typifying species) is highly correlated with vegetative coverage in sandy beaches (Fowler, 1993) and also in semidesert areas with shrub vegetation (Tizón and Quirán, 2009). This predator species has been recorded feeding on aphids, which are strongly associated with vegetation cover (Beck et al., 1967).

Coleoptera predominated in the beach zone, particularly Tenebrionidae and Cicindelinae, which represented 88% of the total beetles found in our study. This across-shore pattern was also found in other studies (Colombini and Chelazzi, 1991; Caldas and Almeida, 1993; Colombini et al., 1996; Chelazzi et al., 2005) and is consistent with gentle slopes (low elevations) and fine and humid sands (see Table 3). Because of its abundance, *Phaleria testacea* was mainly responsible for the across-shore variation pattern in the abundance of the whole group. In agreement with our findings, *Phaleria* species tend to occupy areas with finer and humid sands (Fallaci et al., 2002), being substrate moisture a limiting factor (Colombini et al., 1996, 2008). This is probably related to habitat requirements for oviposition, which ensure the full development of the fossorial immature stages (Caldas and Almeida, 1993; Fallaci et al., 2002). Its foraging activity (detritivorous) is also favoured in this beach fringe (Almeida et al., 1993), where organic matter content tended to increase (see Fig. 1d).

The highest abundance and species richness of Coleoptera shifted from the base of the dunes in winter towards the sea in summer. Similar changes in zonation patterns have also been recorded in some Coleoptera species, notably in *Phaleria* (Caldas and Almeida, 1993; Colombini et al., 2002; Chelazzi et al., 2005) and Cicindelinae (Colombini and Chelazzi, 1991). Temporal variations in zonation patterns of these species have been attributed to changes in microclimatic conditions of the supralittoral zone (Chelazzi et al., 2005). In summer, high temperatures and relative low sand moisture may induce beetles to change their foraging areas and resting location seaward. These changes in zonation could also be closely related to a preference to specific sand characteristics (notably temperature and moisture) associated with breeding and larval habitat requirements (Alwpp, 1983; Fallaci et al., 2002; Uniyal and Bhargav, 2007).

In summary, results of this study showed that beach and dune ecosystems operate as two separate components within the LAZ, in regard to their physical features and to the entomofauna that characterized both ecosystems. The beach is inhabited preferentially by Coleoptera species, which are highly specialized and present specific adaptations to this particular environment, whereas the dune is mainly occupied by more terrestrial (ants) species that occur in a wide variety of habitats. The high values of species richness and abundance of insects reveal that this group has a more significant ecological role than that originally considered so far in sandy beach ecology. Further studies should focus on the biology of the species and its relevance to food webs. It will also be important

to conduct insect deconstructive analyses that take into account beaches with different morphodynamics.

Acknowledgements

This paper is part of the MSc thesis of the first author, at Facultad de Ciencias UdelaR. PEDECIBA (Programa de Desarrollo de Ciencias Básicas) from Uruguay provided logistical and financial support for fieldwork in Barra del Chuy. We are grateful to our colleagues of UNDECIMAR for the assistance in the field and logistic or analytical support. We also specially thank Dr. Martín Bollazzi (Facultad de Agronomía, Montevideo, Uruguay) for the identification of Formicidae specimens. Two referees provided insightful comments that improved our manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ecss.2015.05.011>.

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