ORIGINAL RESEARCH

Environmental Harshness Decreases ant β-Diversity Between Salt Marsh and Neighboring Upland Environments

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Abstract Understanding how wetland organisms interact
with neighbor habitats along environmental gradients is im-
portant to recognize wetland integrity and its connectivity at
landscape-level. We evaluated whether assemblage character-
istics (e.g. α-diversity) of marsh-ants are associated with geo-
graphic changes in environmental conditions, and if these fac-
tors are associated with marsh-upland dissimilarity in ant spe-
cies composition (β-diversity). Ant-samples were collected
both in the marsh and in the neighboring upland habitat at 5-
sites along the South-west Atlantic (SWA) coastline (36°S to
40°S), encompassing two-distinct biogeographic regions.
Generalized Linear Models showed that at the marsh scale,
ant occurrence increased with maximum temperature and
Spartina densiflora cover, but decreased with total-plant cov-
er. Ant richness increased with salinity, *S. densiflora* cover and
marsh area; and ant α-diversity increased with *S. densiflora*
cover and decreased with total marsh plant cover and plant
height. Composition of ant assemblages differed between the
marsh and the upland habitat depending on the site, and β-
diversity decreased with precipitation, salinity, tidal amplitude
and α-diversity of the herbaceous stratum. Then, the abun-
dance and α-diversity of ants varied along SWA marshes in
relation to changes in local environmental factors and the re-
gional landscape. Moreover, changes in species characteristics
across coastal-landscape seem to interact with environmental
gradients, resulting in reduced β-diversity values with increas-
ing environmental harshness. Thus, our results suggest that
the link of geographic changes in the physical environment
with the changes in species traits drives the variation in marsh-
upland dissimilarity across the space.

Keywords Ant assemblages · α-diversity · β-diversity ·
Latitudinal gradients · *Spartina* · Salt marshes · South-west
Atlantic coast

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Introduction

Abundance and diversity of organisms generally vary with
latitude in relation to gradients of physical and environmental
conditions (e.g. Gaston 2000; Hillebrand 2004). In addition, a
given habitat is surrounded by a mosaic of other habitats
throughout its distribution. These neighboring habitats, except
those that are completely hostile (e.g. oceanic islands
surrounded by the sea, Haila 2002; Tscharntke et al. 2012),
have their own pool of species that can influence the abun-
dance and diversity of organisms in the particular habitat, and

vice versa (Gaston 2000; Laurance et al. 2007). This may result in fragments of habitats of the same type situated in different landscape contexts differing in their species compositions (Laurance et al. 2007), and in their suite of shared species (β-diversity). Thus, not only local diversity (i.e. α-diversity), but also β-diversity can vary geographically along environmental and physical gradients, modulating the overall diversity at the landscape scale (Koleff et al. 2003; Tscharntke et al. 2012). Although recently these neighbor's effects have received more attention (Tscharntke et al. 2012), information is still limited, and the role of β-diversity on the overall diversity patterns has yet to be explored, particularly along landscape and geographic gradients in environmental conditions (Tscharntke et al. 2012; Andrew et al. 2012).

The harshness and variability of physical conditions in the environment generally increase with latitude (e.g. higher temperature range, lower intensity of light input, lower accumulated annual rainfall, Stevens 1989; Clarke and Gaston 2006). These changes in environmental conditions may not only affect species abundance and diversity, but also change the species pool and its tolerance to environmental stability. Thus, in highly variable environments, we might expect that organisms develop a more generalist physiology and ecology (Stevens 1989; Clarke and Gaston 2006), which allows them a greater distribution through different habitats. This potential for a widespread distribution could result in decreasing β-diversity (increasing between-habitats similarity) in highly variable environments, decreasing the diversity at the landscape level (Canepuccia et al. 2013). However, opposed results or no relationship between β-diversity and geographic environmental gradients have been found (Koleff et al. 2003; Tscharntke et al. 2012), suggesting that the association of species characteristics with habitats and environmental harshness is far from being fully understood. Thus, investigating these associations is necessary to understand the connectivity between habitats and to predict the consequences of the impending changes in physical stability and stress levels (e.g. changes in rainfall, temperature or sea level) on landscape biodiversity.

Tidal marshes are habitats that develop along low energy coastlines of high and middle latitudes of most continents (Mitsch and Gosselink 1993). These habitats are dominated by a few plant genera with a wide geographical distribution (e.g. *Spartina* spp., Mitsch and Gosselink 1993; Isacch et al. 2006). From the La Plata River outlet (35°13′S) to northern Patagonia (40°50′S, both in Argentina) there are some of the most extensive *Spartina* spp. marshes of the southwest Atlantic coast (Isacch et al. 2006, hereafter SWA). These relatively homogeneous ecosystems are dominated by the dense-flowered cordgrass (*Spartina densiflora* Brong) and the smooth cordgrass (*Spartina alterniflora* Loesel), which are discontinuously distributed along a gradient of tidal

amplitudes and salinity (Isacch et al. 2006; Canepuccia et al. 2013). There is also a marked gradient of increased aridity with latitude (i.e. decreasing precipitation and increasing daily thermal amplitudes; Canepuccia et al. 2013), which creates up to three different biogeographic provinces characterized by the dominance of either grasses or shrubs in upland habitats (Cabrera and Willink 1973; see study area section). As a consequence, different upland habitats surround marshes with similar plant species along their geographic distribution (Canepuccia et al. 2013). This feature provides a unique opportunity to investigate how the species assemblages change between habitats along environmental gradients and climatic conditions, minimizing the artifacts associated with the comparison among different habitat types.

Ants are ubiquitous (Hölldobler and Wilson 1990) and common organisms in marshes (e.g. China: Wu et al. 2013; North America: Childres and Koning 2013; South America: Canepuccia et al. 2009). Given their great diversity, their wide variety of ecological functions, and their high sensitivity to environmental changes (e.g. Folgarait 1998; rainfall and salinity: Fergnani et al. 2008; temperature and plant productivity and diversity: Kaspari et al. 2000; Fergnani et al. 2008), ants are an ideal group to evaluate the responses of species abundance and diversity along environmental and climatic gradients (Andersen 1997; Kaspari et al. 2000). As in many biological assemblages, ants may be segregated at either small or large spatial scales by traits that reflect their location along environmental gradients (e.g. Fergnani et al. 2008; Wittman et al. 2010). Thus, if ant species segregate between neighboring marsh-upland habitats, understanding the influence of both the physical and environmental variables on their distributions might be important to predict biodiversity changes to local or global scale climatic changes.

The purpose of our work was to describe biogeographic patterns of ant diversity, such as gradients of species abundance, richness and segregation between *Spartina* marshes and its neighboring upland habitat along the SWA coastline. Given that species' responses to environment gradients can strongly vary within landscape contexts, we adopted a multiscale approach in which three different spatial scales of diversity were compared: (a) habitat (marsh or upland), (b) landscape (similar marshes surrounded by different upland habitats), and (c) geographic (marsh-upland differences along gradients in physical and environmental conditions). First we investigated if the characteristics of ant assemblages (abundance, richness and α-diversity) in *Spartina* marshes are related to environmental (marsh area, plant cover, plant richness and plant diversity) and physical (tidal range, salinity, temperature and precipitation) variables or are related to

upland landscape characteristics (abundance and identity of upland ants, the type of upland landscape). We evaluated two alternative hypotheses: (a) there is a landscape divergence in species assemblage (e.g. Laurance et al. 2007), or that (b) the species assemblage depends on the characteristics of each local habitat. Here, we predict that although the abundance and richness of species are related to local marsh characteristics (physical and biological variables), its species composition depends on the landscape context. Thus, marshes located in similar landscapes will tend to converge in ant assemblages, while those located in different landscapes will tend to diverge.

To have a better understanding of the drivers of β-diversity, our second aim was to assess the relationship among β-diversity and the gradients of environmental and physical conditions along the SWA coast. Given that we found segregation in species composition between neighboring habitats (β-diversity), we evaluated two alternative hypotheses: (a) this segregation decreases with the harshness and instability of the environment or, (b) that the species segregation depends on the habitat type, independently of the gradients of environmental and physical conditions. We predict an increase in the abundance of species with highly tolerant traits, and poor competitive ability, omnivory and habitat generalists, under conditions of increasing stress (more aridity and salinity) and decreasing environmental stability (increased tidal amplitudes and daily thermal amplitudes). This is based in the fact that a strategy for high tolerance and lower specialization of species living at higher stress conditions allows them a greater spatial distribution (e.g. Stevens 1989) across neighboring habitats, which results in a lower β-diversity with the increase in stress and environmental instability.

Methodology

Study Sites

The study was carried out at five sites located between 35° 13′ S and 40° 50′ S along the Argentinean South West Atlantic (SWA) coast, including most of the SWA *Spartina* marshes (those located between northern Argentinean Patagonia 43°20′ S, and southern Brazil 31°48′ S, Isacch et al. 2006) and their neighboring upland habitats. These tidal marshes are similar in plant composition and topography, and marsh-upland borders are

Fig. 1 Marshes sampled along the SW Atlantic coast. SC: San Clemente (36° 22′ S); MCH: Mar Chiquita (37° 32′ S); PA: Punta Alta (38° 41′ S); BA: Bahía Anegada (39° 48′ S); and BSA: Bahía San Antonio (40° 42′ S). From the upland side, SC and MCH are neighboring by the Pampas grassland landscape (*striped area*), while PA, BA and BSA are neighboring by Monte landscape (*dotted area*). The coast between the arrows shows the area 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 Meteorológico Nacional Argentino)
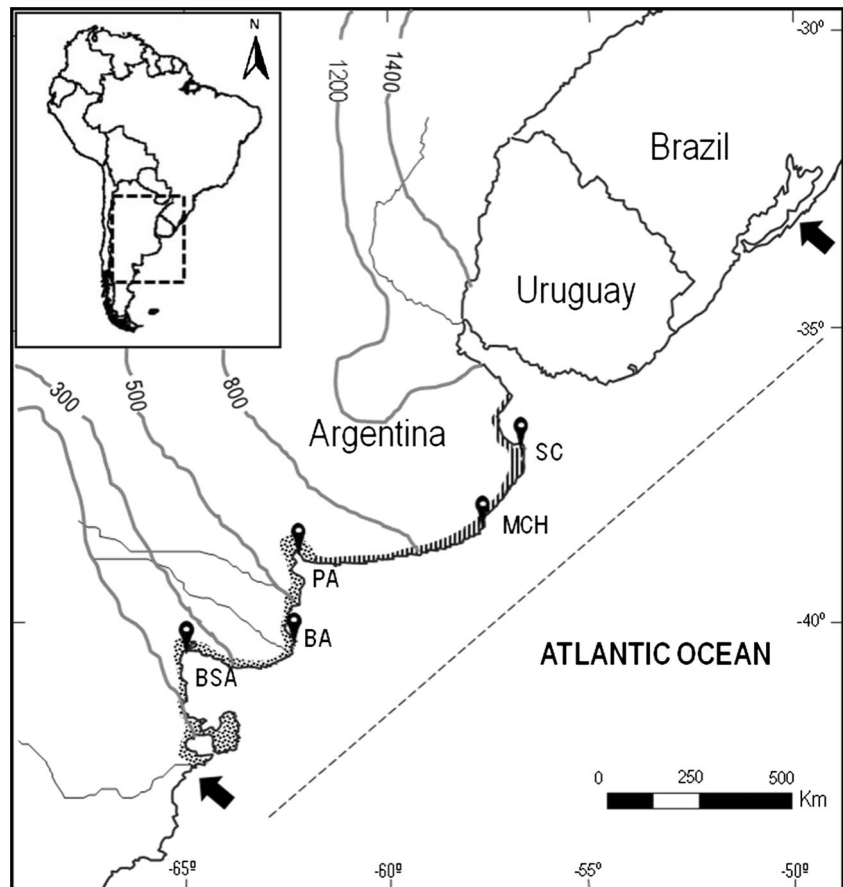
similar in shape (e.g. development and height). These marshes are characterized by two main habitats defined by the intertidal height and the dominance of different plant species. The lower marsh develops at the maritime front and is occupied by a monoculture stand of *Spartina alterniflora*. The high marsh develops at the upper intertidal height and is dominated by *Spartina densiflora* and the perennial glasswort *Sarcocornia perennis* (P. Mill.) A.J. Scott. (Isacch et al. 2006; Canepuccia et al. 2013). The specific sampling sites were: the outlet of La Plata River (San Clemente, SC: 36° 22′ S), the Mar Chiquita coastal lagoon (MCH: 37° 45′ S), the Bahía Blanca estuary (Punta Alta, PA: 38° 51′ S), Bahía Anegada (BA: 39° 48′S), and Bahía San Antonio (BSA: 40° 42′ S, Fig. 1). The northern marshes (SC and MCH) are exposed to microtides of less than 1 m (Isacch et al. 2006, Table 1), have an important freshwater input from the La Plata River estuary, and are characterized by brackish water conditions (lower than 28‰, Canepuccia et al. 2013, Table 1). The southern marshes (PA, BA and BSA) develop in large embayments with a range of mesotide to macrotides (from 1.64 to 6.44 m, see Isacch et al. 2006, Table 1). In these marshes, restricted water circulation, high evaporation (Perillo et al. 2006) and low freshwater input (Isacch et al. 2006) contribute to an average water salinity higher than that of the ocean water (>38‰,

Canepuccia et al. 2013, Table 1). For the upland neighboring side, these *Spartina* marshes are distributed along a marked gradient of increasing aridity southward, mainly caused by a decrease in precipitation (Isacch et al. 2006) and an increase in daily thermal amplitudes (Canepuccia et al. 2013). Furthermore, the northern marshes (SC and MCH) are surrounded by the Pampas grassland vegetation, characterized by an herbaceous stratum dominated by the silver Pampas grass *Cortaderia selloana* (Schult.) Asch. et Graeb. and the spiny rush *Juncus acutus* L. (Canepuccia et al. 2013). Marshes in this biogeographic province have a warm temperate climate (Table 1) and are characterized by abundant precipitation (SC = 950 mm year^{-1}, MCH = 920 mm year^{-1} on average, Isacch et al. 2006). The marshes in the central portion of our study area have a colder and drier climate with intermediate precipitation (PA = 645 mm year^{-1}, BA = 500 mm year^{-1}), while the southernmost marsh has the driest conditions (BSA = 248 mm year^{-1}, Isacch et al. 2006). The marshes of the central and southern sites (PA, BA and BSA) are bordered at the upland side by Monte vegetation (dotted area, Fig. 1), composed mostly by xeric bushes (e.g., *Atriplex lampa* (Moq.) Small, *Cyclolepis genistoides* D. Don, *Frankenia juniperoides* (Hieron.) M.N. Correa, Canepuccia et al. 2013). Therefore, the relatively homogeneous *Spartina* marshes are surrounded by

Table 1 Environmental data: average of tidal amplitude (m), average of salinity (‰), annual precipitation (mm), and temperature data (°C). Plant characteristics in *S. densiflora* marshes are given as cover (%), height (cm), richness (species number), and diversity (Shannon-Wiener index) along SWA coast. Between brackets, the standard error. Different lowercase letters denote significant differences between sites at $P < 0.05$ with Tukey's HSD test. SC: San Clemente (36° 22′ S), MCH: Mar Chiquita (37° 32′ S), PA: Punta Alta (38° 51′ S), BA: Bahía Anegada (39° 48′ S), and BSA: Bahía San Antonio (40° 42′ S). Environmental data were obtained from Canepuccia et al. (2013)

			SC	MCH	PA	BA	BSA
Tidal amplitude			0.75	0.79	2.44	1.64	6.44
Salinity			23.91(2.87)	27.95(1.04)	42.75 (1.34)	38.17(1.02)	40.30 (1.12)
Annual precipitation			950	920	645	500	248
Temperature		Maximum	34.09(1.25)	35.84(1.63)	38.81(1.77)	38.80	38.21(9.32)
		Minimum	−2.76(1.46)	−4.34(1.53)	−5.85(2.03)	−6.11	−6.58(4.46)
		Daily amplitude	24.29(4.3)	24.19(1.77)	26.34(3.09)	27.02	28.33(8.10)
Marsh plants		Cover	42.70(11.27)[ab]	42.96(5.23)[ab]	30.95(5.29)[a]	52.42(9.18)[b]	14.30(8.36)[c]
		Height	116.80(25.24)[a]	67.36(10.54)[b]	57.20(4.46)[bc]	34.20(6.38)[c]	32.70(1.20)[c]
		Richness	2.40(0.89)[a]	1.20(0.45)[b]	2.00(0.00)[a]	2.00(0.00)[a]	2.60(0.55)[a]
		Diversity	0.28(0.20)[ad]	0.05(0.12)[b]	0.47(0.28)[cd]	0.64(0.07)[c]	0.85(0.20)[c]
Upland plants	Herbaceous	Cover	46.00(11.05)[a]	94.62(33.37)[b]	30.96(7.35)[a]	32.94(15.10)[a]	30.49(11.76)[a]
		Height	123.00(4.47)[a]	106.00(5.48)[b]	39.00(2.24)[c]	54.40(8.32)[d]	10.80(2.95)[e]
		Richness	1.20(0.45)[a]	4.60(1.34)[b]	2.60.(0.89)[a]	3.40(0.55)[b]	3.80(0.45)[b]
		Diversity	0.03(0.06)[a]	1.07(0.30)[b]	0.65(0.13)[b]	1.07(0.18)[b]	0.91(0.46)[b]
	Shrubs	Cover	0.00[a]	0.00[a]	0.55(0.16)[b]	0.54(0.31)[b]	0.61(0.25)[b]
		Height	–	–	40.55(11.44)[a]	56.20(10.80)[b]	31.02(11.03)[c]
		Richness	00.00[a]	00.00[a]	3.00(0.00)[b]	3.20(0.45)[b]	2.00(0.00)[c]
		Diversity	–	–	0.66(0.14)[a]	0.98(0.05)[b]	0.66(0.01)[a]

diverse upland matrices that represent two different biogeographic provinces (Fig. 1).

Ant Assemblages and Physical and Environmental Variables

Ant Assemblages Sampling in Marsh and Upland Habitats

We used pitfall traps for sampling epigaeic ant species (e.g. Agosti et al. 2000). Although this trap method has lower efficiency to estimate diversity than hand collecting methods (Gotelli et al. 2011), it is among the most commonly used and standardized methods to estimate and compare the composition of arthropod assemblages. At each study site (SC, MCH, PA, BA and BSA) two 200 m-transects of 20 pitfall traps each, separated by 10 m were placed parallel to the coastline. One transect was located in the middle of the *S. densiflora* marsh (upper intertidal marsh habitat), at a distance of 40–50 m from the marsh-upland edge, and the other 50 m apart from the marsh-upland edge, in the adjacent upland habitat. Sampling was not conducted in the low-marsh zone (dominated by *S. alterniflora*) since pitfall traps would be flooded twice a day by regular tides, resulting in the loss of trapped animals. The traps used were plastic pots of 12 cm diameter and 15 cm depth partly filled with a mix of water, salt and detergent (*sensu* Canepuccia et al. 2009). Pitfall traps were activated for 72 consecutive hours at each site and in each habitat (i.e. marsh and upland) in austral summer (March 2011), when activity, abundance and diversity of ants are generally the highest (e.g. Andersen 1983; Lindsey and Skinner 2001; Pol and Lopez de Casenave 2004). The five sites were sampled during clear-sky weather conditions within a week of low tidal amplitude, thereby avoiding pitfall traps being flooded by tides or rain. Samples were then brought to the laboratory, fixed in 96 % ethanol, and sorted by species. Voucher specimens from each site were deposited in the Museum of Natural Science Lorenzo Scaglia, Mar del Plata, and in the Instituto-Fundación Miguel Lillo, Tucumán, both in Argentina.

Analysis of the ant Assemblage Data

The analysis of ant abundances data was based on the species occurrence in samples, which is recommended for quantifying abundances of social insects (Longino et al. 2002; Gotelli et al. 2011). To estimate richness and α-diversity of ant species, sample-based rarefaction curves were constructed. Species richness was calculated by incidence-based estimators (Chao 2 and Jackknife 1). Species α-diversity was estimated by the Shannon-Wiener diversity index H' (following Magurran 1988). Rarefied richness and α-diversity were computed with the Vegan package version 9 1.15-4 (Oksanen et al. 2015) in R version 2.9.2 (R Development Core Team, http://www.r.project.org).

A Tukey's HSD test following a nested analysis of variance (nested ANOVA, Zar 1999) was used to evaluate the null hypothesis of no differences in occurrence, α-diversity and species richness between habitats as a nested factor within sites. Since community data are mainly multivariate (Clarke and Warwick 2001), to test for differences in ant assemblage composition along the geographical gradient, multivariate analyses were used. To perform permutational analysis of variance (PERMANOVA), the PRIMER 6 software was used (Clarke and Gorley 2006). Bray–Curtis similarity matrices (Clarke and Warwick 2001) were constructed to test the multivariate null hypothesis of no differences in ant assemblage composition among groups. Differences in ant assemblage composition were tested between habitats and among sites (habitat x site). To obtain P-values, all PERMANOVA tests relied on 9999 permutations following the unrestricted raw data permutation method, which is the most appropriate method for one-way cases and it provides a type I error close to α (Anderson et al. 2008). A posteriori, pair-wise comparisons using 9999 random permutations were performed when PERMANOVA tests were significant at the 0.05 level. Differences in ant assemblage composition were further explored using non-metric multidimensional scaling ordination (NMDS), where a stress value below 0.20 gives an adequate representation of the two-dimensional NMDS (Clarke and Warwick 2001).

Environmental and Physical Factors

To characterize the prevailing environmental conditions of each study site, we used the most important physical (i.e. marsh area, mean annual precipitation, temperature, water salinity and tidal amplitude) and biological (i.e. cover, height, richness and diversity of plants) variables associated with the hypotheses proposed to explain changes in the abundance and diversity of organisms (Bertness et al. 1992; Kaspari et al. 2000; Hawkins et al. 2003; Pennings et al. 2005; Fergnani et al. 2008). Physical variables were obtained from Canepuccia et al. (2013, Table 1). To obtain the biological variables, plant characteristics (i.e. cover, height, richness and diversity) were measured in each habitat at each site before ant sampling. The herbaceous and shrub strata were sampled differently due to their different characteristics. The herbaceous vegetation was sampled using a Line Intercept Method (Canfield 1941) with five 10 m-transects placed 50 m apart in each habitat at each site. Transects were placed parallel to the coastline and in the middle of the spatial distribution (across the intertidal) of each marsh height at each site. For the shrub strata, five 5 × 5 m quadrats were used in each habitat at each site to estimate vegetation cover. All individual plants present within the quadrats were counted and measured (height, length and width). Additionally, we

estimated plant height by measuring the height of one randomly chosen plant of each layer (herbaceous or shrub) within each transects or quadrats. A Tukey's HSD test following a two-way ANOVA (Zar 1999) was used to evaluate the null hypothesis of no difference in plant characteristics between habitats and among sites.

Relationship Between ant Assemblages and Physical and Environmental Variables

We used Generalized Linear Models (GLMs) to estimate the relationship among physical and environmental variables (predictor variables) and changes in the characteristics of the ant assemblage among sites. GLMs allow nonnormal data to be analyzed using link functions and exponential family of functions (e.g. normal, Poisson or binomial distributions, Crawley 2007; Bolker et al. 2009).We used a Poisson distribution for richness, and a Gaussian distribution for abundance and diversity (α and β) of ants, as the error distribution. The predictor variables considered for modeling the changes in an assemblage characteristics (occurrence, richness and α-diversity) in marshes along the SWA coast were: marsh surface, tidal amplitude, salinity, precipitation, temperature (maximum, minimum and thermal amplitude), plant characteristics (cover of dominant marsh plant, *S. densiflora*, total cover, height, richness and diversity of marsh plant) and characteristics of the upland ant assemblages (occurrence, richness and α-diversity). We also modeled, using GLMs, the changes in characteristics of upland ant assemblages, and here, the predictor variables considered were: precipitation, temperature (maximum, minimum and thermal amplitude), and plant characteristics (cover, heights richness and diversity of herbaceous and shrub strata of upland plants).

For final model selection, R package glmulti, Version 1.0.7 (Calcagno and de Mazancourt 2010) was applied. To ensure that the multicolinearity of the models was low, we checked variation inflation factors (VIF) among independent variables entering the model. When the VIF of any pair of predictors was larger than 10, the variable with the smallest explanatory power was removed (Neter et al. 1996). Then, the selection procedure was run again. We used two measures to provide further insight into the amount of uncertainty in the model selection. The first measure was the difference in AICc (corrected Akaike Information Criterion) between the best approximating model and all the other models (Burnham and Anderson 2002), termed ΔAICc. In general, a ΔAICc 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 ΔAICc value, termed

"model weight" (Anderson and Burnham 1999; Burnham and Anderson 2002). To evaluate the support of predictor variables we estimated the parameter likelihood (Burnham and Anderson 2002); predictor variables with a model-averaged importance (parameter likelihood) of at least 80 %, were included in our final model. Parameter estimates were calculated by the technique of model averaging (model-averaged inference) from AICc 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. Finally we calculated upper and lower confidence limits by adding or subtracting $2 \times SE$, respectively. These statistics were performed by using R ver. 2.15.2 software (R Development Core Team 2012).

Dissimilarity in ant Assemblages Between Marshes and Upland Habitats

Similarity percentages (SIMPER) analysis was performed on ant occurrence data to determine the identity of the species responsible for the multivariate pattern in the marsh-upland dissimilarity (β-diversity). The SIMPER routine compares average abundance and examines the contribution of each species to dissimilarities (Clarke and Warwick 2001) between marsh and upland assemblages along the SWA coast. A Monte Carlo analysis (Manly 1998) was used to evaluate the null hypothesis of no difference among sites in the marsh-upland dissimilarity in ant species composition. The analysis was made by a random resampling (20 iterations with replacement, matching the number of traps) of the ant species composition for each habitat and among sites. For each iteration we re-estimated dissimilarity percentages (SIMPER) in ant assemblage composition. A Tukey's HSD test following an analysis of variance (ANOVA, Zar 1999) was used to evaluate the null hypothesis of no differences among sites in the dissimilarity of assemblages between marsh-upland environments. As previously described, we used a GLM (Crawley 2007; Bolker et al. 2009) to estimate the relationship among physical and environmental variables and the marsh-upland dissimilarity (β-diversity) in ant species composition along the SWA coast. For the response variable, β-diversity, we used a Gaussian distribution of β-diversity as the error distribution. Here, the predictor variables considered for the models were marsh surface, precipitation, tidal amplitude, salinity, temperature (maximum, minimum and thermal amplitude), plant characteristics (as was previously described) of both

habitats and the richness and α-diversity of ants in both habitats.

Results

Ant Assemblages and Physical and Environmental Variables

We collected a total of 4353 ants (1027 in the marsh and 3326 in the upland habitats) belonging to 49 species and 3 subfamilies (Myrmicinae, Dolichoderinae and Formicinae, see Table S1 in Online Resource). Along the study sites, occurrence, richness (Chao 2 and Jackknife 1estimators) and α-diversity of ants differed between habitats (Table 2). The northernmost sites (SC and MCH) and the southernmost one (BSA) showed higher occurrences, richness and diversity of ants than the central sites (PA and BA). At the same time, SC, MCH and BSA showed higher occurrence, richness and diversity of ants in the upland than in the marsh, while the central sites (PA and SB) did not show differences between habitats (marsh vs. upland, Table 2).

PERMANOVA shows that ant assemblage composition differs between habitats (2 levels, fixed) depending of the sites (5 levels, fixed), with interaction effects (site x habitat, Table 3). MDS analysis showed that the similarity in ant assemblages is higher between high-latitude sites (BA and BSA) and between low-latitudes ones (SC and MCH) than among low and high latitudes sites. PA, located at middle of the latitudinal distribution, showed an intermediate spatial arrangement, with similarities with MCH as well as with high latitude sites (Fig. 2a). When a factor habitat was considered, the ant assemblage of marshes was inside of the spatial arrangement of upland ant assemblages (Fig. 2b). Pair-wise tests showed that ant assemblages differed among the upland habitats (P-per < 0.05, Table 3). The northernmost upland habitat, SC, was dominated by *Pheidole* sp. 6, while MCH was dominated by *Ph. radoszkowskii* Mayr and *Ph. cf. humeridens*. At central sites, PA was dominated by *Solenopsis richteri* Forel, while BA was dominated by *Camponotus rufipes* Fabricius. The southernmost site, BSA, was dominated by *C. punctulatus* Mayr (see Table S1). Assemblage composition also differed among marsh habitats. In this habitat, SC showed lower ant occurrence with dominance of *Ph. aberrans* Mayr. MCH and PA showed higher occurrence of *S. richteri*, while PA was also characterized by a higher occurrence of *C. rufipes*. BA showed a greater occurrence of *Ph. aberrans* and *Pheidole* sp. 1 (gr. *fallax*). Finally, in BSA, there was a higher occurrence of *Pheidole* sp. 1 (gr. *fallax*) and *Dorymyrmex wolffuegeli* Forel. As a result, the ant assemblages also differed

Table 2 Mean (standard error) of observed specis richness, estimated richness by Chao 2 and Jackknife1, and average of α and β-diversity of ants in *S. densiflora* marshes and in the upland habitat along the SWA coast. SC: San Clemente (36° 22' S), MCH: Mar Chiquita (37° 32' S), PA: Punta Alta (38° 51'S), BA: Bahia Anegada (39° 48'S), and BSA: Bahía San Antonio (40° 42' S). SC and MCH are limiting from the upland by the Pampa grassland. PA, BA and BSA are limiting by Monte vegetation. Different lowercase letters denote significant differences between habitats (marsh and upland) and among sites (SC, MCH, BB, BA, BSA) at p < 0.05 with Tukey's HSD test

Sites	SC		MCH		PA		BA		BSA	
Habitat	Upland	Marsh	Upland	Marsh	Upland	Marsh	Upland	Marsh	Upland	Marsh
Occurrences	4.15(2.13)[a,c]	0.15(0.49)[b,f]	7.05(1.54)	3.70(2.87)[c]	1.80(0.95)[d]	1.80(1.20)[d]	1.85(0.99)[d]	1.40(1.19)[d,f]	5.40(1.05)[a]	0.50(0.61)[b,d]
Observed richness	18	2	20	17	12	9	8	6	16	2
Estimated richness: Chao2	23.94(7.19)	2.48(1.27)	37.10(22.46)	19.14(3.25)	38.60(20.22)	12.80(5.05)	9.90(3.57)	6.95(2.12)	21.70(6.18)	2.00(<0.001)
Estimated richness: Jackknife1	22.75(2.53)	2.95(0.95)	25.70(2.70)	19.85(1.65)	19.60(2.69)	12.80(1.90)	9.90(1.34)	7.90(1.34)	21.70(3.33)	2.00(<0.0001)
α-diversity	0.92(0.52)[b]	0.03(0.15)[a]	1.43(0.38)[c]	0.91(0.72)[b]	0.47(0.39)[a,d,e]	0.33(0.49)[a,d,e]	0.54(0.43)[d,b,e]	0.30(0.40)[d]	1.18(0.31)[b,c]	0.03(0.11)[a]
β- diversity	99.11(0.52)[a]		71.55(23.91)[b]		52.38(6.57)[c]		84.41(2.72)[d]		88.80(3.55)[e]	

Table 3 Summary of the PERMANOVA main tests to assess differences in the structure of the whole ant assemblages, between sites (SC, MCH, PA, BA and BSA) and habitats (marsh and upland) along SWA coast. Pair-wise comparison, * denote P-perm < 0.01

Source of variation	df	MS	Pseudo-F	P-value
Site	4	29,753	36.25	0.001
Habitat	1	30,174	36.76	0.001
Site x Habitat	4	13,814	16.83	0.001
Residuals	190	820.78		
Pair-wise comparison				
	Pseudo-$F_{1,4}$			
Sites	Upland	Marsh		
SC-MCH	4.750*	4.813*		
SC-BB	4.171*	6.868*		
SC-BA	4.587*	3.607*		
SC-BSA	5.956*	2.568*		
MCH-BB	6.010*	2.312*		
MCH-BA	6.854*	3.803*		
MCH-BSA	7.926*	4.443*		
BB-BA	4.847*	5.304*		
BB-BSA	6.150*	5.531*		

between habitats (upland and marsh, Table 3, Fig. 2, for details of each ant species changes among sites and between habitats see Table S1).
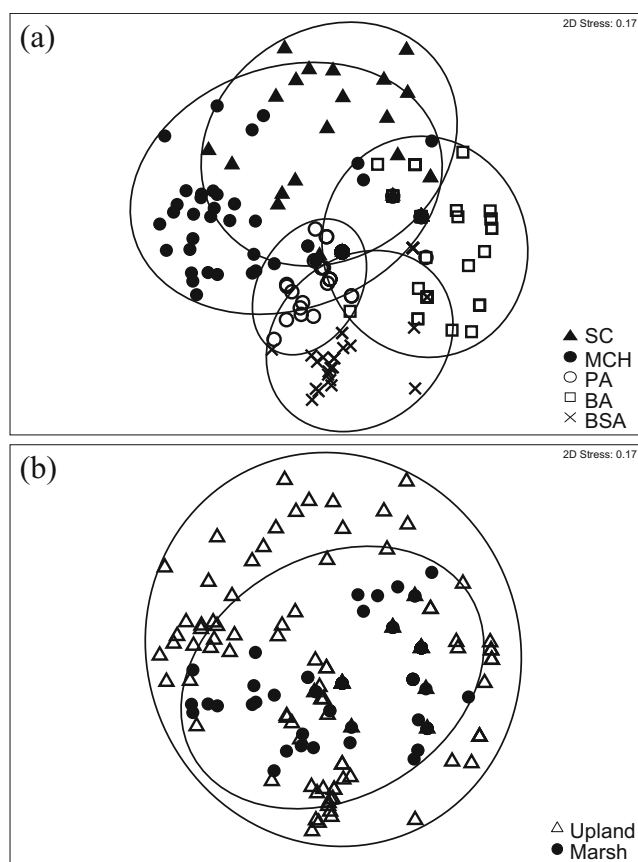

Fig. 2 Non-metric multidimensional scaling (NMDS) ordination plots using ant species abundance based on Bray–Curtis similarity matrices. (a): Two-dimensional arrangements of habitats: upland or marsh; and (b): sites: SC: San Clemente (36° 22′ S); MCH: Mar Chiquita (37° 32′ S); PA: Punta Alta (38° 41′ S); BA: Bahía Anegada (39° 48′ S); and BSA: Bahía San Antonio (40° 42′ S)

Ant Assemblages and Physical and Environmental Variables Relationship

Plant assemblage composition and characteristics differed between sites (ANOVA, $p < 0.05$, Table 1). Accounting for the 49 % of the variation, GLMs analysis indicated that the best model for ant occurrences in the marsh included the positive relationship with *S. densiflora* cover and maximum temperature, and the negative relationship with total plant cover and height of marsh plants. These four variables showed high parameter likelihood (>0.9) and significant confidence intervals (Table S2A). For the richness of marsh ants, the best model account for the 50 % of their variation and included the positive relationship with salinity, *S. densiflora* cover, α-diversity of herbaceous stratum of the upland, α-diversity of upland ants, and the negative relationship with the total marsh plants cover (Table 4A). However, α diversity of upland ants showed the lower parameter likelihood (0.58) and no significant confidence interval (Table S2A). Indeed there is one model with ΔAICc < 2 of the best model (Table 4A) that excluded α diversity of upland ants, and keeping the other four variables, which show high parameter likelihood (>0.9) and significant confidence intervals (Table S2A). Finally, the best model for the α-diversity of marsh ants (accounted for 37 % of the variation) included the positive relationship with *S. densiflora* cover and the negative relationship with cover and heights of marsh plants (Table 4A). These three variables showed high parameter likelihood (>0.9) and significant confidence intervals (Table S2A). Also there was another model with ΔAICc < 2, which also includes the positive relationship with α-diversity of upland ants, however this last variable showed low (0.52) parameter likelihood and no significant confidence interval (Table S2A).

Accounting for the 69 % of the variation, the best model for ant occurrences in the upland included the positive relationship with herbaceous strata cover and the negative relationship with the heights of shrub stratum and precipitation (Table 4B). These predictor variables presented high parameter likelihood (1) and significant confidence intervals (Table S2B). For the richness and α-diversity of the upland ants the best models included the positive relationship with herbaceous stratum cover, and the negative relationship with precipitation and heights of shrub stratum (Table 4B). Those three variables showed high parameter likelihood (>0.9) and significant confidence intervals (Table S2B). For α-diversity of the uplands ants the best model also included the positive relationship with height of herbaceous strata, but this variable showed low parameter likelihood (0.3) and no significant confidence interval (Table S2B). Indeed a second model for α-diversity of the uplands ants excluded this last parameter (Table S2B).

Table 4 Generalized Linear Models explaining the environmental and physical variables related to abundances (aa$_m$), richness (ar$_m$) and α-diversity (aα$_m$) of ants in marsh (A), abundances (aa$_u$), richness (ar$_u$) and α-diversity (aα$_u$) in upland (B), and marsh-upland dissimilarity, β-diversity, in ant assemblages composition: β (C). Number of parameters: K in each model included the intercept and each explanatory variable. Models with strong support are shown (i.e. ΔAICc < 2). Global models are also shown; AICc weight: AICcw. To eliminate multicolinearity of the models when the variation inflation factors (VIF) of any pair of predictors was larger than 10, the variable with the smallest explanatory power was removed. The physical explaining variables were: tides (td), salinity (sl), marsh surface (s), annual precipitation (pr), maximum (tma) and minimum temperature (tmi), thermal amplitude (ta). The biological explaining variables were: Spartina densiflora cover (sd); cover (mc); height (mh); richness (mr) and α-diversity (mα) of total marsh plants; cover (hc); height (hh); richness (hr) and α-diversity (hα) of plants of the herbaceous stratum of upland; and cover (shc); height (shh); richness (shr) and α-diversity (shα) of the shrub stratum of upland. Also variables estimated of ant assemblages (aa$_m$, ar$_m$, aα$_m$ aa$_u$, ar$_u$, and aα$_u$) were considered as biological explaining variables

(A) Marsh

	Model	Explanatory variables	K	AICc	AICcw	R^2
aa$_m$	1	sd + mc+ mh + tmax	5	136.11	0.937	0.49
	Global	ti+sl+pr+tmi+tma+ta+s+sd+mc+mh+mr+mα+aa$_u$	14			
ar$_m$	1	sd + mc + sl + aα$_u$ + hα	6	284.35	0.584	0.50
	2	sd+mc+sl+hα	5	285.03	0.415	0.50
	Global	ti+sl+pr+tmi+tma+ta+s+sd+mc+mh+mr+mα+ar$_u$+aα$_u$	15			
aα$_m$	1	sd + mc + mh	4	122.97	0.570	0.37
	2	sd + mc + mh + aα$_u$	5	123.56	0.426	0.37
	Global	ti+sl+pr+tmi+tma+ta+s+sd+mc+mh+mr+mα+ar$_u$+aα$_u$	15			

(B) Upland

	Model	Explanatory variables	K	ΔAICc	AICcw	R^2
aa$_u$	1	pr+hc+shh	4	357.96	1	0.69
	Global	pr+tmi+tma+ta+hc+hh+hr+hα+shc+shh+shr+shα	13			
ar$_u$	1	pr+shh+hc	4	360.01	0.982	0.59
	Global	pr+tmi+tma+ta+hc+hh+hr+hα+shc+shh+shr+shα	13			
aα$_u$	1	pr+hc+shh	4	113.043	0.688	0.45
	2	pr+hc+shh+hh	5	114.649	0.308	0.45
	Global	pr+tmi+tma+ta+hc+hh+hr+hα+shc+shh+shr+shα	13	−65.32	2.32E-03	

(C) β-diversity

	Model	Explanatory variables	K	ΔAICc	AICcw	R^2
β	1	ti+sl+pr+hr	5	−362.85	0.520	0.95
	2	ti+sl+pr+hr+aα$_u$	6	−361.29	0.239	0.95
	Global	ti+sl+pr+tmi+tma+ta+s+sd+mc+mh+mr+mα+hc+hh+hr+hα+shc+shh+shr+shα+ar$_m$+ar$_u$+aα$_m$+aα$_u$	25			

Marshes-Upland Dissimilarity in ant Assemblage and Physical and Environmental Variables

There were differences in ant assemblage compositions between marsh and upland at all sites (p$_{perm}$ < 0.01, Table 3, Fig. 2). SIMPER analysis revealed decreasing dissimilarities between upland and marsh assemblages from the outermost to the central sites in the latitudinal gradient, with the highest values of dissimilarity (β- diversity) at SC and BSA, intermediate values at MCH and BA, and the lowest value at PA (Table 2). At SC, two species contributed to about 50 % of the Bray-Curtis dissimilarity (99.32 %) between marsh and upland. These species were *Pheidole* sp. 6 (25.11 %) and *S. richteri* (15.18 %), which were more frequent in the upland habitat. With lower Bray–Curtis dissimilarity (75.80 %), a similar pattern was observed at MCH. There, *Ph.*

radoszkowskii (13.45 %) and *Ph. cf. humeridens* (11.17 %) were the most responsible for marsh-upland differences, being both more frequent in the upland habitat. PA showed the lowest dissimilarity (53.67 %). There, three species contributed to about 50 % of the marsh-upland dissimilarity: *Ph. aberrans* (9.4 %), which was more frequent upland; and *S. richteri* (36.24 %) and *D. wolffuegeli* (9.3 %), which was more frequent in the marsh. At BA, the average dissimilarity of ant assemblages between marsh and upland habitats reached 85.75 %. There, four species accounted for 79 % of marsh-upland dissimilarity: *C. rufipes* (26.28 %) and *Solenopsis invicta* Buren 1972 (12.65 %), which were more frequent upland; and *Ph. aberrans* (20.72 %) and *Pheidole* sp. 1 (gr. *fallax*) (20.03 %), which were more abudant in the marsh. Finally, at BSA, the Bray-Curtis dissimilarity between marsh and upland habitats rose again (92.37 %). Five species

contributed more than two thirds to this dissimilarity: *Pheidole* sp. 1 (gr. *fallax*) (22.51 %), *S. richteri* (18.32 %), *C. punctulatus* (13.98 %), *Dorymyrmex exanguis* Forel (11.36 %) and *D. wolffuegeli* (9.21 %); all were more frequent in the upland habitat (for details of ant species changes among sites and between habitats see Table S1).

GLMs indicated that the best model for predicting β-diversity changes between marsh and upland in ant species assemblages include the negative relationship with precipitation, salinity, tidal amplitudes and richness of herbaceous stratum (Table 4C). This model accounted for 95 % of the β-diversity. There were also another model with ΔAICc < 2 (Table 4C) which also included the negative relationship with α-diversity of ants in marsh, and the positively relationship with α-diversity of ants in upland (Table S2C, see Online Resource). However, the two ant α-diversities, those from the upland and those from the marsh, showed low parameter likelihood (<0.4), and were not significant (Table S2C). The other variables (precipitations, salinity, tidal amplitudes and α-diversity of herbaceous stratum) showed higher support (parameter likelihood > 0.9) and confidence intervals excluding zero (Table S2C).

Discussion

We found that ant assemblages varied in marshes and upland habitats based on physical (temperature, salinity, precipitation) and biological (cover, height and diversity of plants) variables. Furthermore, the changes in species characteristics (e.g. tolerance to environmental harshness, position in the trophic web) can combine with the changes in the physical and biological variables to exert important effects on the assemblage differences (β-diversity) between these marshes and the upland habitats.

Ant Assemblages Characteristics and Physical and Environmental Variables

Ant abundance was positive correlated with maximum temperature. Along the study area, the variation range of maximum temperature is 4 °C, such difference could have important effects on thermophilic organisms, such as many ant species (Brown 1973; Kaspari et al. 2000). Higher temperatures can allow higher foraging rates and more energy accumulated, decreasing physiological and thermoregulation costs (Lennon et al. 2000; Kaspari et al. 2000), and extinction rates (Sanders et al. 2007), which may result in higher ant abundances in marshes located at sites with higher temperatures.

Net primary productivity is often temperature limited (e.g. Lieth 1975), and this may be related with the increase in ant abundance, richness and α-diversity in marshes with the increase of *S. densiflora* cover. Then,

the ant abundances-maximum temperature relationship arises, at least in part, as a result of net primary productivity-ant relationship. Considering vegetation cover as a surrogate of net primary production, its increase can have important community effects (Hutchinson 1959), providing more food, refuges and potential niches for ants (e.g. Kaspari et al. 2000) in those marshes with higher plant cover. However, abundances, richness and α-diversity of ants also decreased with increasing total marsh plant cover. This inconsistency could be the result of different structures and forms of primary producers that may differentially modify the habitat structure for ants (e.g. Fergnani et al. 2010). Along the study range, the succulent *Sarcocornia perennis* (co-dominant species with *S. densiflora* grasses, Isacch et al. 2006; Canepuccia et al. 2013) has a more open-leaves structure than the compact *S. densiflora* grass. In addition, *S. densiflora* grasses are known to provide critical food resources (e.g. insect prey, seeds) and refuges for many terrestrial organisms in marshes (Canepuccia et al. 2008, 2010). Thus, ants could vary their assemblage composition along the SWA marshes in response to the variations in plant characteristics dominating these wetlands.

In addition, lower latitude plants were about ten times taller than higher latitude ones. Given that marsh plants height increases with environment productivity (Valiela et al. 1985; Valiela 2015), we expected taller plants to increase niche availability and foraging opportunities for ants. However, richness and α-diversity of ants decreased with increasing plant height. This relation could be the result of the importance of sun exposure (decreased by the canopy closure, Valiela 2015) on thermophilic organisms such as some ant species (Lassau and Hochuli 2004; Fergnani et al. 2013). The concomitant increase of obstruction may also hamper ant movements (Lassau and Hochuli 2004) and efficiency (Fergnani et al. 2013). Thus plant height appears to constitute a selective filter for ant colonization, influencing assemblage composition.

The species richness of ants also increased with increasing salinity, in contrast with the negative effect of salinity on ants occurring in other coastal environments (e.g. Kaspari et al. 2008). Tidal marshes are highly stressful environment for plants (Bertness et al. 1992; Canepuccia et al. 2010) and consumers (Crain 2008; Canepuccia et al. 2010), by the salt accumulation due to daily tidal flooding (Bertness et al. 1992). As a result, tidal marshes generally exhibit a salinity gradient from low to high marsh that corresponds with elevation and the frequency of tidal inundation (Bertness et al. 1992). This apparently contradictory result could arise, in part, because of the salinity gradient could operate as an environmental filter, allowing different ant species along the gradient depending on their tolerance to salt

stress. Thus, marshes flooded by seawater of higher salinity (PA and BSA: more than 40 ppm), could locally have a broader salinity gradient between the ocean side to the upland limit, than those marshes exposed to lower salinities (SC and MCH: lower than 28 ppm) allowing a higher ant diversity. In fact, plant diversity also increases with salinity in these marshes (Canepuccia et al. 2013), which also indicate an increase in niche availability for ants.

The increase in abundance, richness and α-diversity of upland ants with increasing productivity is a well known pattern for ants in different upland habitats (e.g. Kaspari et al. 2000; Retana and Cerda 2000). As in marshes, the increase of herbaceous cover may imply an increase of food, refuges and potential niches for ants. Unexpectedly, and given the negative effects of drought stress on organisms' physiology (Hawkins et al. 2003), the abundance, richness and α-diversity of ants decrease as precipitation increase. Although the underlying mechanisms are still poorly understood, ants are often more diverse and successful in dry systems (Dunn et al. 2009). A possible cause for this pattern is that high precipitation can increase the soil moisture, which can have negative effects on ants nesting site (Wang et al. 2001; Lassau and Hochuli 2004). Also, ants strongly adapted to aridity (Andersen 2007; Delsinne et al. 2010), are negatively affected by precipitation deficit only when it is lower than 200 mm year^{-1} (Delsinne et al. 2010), limit below which its desiccation risk increases (Kaspari 1993; Segev 2010). Along our study range, however, the precipitation gradient (950 mm year^{-1} at the N to 248 mm year^{-1} at the S) is above this limit.

Another plausible scenario for the ant-precipitation relationship is that precipitation gradient differentially changes the structure of species assemblages. For example, granivorous species have less profit at lower precipitation values than omnivorous ones because of limitation in seed production (Kaspari and Valone 2002). In our study range, the greater abundance of granivorous species (e.g. some *Pheidole* like cf. *humeridens*) were found at lower latitudes, coinciding with the higher rainfall amount (950 mm year^{-1}), while carnivorous/omnivorous species (e.g. *Dorymyrmex exanguis* Forel and *Forelius lilloi* Cuezzo) were more abundant at the higher latitudes and with lower rainfall amount (248 mm year^{-1}).

Similarly to what we found in marshes, the richness and α-diversity of ants decreased as increasing shrub height in the upland. The same variables and explanations may play a role in this sense (see above). Thus, geographic gradients in physical variables (e.g. gradients in temperature, precipitation and salinity) may have direct and indirect effects (through vegetation structure variation, cover, diversity and height of plants) not only on the abundance and diversity of ant, but also on the composition and function of the ant assemblage.

Marshes-Upland Dissimilarity in ant Assemblages

Although there is some agreement about the decrease in β-diversity with increasing latitude, there is still controversy about what factors and how they modulate these global variations (Koleff et al. 2003; Tscharntke et al. 2012). In our study, the best model to explain variation in β-diversity between marsh and upland habitats in ant assemblages' composition included the negative relationship with precipitation, salinity, tidal amplitude and richness of herbaceous stratum. Physical factors can act as environmental filters (Keddy 1992), varying the number and the type of species that one habitat can receive from their neighboring habitats. Here, changes in species' traits along geography may play an important role in the variation of β-diversity. Those organisms adapted to live in highly variable physical conditions usually develop more generalized physiological and ecological characteristics to cope with these environmental conditions (Stevens 1989). The tolerance to wide ranges in physical-environmental conditions results in species being able to become more widespread (Stevens 1989; Clarke and Gaston 2006). In fact, several marsh plants, which are adapted to highly variable physical conditions (e.g. daily tidal flooding, broad salinity ranges, Bertness 1991; Bertness et al. 1992) are among the most widely distributed worldwide (Adam 1993; Mitsch and Gosselink 1993). Conversely, more stable and benign physical conditions promote greater specialization in the use of (Stevens 1989; Clarke and Gaston 2006) and competition for resources (Tilman 1982; Grime 2001). This may result in a reduction of the number of species shared between neighboring habitats.

In our study range, the southernmost site (BSA) is exposed to greater environmental stress (higher salinity) and habitat variability (higher tidal range and daily temperature ranges). This site shows a greater abundance of omnivorous and generalist ant species such as *Pheidole* sp. 1 (gr. *fallax*), *C. punctulatus* and *D. exanguis* (Folgarait 1998; Wilson 2003), and species adapted to habitat instability (such as landscape flood, e.g. *C. punctulatus*, Folgarait et al. 2004). The northernmost sites (SC and MCH), in contrast, are less environmentally stressful (lower salinity, tidal range and daily temperature ranges) and show a greater abundance of predatory and highly competitive ants such as *Linepithema humile* Mayr (Kabashima et al. 2007) and *S. richteri* (Gonçalves and Nunes 1984; Folgarait et al. 2004). Therefore, if a low stress level increases the specialization in habitat and resource use of organisms (Bertness and Callaway 1994), we would also expect higher differences in the assemblage composition between habitats. Indeed, β-diversity of plants in this marsh-upland system follows a similar pattern (Canepuccia et al. 2013). There is also an inverse relationship of limnofauna β-diversity with latitude, partially explained by increased specialization of organisms towards the tropics (Hof et al. 2008). Then, a possible scenario for the β-diversity-hardness

association could be related with the stress gradient hypothesis (Bertness and Callaway 1994; Bertness and Ewanchuk 2002) in which the importance of negative interactions (e.g. competition) decreases at higher levels of environmental stress, while the importance of the positive ones (e.g. facilitation) increases, promoting, therefore, the observed decrease in β-diversity. Thus, besides local species interactions, the regional processes (e.g. Ricklefs 1987; Soininen et al. 2007), may probably modulate the differences in β-diversity of marsh-upland system along the SWA coast.

Overall, our results show that the abundances and α-diversity of ants vary geographically along the SWA coast in relation with some physical and biological factors correlated or not with latitude. In addition, assemblages of marsh ants were a subset of species already known for the upland habitats. This result suggests that there is not exclusive ant species in SWA marshes, but highlight the importance of these coastal wetlands for these organisms. The differences in the assemblage composition of ants between these neighboring habitats (β-diversity) varied along SWA coast with the gradients in physical and biological factors. Here, the higher specialization of species living in more benign environmental conditions seem to prevent assemblage similarities between neighboring habitats. Thereby, the changes in traits of species seem to interact with the gradients in the physical and biological factors, reducing β-diversity with the increase in stress and environmental instability. We hypothesize that the relative values of α and β-diversity are driven by multiple factors related with the shifts in landscape-wide species pools, together, or even synergistically with the environmental values of stability or stress.

References

Adam P (1993) Saltmarsh ecology. Cambridge studies in ecology. Cambridge University Press, Cambridge

Agosti D, Majer JD, Alonso LE, Schultz TR (2000) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington DC

Andersen AN (1983) Species diversity and temporal distribution of ants in the semi-arid mallee region of northwestern Victoria. Australian Journal of Ecology 8:127–137

Andersen AN (1997) Using ants as bioindicators: multiscale issues in ant community ecology. Conservation Ecology 1:8–21

Andersen AN (2007) Ant diversity in arid Australia: a systematic overview. In: Snelling RR, Fisher BL, Ward PS (eds) Advances in ant systematics (Hymenoptera: Formicidae): homage to EO Wilson- 50 years of contributions, memoirs of the American Entomological Institute., pp 19–51

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

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

Andrew ME, Wulder MA, Coops NC, Baillargeon G (2012) Beta-diversity gradients of butterflies along productivity axes. Global Ecology and Biogeography 21:352–364

Bertness MD (1991) Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology 72:138–148

Bertness MD, Callaway R (1994) Positive interactions in communities: a post cold war perspective. Trends in Ecology & Evolution 9:191–193

Bertness MD, Ewanchuk PJ (2002) Latitudinal and climatedriven variation in the strength and nature of biological interactions in New England salt marshes. Oecologia 132:392–401

Bertness MD, Gough L, Shumway SW (1992) Salt tolerances and the distribution of plants across a New England salt marsh. Ecology 72: 1842–1851

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 in Ecology & Evolution 24:127–135

Brown WL (1973) A comparison of the Hylean and Congo-West African rain forest ant faunas. In: Meggers BJ, Ayens ES, Duckworth WD (eds) Tropical forest ecosystems in Africa and South America: a comparative review. Smithsonian Institution Press, Washington DC, pp 161–185

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, monografía n° 13.Washington, DC. Programa regional de Desarrollo Científico y Tecnológico, departamento de Asuntos Científicos, Organización de Estados Americanos, Washington

Calcagno V, de Mazancourt C (2010) glmulti: an R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34:1–29

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

Canepuccia AD, Cicchino A, Escalante A, Novaro A, Isacch JP (2009) Differential responses of marsh arthropods to rainfall-induced habitat loss. Zoological Studies 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. Journal of Experimental Marine Biology and Ecology 396:42–47

Canepuccia AD, Pérez CF, Farina JL, Alemany D, Iribarne OO (2013) Dissimilarity in plant species diversity between salt marsh and neighboring environments decreases as environmental harshness increases. Marine Ecology: Progress Series 494:135–148

Canfield R (1941) Application of line interception in sampling range vegetation. Journal of Forestry 39:388–394

Childres ES, Koning AA (2013) *Polydomous Crematogaster pilosa* (Hymenoptera: Formicidae) colonies prefer highly connected habitats in a tidal salt marsh. Florida Entomologist 96:235–237

Clarke A, Gaston KJ (2006) Climate, energy and diversity. Proceedings of the Royal Society B: Biological Sciences 273:2257–2263

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

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

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

Delsinne T, Roisin Y, Herbauts J, Leponce M (2010) Ant diversity along a wide rainfall gradient in the Paraguayan dry Chaco. Journal of Arid Environments 74:1149–1155

Dunn RR, Agosti D, Andersen AN, Arnan X, Bruhl CA, Cerda X, Ellison AM, Fisher BL, Fitzpatrick MC, Gibb H, Gotelli NJ, Gove AD, Guenard B, Janda M, Kaspari M, Laurent EJ, Lessard JP, Longino JT, Majer JD, Menke SB, McGlynn TP, Parr CL, Philpott SM, Pfeiffer M, Retana J, Suarez VA, Vasconcelos HL, Weiser MD, Sanders NJ (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. Ecology Letters 12:324–333

Fergnani P, Sackmann P, Cuezzo F (2008) Environmental determinants of the distribution and abundance of the ants, *Lasiophanes picinus* and *L. valdiviensis*, in Argentina. Journal of Insect Science 8:1–16

Fergnani PN, Sackmann P, Ruggiero A (2010) Richness-environment relationships in epigaeic ants across the Subantarctic-Patagonian transition zone. Insect Conservation and Diversity 3:278–290

Fergnani PN, Sackmann P, Ruggiero A (2013) The spatial variation in ant species composition and functional groups across the Subantarctic-Patagonian transition zone. Journal of Insect Conservation 17:295–305

Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7:1221–1244

Folgarait PJ, D'Adamo P, Gilbert LE (2004) A grassland ant community in Argentina: the case of *Solenopsis richteri* and *Camponotus punctulatus* (Hymenoptera: Formicidae) attaining high densities in their native ranges. Annals of the Entomological Society of America 97:450–457

Gaston K (2000) Global patterns in biodiversity. Nature 405:220–227

Gonçalves CR, Nunes AM (1984) Formigas das praias e restingas do Brasil. In: Lacerda LD, Araújo DSD, Cerqueira R, Tureq B (eds) Restingas: origem, estrutura, processos. CEUFF, Niterói, pp 373–378

Gotelli NJ, Ellison AM, Dunn RR, Sanders NJ (2011) Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. Myrmecological News 15:13–19

Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties, 2nd edn. Wiley and Sons, Chichester

Haila Y (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecological Applications 12:321–334

Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology 24:3105–3117

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. American Naturalist 163:192–211

Hof C, Brändle M, Brandl R (2008) Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types. Global Ecology and Biogeography 17:539–546

Hölldobler B, Wilson E (1990) The ants. Belknap, Harvard University Press, Cambridge

Hutchinson GE (1959) Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93:145–159

Isacch JP, Costa CSB, Rodríguez-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. Journal of Biogeography 33:888–900

Kabashima JN, Greenberg L, Rust MK, Paine TD (2007) Aggressive interactions between *Solenopsis invicta* and *Linepithema humile* (Hymenoptera: Formicidae) under laboratory conditions. Journal of Economic Entomology 100:148–154

Kaspari M (1993) Body size and microclimate use in Neotropical granivorous ants. Oecologia 96:500–507

Kaspari M, Valone TJ (2002) On ectotherm abundance in a seasonal environment- studies of a desert ant assemblage. Ecology 83:2991–2996

Kaspari M, Alonso L, O'Donnell S (2000) Three energy variables predict ant abundance at a geographical scale. Proceedings of the Royal Society B: Biological Sciences 267:485–489

Kaspari M, Yanoviakc SP, Dudley R (2008) On the biogeography of salt limitation: a study of ant communities. Proceedings of the National Academy of Sciences 105:17848–17851

Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164

Koleff P, Lennon JJ, Gaston KJ (2003) Are there latitudinal gradients in species turnover? Global Ecology and Biogeography 12:483–498

Lassau SA, Hochuli DF (2004) Effects of habitat complexity on ant assemblages. Ecography 27:157–164

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

Lennon JJ, Greenwood JJD, Turner JRG (2000) Bird diversity and environmental gradients in Britain: a test of the species-energy hypothesis. Journal of Animal Ecology 69:581–598

Lieth H (1975) Modeling the primary productivity of the world. In: Lieth H, Whittaker RH (eds) Primary productivity of the biosphere. Springer, NewYork, pp 237–263

Lindsey PA, Skinner JD (2001) Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. Journal of Arid Environments 48:551–568

Longino JT, Coddington JA, Colwell RK (2002) The ant fauna of a tropical rain forest: estimating species richness three different ways. Ecology 83:689–702

Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton

Manly BFJ (1998) Randomization, bootstrap and Monte Carlo methods in biology, 2nd edn. Chapman and Hall Press, London

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

Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996) Applied linear statistical models, 4th edn. Times Mirror Higher Education Group, Chicago

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2015) Vegan: community ecology package. R package version 2.2-1. http://CRAN.R-project.org/package=vegan

Pennings SC, Grant MB, Bertness MD (2005) Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. Journal of Ecology 93:159–167

Perillo GME, Piccolo MC, Marcovecchio J (2006) Coastal oceanography of the western south Atlantic continental shelf (33 to 55° S) (5° W). In: Robinson AR, Brink KH (eds) The sea, ideas and observations on progress in the study of the seas: the global coastal ocean. Harvard University Press, Boston MA, Interdisciplinary regional studies and syntheses, pp 295–328

Pol R, Lopez de Casenave J (2004) Activity patterns of harvester ants *Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* in the Central Monte Desert, Argentina. Journal of Insect Behavior 17:647–661

R Development Core Team (2012). R : A Language and Environment for Statistical Computing . R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Retana J, Cerda X (2000) Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. Oecologia 123:436–444

Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. Science 235:167–171

Sanders NJ, Lessard J-P, Fitzpatrick MC, Dunn RR (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16:640–649

Segev U (2010) Regional patterns of ant-species richness in an arid region: the importance of climate and biogeography. Journal of Arid Environments 74:646–652

Soininen J, McDonald R, Hillebrand H (2007) The distance decay of similarity in ecological communities. Ecography 30:3–12

Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. American Naturalist 133:240–256

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton

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. Biological Reviews 87:661–685

Valiela I (2015) The Great Sippewissett Salt Marsh Plots—some history, highlights, and contrails from a long-term study. Estuaries and Coasts 38:1099–1120

Valiela I, Teal JM, Volkmann S, Van Etten R, Allen S (1985) Decomposition in salt marsh ecosystems: the phases and major factors affecting disappearance of above-ground organic matter. Journal of Experimental Marine Biology and Ecology 89:1–26

Wang C, Strazanac JS, Butler L (2001) Association between ants (hymenoptera: formicidae) and habitat characteristics in oak-dominated mixed forests. Environmental Entomology 30:842–848

Wilson EO (2003) Pheidole in the new world: a dominant, hyperdiverse ant genus. Harvard University Press, Cambridge

Wittman SE, Sanders NJ, Ellison AM, Jules ES, Ratchford JS, Gotelli NJ (2010) Species interactions and thermal constraints on ant community structure. Oikos 119:551–559

Wu H, Batzer DP, Yan X, Lu X, Wu D (2013) Contributions of ant mounds to soil carbon and nitrogen pools in a marsh wetland of Northeastern China. Applied Soil Ecology 70:9–15

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