

Research Article

Structural Changes in Macroinvertebrate Communities Associated with Reduction in the Management of Coastal Saltpans

P. C. Tavares, D. Alves, and M. Shapouri

CVRM, Geo-Systems Centre, Departamento de Minas, Instituto Superior Técnico, Avenue Rovisco Pais 1, 1049-001 Lisboa, Portugal

Correspondence should be addressed to M. Shapouri, maryamshapouri@gmail.com

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Salt pans with different management levels were studied for macroinvertebrate community and abiotic variables like water depth, water conductivity, and organic matter in sediments. Significant variation was observed between salt pans, between ponds within salt pans, and between periods within ponds for abundance, and also between salt pans for biomass. Environmental variables varied significantly between salt pans and between ponds. Significant positive correlations occurred between depth and total abundance, between depth and Corixidae abundance, and also between organic matter in sediments and diversity. Significant negative correlations were observed between depth and diversity and between organic matter in sediments and total abundance. Multidimensional Scaling and Canonical Correspondence Analysis confirmed results of analysis of variance and correlations. Invertebrate communities were numerically dominant as also revealed by ABC method. Abandoned salt pan ponds show the largest changes in water depth, with communities dominated by some opportunist species, varying within short temporal scales, which is typical from highly disturbed systems.

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1. Introduction

Macroinvertebrate abundances and diversity can reveal large temporal and spatial variation in coastal wetlands. Part of variation is associated with biological cycles and is inherent to species or subspecies but is also under the control of climate, tides, and management practices which influence several environmental variables. Biological cycles are partly controlled by environmental variables such as temperature, moisture, or light duration; in inshore aquatic habitats, gradients are usually established over small spatial scales for variables like water depth, hydrodynamics, salt concentration, and organic enrichment, which also strongly influence macroinvertebrate communities [1]. Salt concentration is the major factor referred as controlling macroinvertebrate communities in lotic systems [2] and lentic systems, for example, salt pans [3–5]. Water depth and salinity is on the basis of overall changes in macroinvertebrates of salt pans [5], but little is known about the relation between the

management state of salt pans and their communities since water management also affects other factors like organic loads entering in the pond systems; from active salt pans to totally abandoned salt pans there is a gradient of conditions, and also among abandoned salt pans we may distinguish between closed and permanently opened to tides.

Water management is crucial to human-made and human-modified systems within coastal wetlands (e.g., flooded pasture landscape, ricefields, or salt pans). They are highly productive and provide food and nursery habitats for invertebrates which represent an important sink of food resources for predators; those with suitable conditions such as low water depths and highly energetic insect midges are largely used by breeding populations of birds; they are also used by waders during high tides and shorebirds during severe weather [6]. These seminatural areas have strongly been affected by human pressure, since both structural changes and anthropogenic pollution occur, which led to the loss of their natural value, and to the reduction of several

TABLE 1: Description of type of saltpan, variables, and indices.

variable	symbol	Description
Type of saltpan	Type L-I	Partly managed for salt production (maintenance of low water depths); saltpans: Esteiro-Furado ² : EF1, EF2, EF3 Passa ⁴ : PAS1, PAS2, PAS3 Praias-Sado ¹ : PS1, PS2, PS3
	Type L-II	Nonmanaged for salt production (oscillation from high water depths to dry land); saltpans: Atalaia ² : AT1, AT2, AT3 (**) Gala ³ : GAL1, GAL2, GAL3 (*) Vaia ¹ : VAI1, VAI2, VAI3, VAI4 (**) Vasa-Sacos ² : VS1, VS2, VS3 (**) Vau-Nascente ² : VN2, VN3, VN4 (*) Vau-Poente ² : VP1, VP2, VP3, VP4, VP5 (*)
Total abundance	N	Total number of individuals of all groups
Relative abundance	P_i	Abundance of group i
Total biomass	B	Dry weight of total individuals
Relative biomass	B_i	Mean dry weight of group i
Percentage of organic matter	OM_i	% of dry weight "loss in ignition" of group i
Species richness	S	Number of species
Margalef index	d	$(S - 1)/\log_e(N)$
Shannon-Wiener	H'	$-\sum[P_i \cdot \log_e(P_i)]$
Pielou's evenness	J'	$H'/\log_e(S)$
Simpson index	$1 - \lambda'$	$1 - \sum[N_i \cdot (N_i - 1)/(N \cdot (N - 1))]$

Legend: ¹Sado estuary, ²Tejo estuary, ³Mondego estuary, ⁴Ria de Aveiro, (*) *P. varians* production, (**) no production = abandoned.

ecosystem services. In the coastal Portuguese saltpans, large areas have been progressively abandoned or destroyed. Species diversity and the uniqueness of species found can be used to assess the effect of human pressure on these areas. The channel and pond network of saltpans has an enormous potential as experimental areas to test the effect of management or its absence on communities. The present work aims to assess the relation between short temporal and spatial changes in macroinvertebrate communities and the management state of saltpans as revealed by water depth, salinity, and organic loads.

2. Materials and Methods

2.1. Study Area. The study area (Figure 1) included the following four coastal wetlands, Ria de Aveiro, Mondego estuary, Tagus estuary, and Sado estuary, Portugal. Two main types of saltpans were considered according to their level of management: with/without salt production (L-I, L-II, see Table 1); in the second type two other subtypes were also distinguished: *P. varians* production/no production. The study of intersaltpan variation was carried out through saltpans controlled for the same type of fauna (in the overall period of sample collection) belonging to different geographic areas and the same geographic area for Tejo and Sado estuaries (saltpan related effect). Intrasaltpan variation was studied in some saltpans through variation between

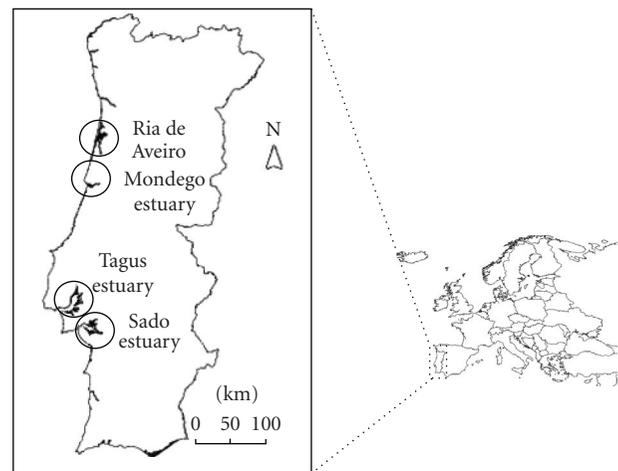


FIGURE 1: Maps of Europe and Portugal and the localization of coastal wetlands in the study; the coastal lagoon of Aveiro (Ria de Aveiro), and the estuaries of Mondego, Sado, and Tejo (Tagus estuary).

ponds (pond related effect) and variation between weeks (temporal related effect). Pond related effect was considered for Passa in 2001, Atalaia in 2000, Vasa-Sacos in 2000, and Vau in 2000, 2001 and 2002. Temporal related effect was considered for Esteiro-Furado in 2000, Gala in 2001, Vaia

in 2001, and 2002, and Praias-Sado in 2002. Vau, Vaia, and Esteiro-Furado were considered in the study of inter-year variation for 2000, 2001, and 2002.

2.2. Sampling Methods. Macroinvertebrate samples were collected along 10 m transects with a 1000 μm mesh size (70 cm \times 30 cm mesh mouth) manually dragging system in the shallow-water column (<45 cm) which included suspended and surface sediment. Three types of replicates were considered: pond replicates (ponds in the same saltpan, $n \geq 3$), spatial replicates (sampling points in the same pond, $n \geq 3$), and temporal replicates (different single-week time periods in the same pond, $n \geq 3$). Environmental variables were characterized simultaneously to sample collection, and they included mean and maximum water depth (cm), salt concentration in water (%), water conductivity (mS cm^{-1}), pH in water and surface sediment, redox potential in water, and surface sediment (mV), temperature in water and surface sediment ($^{\circ}\text{C}$). Salt concentration was obtained using a traditional handled refractometer, and other parameters were measured using a CyberScan PC 300 multiparameter meter (Eutech Instruments). Sediment samples were collected with 3 petri dishes in each sampling point to the determination of percentage of organic matter in surface sediments.

2.3. Sample Treatment. Macroinvertebrate samples were sieved after collection, separated according to taxonomic groups, and promptly frozen at -20°C in the same day of collection. Each saltpan was sampled at each day, but the sampling work of different saltpans was performed in the same sampling period. This method was possible due to the low number of taxonomic groups in saltpans; macroinvertebrates were always identified according to the lowest taxonomic level as possible. Sediment samples were also frozen in the petri dishes. Dry weight (DW) was determined for biomass estimation in macroinvertebrate samples; samples were dried until constant weight at 60°C . Percentage of organic matter in invertebrates and percentage of organic matter in the surface sediment were determined in subsamples through “loss on ignition” (LOI) method at 450°C , after dry weight quantification; Percentage of organic matter was given by the equation $\% \text{OM} = [(DW_{\text{before ignition}} - DW_{\text{after ignition}}) / DW_{\text{before ignition}}] \times 100$.

2.4. Data Analysis. The structure of macroinvertebrate communities was characterized according to total and relative abundances, diversity, biomasses (dry weight), and percentage of organic matter. Diversity was measured through several ecological indices: Species Richness (S), Margalef index, Shannon-Wiener index (H'), Simpson's index ($1 - \lambda'$), and Evenness index, as presented in Table 1. Biomass has been considered as a measure of secondary production [7]. The principles of diversity indices were referred in [8, 9]. Dominance was represented by λ' and because it is considered as a measure of concentration, $1 - \lambda'$ was considered as a diversity index. Multivariate analysis was used in the study of community structure according to the

main principles referred in other studies, that is, [10]. Primer 5.0 for Windows version 5.2.9 (Primer-E Ltd) was used for index estimation and Grouping analysis [11]; Clustering and Multidimensional Scaling (MDS) were applied, and results of this last one were graphically presented here. Square root transformation was applied to data and Similarity Matrix was used. Bray-Curtis similarity was chosen as measure of similarity. ANOSIM one-way and two-way crossed analysis was applied in Primer to check for differences between periods, ponds, saltpans, and saltpan's types. Pearson correlation coefficient was used in the relation between abiotic parameters and community descriptors. BIOENV analysis was also applied in Primer. Brodgar version 2.1.0 (Highland Statistics Ltd) [12] was used for Canonical Correspondence Analysis (CCA) based on square root transformed abundances. Abundance and biomass Curves method, also referred as the ABC method, was applied as proposed by [13] and discussed by [14, 15]. Correlation coefficients or analysis of variance were performed through parametric tests using Statistica 5.5 with 5% as threshold for significance.

3. Results

Insects accounted for the highest number of taxonomic groups (11 taxa), and the highest number of individuals per group per sample (31488 individuals), and were represented by different life stages (Table 2); Corixidae (nymph and adult), Chironomidae (larvae and pupae), Hydrophilidae (larvae and adult), and Dytiscidae (larvae and adult) occurred in most saltpans. The crustacean *P. varians* dominated in part of saltpans nonmanaged for salt production. Insecta larvae from Ephydriidae occurred in Passa, Esteiro-Furado, and Praias-Sado, all active saltpans. The crustacean *A. salina* occurred in Esteiro-Furado (L-I saltpans, see Table 1). The isopod *L. rugicauda* occurred in Vau-Poente, the polychaetes *C. capitata* and *H. diversicolor* occurred in Vaia, and the gastropod *H. ulvae* occurred within macroalgae in Vaia and Gala (L-II saltpans, Table 1).

3.1. Saltpan Related Effect. Total abundance varied significantly between saltpans in 2000 (one-way ANOVA, $F_{4,28} = 10.0$, $P < .001$); total abundance in Esteiro-Furado was significantly higher than in Vau, Atalaia, and Vasa-Sacos, and total abundance in Vaia was significantly higher than in Vasa-Sacos (Tukey, $P < .05$). Total abundance also varied significantly between saltpans for 2001 (one-way ANOVA, $F_{3,40} = 3.32$, $P < .05$). The highest relative abundance values were observed for the crustacean *A. salina* in Esteiro-Furado, followed by Corixidae adults in Vaia during 2000. During 2000, relative abundance varied significantly between saltpans in several macroinvertebrate groups, as shown in Table 3 (one-way ANOVA). Vaia showed significantly higher abundance of Corixidae adults than other saltpans, and Vau showed significantly higher abundance of Corixidae adults than Esteiro-Furado, Vasa-Sacos, or Atalaia (Tukey, $P < .05$). Vau showed significantly higher abundance of Corixidae nymphs than Vasa-Sacos or Esteiro-Furado (Tukey, $P < .05$). Esteiro-Furado showed significantly higher

TABLE 2: Taxonomic groups in macroinvertebrate communities.

	Genus or species	Life stage	Code
Malacostraca,			
Amphipoda, Corophiidae	<i>Corophium insidiosum</i>		CPH
Amphipoda Gammaridae	<i>Gammarus subtypicus</i>		ANF
Isopoda, Sphaeromatidae	<i>Lekanosphaera rugicauda</i>		ISO
Decapoda, Palaemonidae	<i>Palaemonetes varians</i>		CAM
Branchiopoda, Anostraca, Artemidae	<i>Artemia salina</i>		ART
Insecta,			
Heteroptera, Corixidae	<i>Corixa</i> sp.	nymph (a); adult (a)	COR-N; COR-A
Heteroptera, Noctonectidae		nymph (a)	NOCT
Diptera, Chironomidae	<i>Chironomus</i> spp.	larvae (a); pupae (a); adult (t)	CHI-L; CHI-P; CHI-A
Diptera, Ephydriidae	<i>Ephydra</i> sp.	larvae (a); pupae (a); adult (t)	EPHY-L; EPHY-P; EPHY-A
Diptera, Dolichophoridae		larvae (a)	DOLI
Diptera, Limoniidae		larvae (a)	DIP
Diptera, Culicidae			DIPT
	<i>Berosus</i> sp.	larvae (a); adult (t)	BER-L; BER-A
Coleoptera, Hydrophilidae	<i>Enochrus</i> sp.	larvae (a); adult (t)	ENO-L; ENO-A
	<i>Hydrobius</i> sp.	larvae (a); adult (t)	HDB-L; HDB-A
Coleoptera, Dytiscidae	<i>Coelambus</i> sp.	larvae (a); adult (t)	DYT-L; DYT-A
Gastropoda, Hydrobiidae	<i>Hydrobia ulvae</i>		GAS
Polychaeta,			
Nereididae	<i>Hediste diversicolor</i>		HED
Polychaeta, Capitellidae	<i>Capitella capitata</i>		CAP
Oligochaeta n.i.			OLI

(a) aquatic, (t) terrestrial.

abundance of Ephydriidae pupae than Vasa-Sacos, Vau, or Atalaia (Tukey, $P < .05$). In 2001 relative abundance varied significantly between saltpans for several groups as presented in Table 3 (one-way ANOVA); Vaia showed significantly higher abundance of Corixidae adults or nymphs than other saltpans (Tukey, $P < .05$), Passa showed significantly higher abundance of Chironomidae larvae than others (Tukey, $P < .05$), Vau showed significantly higher abundance of *Berosus* sp. larvae than others (Tukey, $P < .05$), and Gala showed significantly higher abundance of *Berosus* sp. adults than Vaia or Passa (Tukey, $P < .05$). In 2002, relative abundance varied significantly between saltpans for three groups as observed in Table 3 (one-way ANOVA); Vau showed significantly higher abundance of *L. rugicauda* (Tukey, $P < .05$), and Praias-Sado showed significantly higher abundance of Ephydriidae (Tukey, $P < .05$) comparing to other saltpans.

Total dry biomass in macroinvertebrates varied significantly between saltpans in 2000 (one-way ANOVA, $F_{4,24} = 17.8$, $P < .001$); Esteiro-Furado showed significantly higher total biomass than other saltpans, and Vaia showed significantly higher total biomass than Vau, Atalaia, and Vasa-Sacos (Tukey, $P < .05$). Mean percentage of organic matter in macroinvertebrates varied significantly between saltpans in 2000 (one-way ANOVA, $F_{4,24} = 12.6$, $P < .001$) and Esteiro-Furado revealed a significantly higher value than other saltpans (Tukey, $P < .05$). Biomass also varied significantly between saltpans for Corixidae adults (one-way ANOVA, $F_{3,19} = 97.6$, $P < .001$) and Vaia showed significantly higher value than other saltpans in 2000 (Tukey, $P < .05$). The highest biomass values were observed for Corixidae adults at Vaia, followed by *A. salina* at Esteiro-Furado. Percentage of organic matter in macroinvertebrates

TABLE 3: Significant differences between salt pans and between ponds for relative abundances of macroinvertebrate groups (one-way ANOVA).

(a) Saltpan related effect			
	2000	2001	2002
Corixidae adult	$F_{4,28} = 440.9, P < .001$	$F_{3,40} = 6.7, P < .01$	
Corixidae nymph	$F_{4,28} = 2.5, P < .05$	$F_{3,40} = 6.2, P < .01$	
Ephydriidae larvae	$F_{4,28} = 3.1, P < .05$		
Ephydriidae pupae	$F_{4,28} = 3.6, P < .05$		$F_{3,40} = 10.8, P < .01$
Chironomidae larvae		$F_{3,40} = 2.9, P < .05$	
Berosus sp. larvae		$F_{3,40} = 6.6, P < .01$	
Berosus sp. adult		$F_{3,40} = 3.8, P < .05$	
<i>L. rugicauda</i>		$F_{3,40} = 3.6, P < .05$	$F_{3,40} = 32.2, P < .001$
<i>P. varians</i>			$F_{2,7} = 5.3, P < .05$

(b) Pond related effect			
	2000	2001	2002
Corixidae nymph	${}^1F_{2,6} = 7.2, P < .05$		
Ephydriidae pupae		${}^3F_{4,9} = 11.2, P < .01$	
Chironomidae larvae	${}^1F_{2,4} = 9.3, P < .05$		
Chironomidae pupae	${}^1F_{2,4} = 21.6, P < .01$		
Berosus sp. larvae	${}^1F_{2,4} = 5.3, P < .05$		
<i>Enochrus</i> sp. adult	${}^2F_{2,4} = 43.0, P < 0.01$		

Legend: ¹Atalaia ponds; ²Vasa-Sacos ponds; ³Vau ponds (VP2, VP3, VP4).

TABLE 4: Significant Pearson correlation coefficients r (Pearson $r, P < .05$) between total abundance, total biomass, diversity indices, and percentage of organic matter in macroinvertebrate communities.

	Total abundance	Total biomass (dry weigh)
Total abundance	—	$r = 0.70, P < .001$
Species richness	$r = -0.40, P < .05$	$r = -0.39, P < .05$
Margalef index	$r = -0.53, P < .01$	$r = -0.48, P < .01$
Shannon-Wiener	$r = -0.69, P < .001$	$r = -0.46, P < .05$
Pielou's evenness	$r = -0.59, P < .01$	n.s.
Simpson's index	$r = -0.70, P < .001$	$r = -0.45, P < .05$
OM in macroinvertebrates (%)	$r = 0.88, P < .001$	$r = 0.70, P < .001$

n.s. : nonsignificant.

varied between salt pans for Corixidae nymphs (one-way ANOVA, $F_{3,15} = 3.4, P < .05$), *P. varians* (one-way ANOVA, $F_{3,12} = 7.4, P < .01$), and Ephydriidae pupae (one-way ANOVA, $F_{2,6} = 33.9, P < .001$).

Esteiro-Furado samples were clearly grouped in a single separated group as shown in MDS, considering abundances (Figure 2) and biomass (Figure 3) in 2000. Grouping analysis in other years gave some relevance to Passa (PAS1) in 2001, and Vau (VP) in 2002 which represented the most different samples comparing to others (Figure 2). ANOSIM one-way analysis confirmed significant differences through dissimilarities between overall sampled salt pans (Global $R = 0.51$; significance level 0.1%, $P < .001$) and between saltpan's types; between salt pans with/without salt production (Global $R = 0.68$; significance level 0.1%, $P < .001$) and between salt pans with salt production/*P. varians* production/no production (Global $R = 0.35$; significance

level 0.1%, $P < .001$) (see Table 1). Two-way crossed analysis of factors Saltpan \times Type also revealed significant effects (Global $R = 0.35$ for salt/no production, and Global $R = 0.38$ for salt/*P. varians*/no production; significance level 0.1%, $P < .001$).

Diversity indices varied significantly between salt pans in 2000, considering Species Richness (one-way ANOVA, $F_{4,28} = 2.9, P < .05$), Margalef index (one-way ANOVA, $F_{4,28} = 4.1, P < .05$), or Shannon-Wiener index (one-way ANOVA, $F_{4,28} = 5.3, P < .01$); Vasa-Sacos revealed significantly higher diversity than Esteiro-Furado using Margalef index and significantly higher diversity than Esteiro-Furado or Vau using Shannon-Wiener index (Tukey, $P < .05$). Diversity indices varied significantly between salt pans in 2001 considering Shannon-Wiener index (one-way ANOVA, $F_{3,40} = 3.8, P < .05$); Vau revealed significantly higher value than Passa (Tukey, $P < .05$).

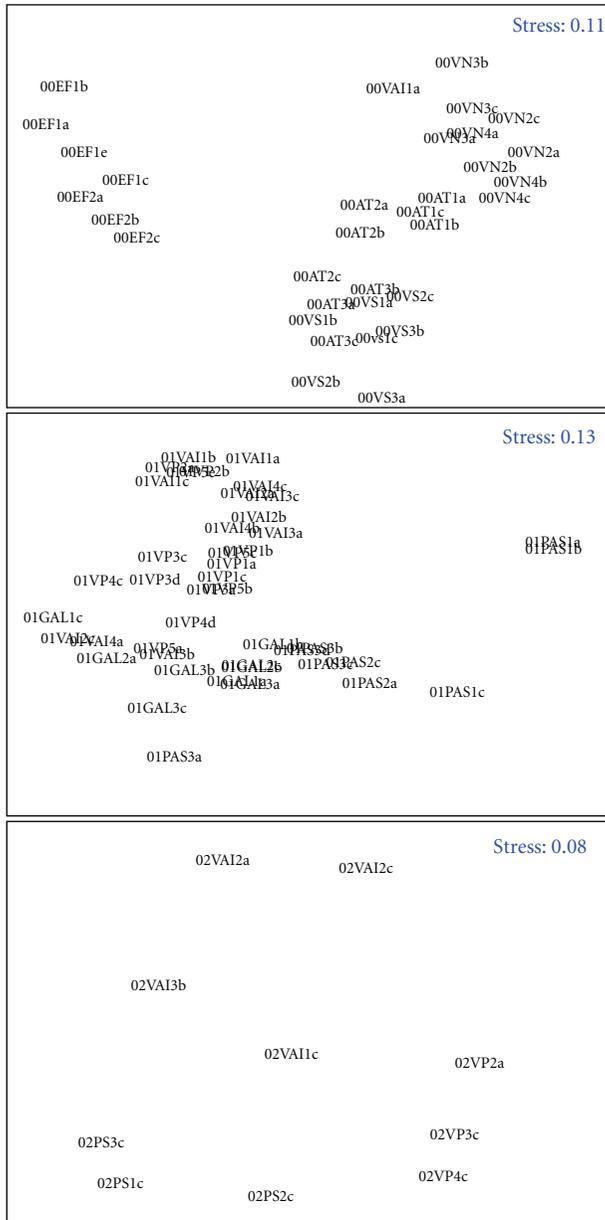


FIGURE 2: Plot of Multidimensional Scaling (MDS) using Bray-Curtis similarity matrix of macroinvertebrate abundances from 2000 (up) to 2002 (down). 1,2,3: pond replicates; a, b, c: spatial replicates within pond; 00, 01, 02: years; VN/VP: Vau; VAI: Vaia; AT: Atalaia; EF: Esteiro-Furado; VS: Vasa-Sacos; PAS: Passa, GAL: Gala; PS: Praias-Sado.

Mean water depth varied significantly between salt pans in 2001 (one-way ANOVA, $F_{3,35} = 15.6$, $P < .001$) and 2002 (one-way ANOVA, $F_{6,16} = 3.9$, $P < .05$). Maximum water depth varied significantly between salt pans in 2002 (one-way ANOVA, $F_{2,6} = 6.9$, $P < .05$) and Vau revealed significantly higher depth than Praias-Sado (Tukey, $P < .05$). Salt concentration in water varied significantly between salt pans in 2001 (one-way ANOVA, $F_{3,27} = 26.0$, $P < .001$) and 2002 (one-way ANOVA, $F_{2,6} = 14.3$, $P < .01$). Vau showed

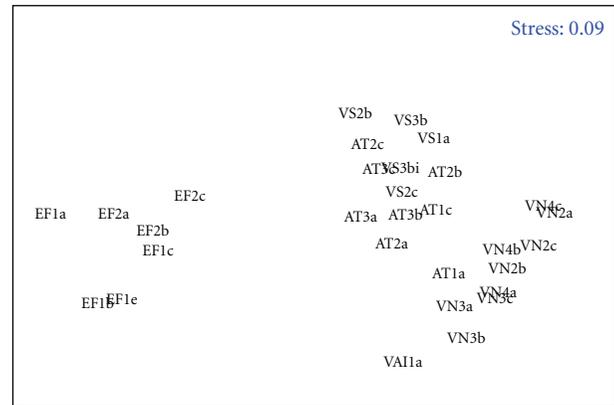


FIGURE 3: Plot of Multidimensional Scaling (MDS) using Bray-Curtis similarity matrix of macroinvertebrate biomasses (dry weight) in 2000. 1,2,3: pond replicates; a, b, c: spatial replicates within pond; VN: Vau; VAI: Vaia; AT: Atalaia; EF: Esteiro-Furado; VS: Vasa-Sacos.

significantly lower salt concentration than Vaia or Praias-Sado in 2002 (Tukey, $P < .05$). Water conductivity varied significantly between salt pans in 2001 (one-way ANOVA, $F_{3,31} = 64.8$, $P < .001$) and 2002 (one-way ANOVA, $F_{2,7} = 12.5$, $P < .01$). Vau also showed significantly lower conductivity than Vaia and Praias-Sado in 2002 (Tukey, $P < .05$). Percentage of organic matter in sediment varied significantly between salt pans in 2002 (one-way ANOVA, $F_{3,53} = 3.8$, $P < .05$).

Significant positive correlations were observed between total abundance and total biomass, between total abundance and percentage of organic matter in macroinvertebrates, and between total biomass and percentage of organic matter in macroinvertebrates (Table 4). Significant negative correlations were observed between diversity and total abundance and between diversity and total biomass (Table 4). Abundance curve was above the biomass curve throughout its length for Vau, Atalaia, Esteiro-Furado, and Vaia. In Vasa-Sacos, biomass and abundance curves were close from each other, they crossed each other twice, and biomass curve was above the abundance curve in a small part of its length (Figure 4).

3.2. Pond Related Effect. Total abundance varied significantly between ponds of Vasa-Sacos in 2000 (one-way ANOVA, $F_{2,4} = 83.9$, $P < .001$) and between ponds of Vau in 2002 (one-way ANOVA, $F_{4,9} = 4.8$, $P < .001$). Relative abundances varied significantly between ponds of salt pans for several macroinvertebrate groups (Table 3).

Grouping analysis of abundances revealed that ponds from the same salt pan might be in different groups, as in the case of ponds from Atalaia in 2000 (Figure 2). ANOSIM one-way analysis confirmed significant differences between salt pan ponds (Global $R = 0.73$; significance level 0.1%, $P < 0.001$). Two-way crossed analysis of factors Saltpan \times Pond revealed significant effect (Global $R = 0.64$; significance level 0.1%, $P < .001$).

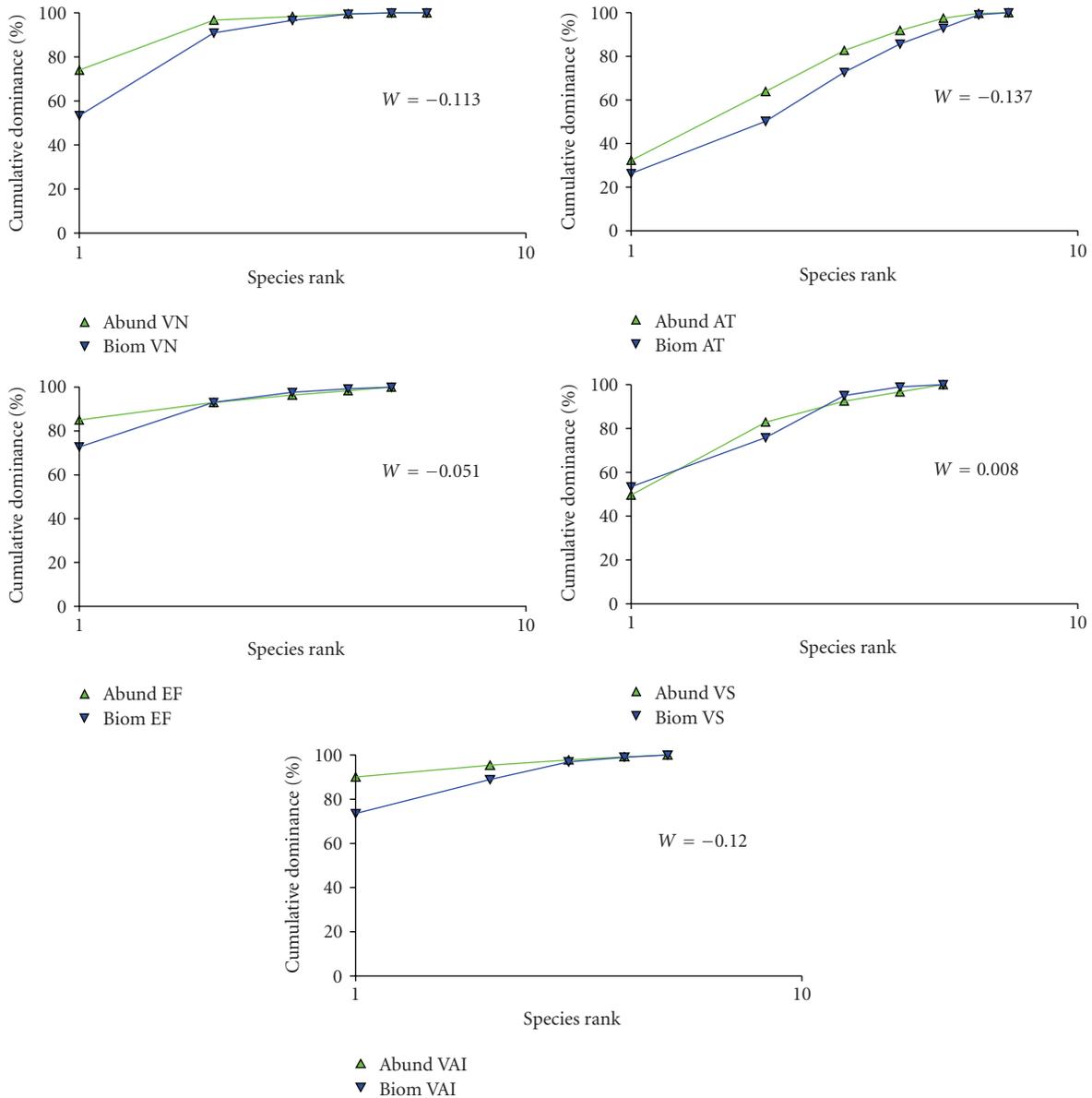


FIGURE 4: Abundance biomass curves for macroinvertebrate communities in 2000. abund: Abundance; biom: Biomass; VN: Vau; AT: Atalaia; EF: Esteiro-Furado; VS: Vasa-Sacos; VAI: Vaia.

Diversity indices varied significantly between ponds of Atalaia in 2000 for Species Richness (one-way ANOVA, $F_{2,6} = 6.6, P < .05$) and Margalef index (one-way ANOVA, $F_{2,6} = 5.6, P < .05$). Diversity indices varied significantly between ponds of Vasa-Sacos in 2000 for Margalef index (one-way ANOVA, $F_{2,4} = 8.2, P < .05$) and Shannon-Wiener index (one-way ANOVA, $F_{2,4} = 7.0, P < .05$). Diversity indices also varied significantly between ponds of Vau in 2001 for Margalef index (one-way ANOVA, $F_{4,9} = 4.3, P < .05$) and Shannon-Wiener index (one-way ANOVA, $F_{4,9} = 7.0, P < .05$).

Mean water depth varied significantly between ponds of Vau in 2002 (one-way ANOVA, $F_{3,8} = 20.5, P <$

.001). Conductivity also varied significantly between ponds of Vau in 2002 (one-way ANOVA, $F_{3,8} = 123.9, P < .001$). Redox Potential in water varied significantly between ponds from Vau in 2002 (one-way ANOVA, $F_{3,7} = 6.2, P < .05$). Percentage of organic matter in sediment varied significantly between Vaia ponds, VAI-R1 (channel), VAI-R2 (1st evaporation pond), and VAI-R3 (2nd evaporation pond), (one-way ANOVA, $F_{2,7} = 84.4, P < .001$) and also between Vau ponds, VP1, VP2, VP3, and VP4 (one-way ANOVA, $F_{3,11} = 6.6, P < .01$) in 2002. VAI-R3 showed a mean value significantly higher than VAI-R2 and VAI-R1, and VP4 showed a mean value significantly higher than VP1 (Tukey, $P < .05$).

TABLE 5: Significant Pearson correlation coefficients r (Pearson r , $P < .05$) between abiotic variables, and total abundance, diversity indices, relative abundance, and percentage of organic matter in macroinvertebrate communities.

	Max_depth	Mean_depth	Salt	OM in sediments (%)
Total abundance	$r = 0.42, P < .05$	$r = 0.42, P < .05$	n.s.	$r = -0.48, P < .05$
Species richness	n.s.	n.s.	$r = 0.42, P < .05$	$r = 0.50, P < .01$
Margalef index	n.s.	n.s.	n.s.	$r = 0.60, P < .01$
Shannon-Wiener	$r = -0.41, P < .05$	$r = -0.57, P < .01$	n.s.	$r = 0.70, P < .001$
Pielou's evenness	$r = -0.46, P < .05$	$r = -0.59, P < .01$	n.s.	$r = 0.62, P < .01$
Simpson's index	n.s.	$r = -0.53, P < .01$	n.s.	$r = 0.63, P < .01$
Relative abundance (COR-N)	n.s.	$r = 0.42, P < .05$	n.s.	n.s.
OM in macroinvertebrates (%)	n.s.	n.s.	n.s.	$r = 0.52, P < .05$

Legend: Max_depth - maximum water depth (cm); Mean_depth: mean water depth (cm); Salt: salt concentration in water (%); OM: percentage of organic matter (%); COR-N: Corixidae nymph; n.s.: non significant.

3.3. *Temporal Related Effect.* Significant variation was observed between weeks at Gala in 2001 for abundance of Chironomidae pupae (one-way ANOVA, $F_{2,6} = 9.4, P < .05$). No significant variation was observed between weeks for total abundance or diversity in Gala. No significant variation was observed between weeks for macroinvertebrates in the other saltpan ponds tested for the temporal related effect, Vaia, Esteiro-Furado, and Praias-Sado (ANOVA, $P > .05$). ANOSIM one-way analysis did not revealed significant dissimilarities between periods (Global $R = 0.23$), and no significant effect was observed for two-way analysis of factors Saltpan \times Period ($R = 0.19$). No significant variation was observed between weeks for abiotic variables.

3.4. *Environment and Macroinvertebrates.* Mean water depth was significantly negatively correlated with water conductivity in 2002 (Pearson $r = -0.34, P < .05$). Mean water depth was significantly positively correlated with redox potential in water in 2002 (Pearson $r = 0.44, P < .01$). Redox potential in water was significantly negatively correlated with pH in water during 2001 (Pearson $r = -0.40, P < .001$). Significant positive correlations were observed between water depth and total abundance and between water depth and abundance of Corixidae nymphs (Table 5). Significant negative correlation was observed between water depth and diversity (Table 5). Percentage of organic matter in sediment was significantly negatively correlated with total abundance and significantly positively correlated with diversity (Table 5). BIOENV analysis confirmed significant positive correlations between some macroinvertebrate groups and abiotic variables such as organic matter in sediments and water conductivity. Conductivity was a very important variable since it was present in almost all results. The most relevant results were observed for gastropods ($r = 0.96$), amphipods ($r = 0.93$), and also larvae of insects from Hydrophilidae (*Berosus* sp., $r = 0.91$; *Enochrus* sp., $r = 0.93$) and Dytiscidae ($r = 0.94$).

Higher conductivity values and the presence of Ephydriidae larvae in PAS1 pond in 2001 and lower conductivity values of VP3, VP4, and VP5 ponds in 2001 were in accordance with CCA (Figure 5). CCA confirmed the negative correlation between water depth and conductivity, in 2002.

Higher water depth, lower conductivity and the presence of *P. varians* increment at VP3 pond in 2002 were also reflected in CCA. The displacement of VP4 pond relative to other ponds in CCA was in accordance with the higher percentage of organic matter in sediment observed in this pond. The presence of Ephydriidae larvae, pupae and adults, and Dytiscidae and Hydrophilidae adults in Praias-Sado ponds in 2002 also seem to be in accordance with placement of these ponds together in CCA.

4. Discussion

Macroinvertebrate communities in the studied saltpans were characterized by a higher numerical dominance and a lower diversity than communities reported in several Portuguese estuaries and coastal lagoons [16]. Despite these saltpans being part of coastal environments, they provide a very particular type of environment with limiting factors for fauna like salinity [4]. Salinity gradients have been related to diversity and abundance of macroinvertebrate communities in other inland ecosystems, for example, rivers. In [17] rising salinities affected the number of species but not other diversity, evenness, or abundance values; the study found that the species composition of the community was influenced by the salinity for a small group of species, mainly crustaceans. Saltpans also differ between each other as assessed through the studied saltpans and in comparison with other studies [18, 19]. Results provided newly important information about variation of macroinvertebrate communities in saltpans under different management states, in special referring to those no longer used in salt production. A well-marked spatial heterogeneity was observed for the macroinvertebrate community between ponds within the saltpan system and also for intersaltpan variation within the same wetland system, that is, Tejo estuary, as in the case of Esteiro-Furado saltpans.

The most relevant variations observed for macroinvertebrate communities were observed in the analysis of three factors: pond, saltpan, and saltpan's type. Regarding this last one, the largest differences for macroinvertebrate fauna were observed between saltpans with salt production and saltpans without salt production, which included saltpans

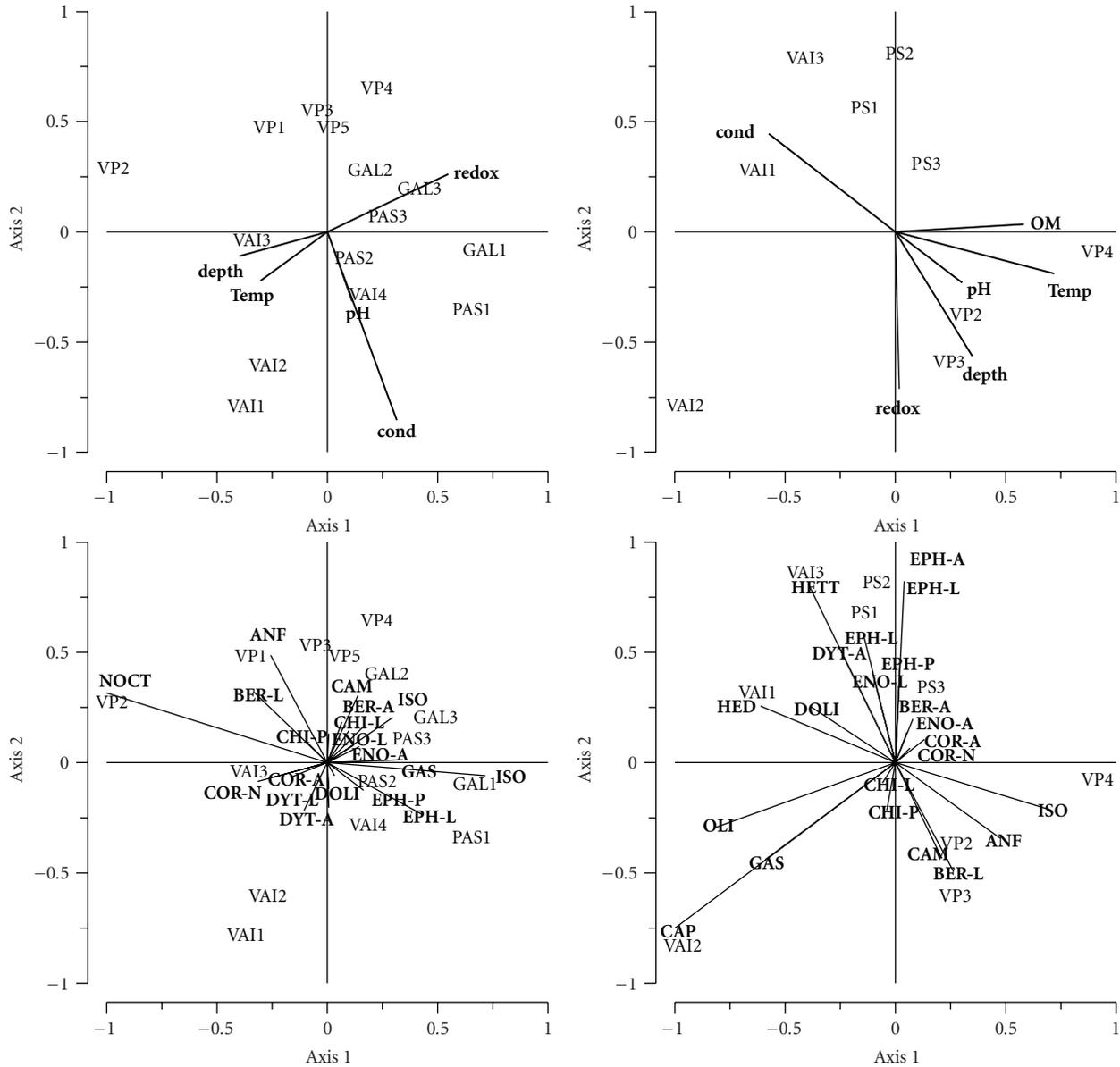


FIGURE 5: Biplots of sampling points and explanatory variables (up) and biplots of sampling points and response variables (down) from Canonical Correspondence Analysis (CCA) using abundances in 2001 (left) and 2002 (right). 1, 2, 3, 4: pond replicates; VP: Vau; VAI: Vaia; PAS: Passa; GAL: Gala; PS: Praias-Sado; COR: Corixidae; CHI: Chironomidae; BER: *Berosus* sp.; ENO: *Enochrus* sp.; DYT: Dytiscidae; CAM: *P. varians*; ANF: *G. subtypicus*; ISO: *L. rugicauda*; EPHY: Ephydriidae; ART: *A. salina*; CPH- *C. insidiosum*; GAS: *H. ulvae*; DOLI: Dollicophoridae; NOCT: Noctonectidae; CAP: *C. capitata*; HED: *H. diversicolor*; HETT: *Oligochaeta* n.i.; cond: water conductivity (mS cm^{-1}); redox: Redox Potential in water (mV); depth: mean water depth (cm); Temp: water temperature ($^{\circ}\text{C}$); OM: percentage of organic matter in surface sediment (%).

with *P. varians* production and abandoned salt pans (no production). The occurrence of *P. varians* production in some salt pans no longer used for salt production justifies the maintenance of high water levels during almost all the year, a condition which is achieved in abandoned-closed salt pans before the dry season. This explains in part the similarity of fauna observed between salt pans with *P. varians* and abandoned ones. The analysis of temporal changes on macroinvertebrate communities was limited to the sampling periods occurred from March to May, including only the

first part of the dry season. After this period the most part of ponds in abandoned-closed salt pans turns completely dry. Every time it occurred the aquatic diversity was lost temporally, with the exception of cysts of *Artemia salina*. Water inputs to abandoned salt pans depend on rainfall, runoff, and also tides in the case of abandoned-opened salt pans. The re-establishment of communities largely depended on recolonization by settlers of species existing in the surrounding saltmarsh which is influenced by marginal parts of aquatic (i.e., estuarine) and terrestrial environments as

observed through the analysis of diversity. Abiotic conditions found within saltpan ponds along the time may represent limiting factors for the settlement of such a pool of species. Because the saltmarsh seems to function as a reservoir of species, it is normal that several groups are quite adapted to a changing environment regarding salt concentration and show a quite large range of tolerance to salt concentrations. Others are particularly adapted to sharp ranges of salinity, and abundances were related to conductivity. Part of species came directly from terrestrial environment like those insects having only part of life cycle in aquatic systems as larvae stages and also those seemed to tolerate rising salinities. This is interesting in the point of view of biodiversity that can complete life cycles under the effects of rising temperatures during drastic climate events.

Macroinvertebrate communities in the study were numerically dominated by insect groups. Despite having a reduced body size, these groups represented high biomass peaks due to temporary high abundances describing a patchy distribution. Short-term patch dynamics was investigated for macroinvertebrate colonization on decaying detritus, and a strong linkage was found between abundance patterns and short-term variations of detritus mass [20]. The recruitment of invertebrates into a substrate depends mostly on the establishment of first settlers into the substrate, which in turn depends on substrate conditions and species biological cycles [21]. Most of them are considered opportunists as they take advantage of the disappearance of others, occupying their ecological niches during extreme conditions. These groups are well adapted to a changing environment, and they typically colonize the substrate after disturbances in the habitat. Saltpans are a good example of permanently disturbed systems due to their shallow-water columns affected by evaporation rates and water inputs; the range of disturbance is influenced by the water management.

The short temporal scales that characterized variation of abiotic variables are related to inundation/evaporation cycles and contributed for a permanent state of high disturbance in macroinvertebrate communities establishing inside saltpans. Although a permanent source of disturbance is observed through changes in water depth, the extent of disturbance varied between saltpans with different levels of management. The disturbance is enlarged if water evaporation and water inputs do not compensate each other, a very common situation in abandoned saltpans. Biological cycles must have here a huge importance on the temporal variability of the community structure, since the temporal scale of 3-4 weeks per saltpan pond revealed in some cases differences in the community structure even when no significant variation occurred in abiotic variables between successive single-week periods. However it did not represent a uniformity, since significant differences occurred for abiotic variables and macroinvertebrate communities between saltpans with different levels of management. Reduction of saltpans' management resulted in differences in the structure of communities.

Abiotic conditions that were affected by saltpans' management, like water depth, salt concentration as revealed by water conductivity, and organic matter in sediments, all

were related to community structure. In managed ponds for salt production (e.g., Esteiro-Furado, Passa) communities were numerically dominated by insects from Ephydriidae larvae stages since the water management increased salt concentration. In nonmanaged ponds (e.g., Vaia, Vau, Atalaia) communities were numerically dominated by insects from Chironomidae, Corixidae, or Hydrophilidae, with several life stages succeeding each other (larvae, pupae, and adult). However, in abandoned ponds the diversity was not maintained because the water column suffered quick reductions which occurred very early in the dry season. Among totally abandoned saltpan ponds, Vaia revealed the highest disturbance condition due to the influence of tides (it was permanently opened to water from estuary) originating short-time periods between disturbance events.

A very particular opportunist Polychaete, *Capitella capitata*, occurred here. Opportunist species are the first to settle after disturbance since they can use the habitat during the conditions not favorable for less tolerant species; they can easily adapt to new refuges left by other species thus using available food resources which enable them to produce high biomass peaks. It is the case of *C. capitata* which takes advantage from increasing organic loads. If conditions remain more stable, other species can recolonize because a movement of individuals can occur from the adjacent habitats. The stages of colonization phase in saltpan ponds that were most disturbed were highly dynamic but predictable according to abiotic conditions and available colonizers in the macrobenthic community, as observed in the study. Post colonization succession stages are more stable but less predictable, maybe due to intricate biotic relations [22]. The small scale dispersion of aquatic invertebrates is usually associated to adult stages of surrounding terrestrial environment in opposition to large-scale dispersion of larvae stages [23]; the first dispersion scale seemed to be more important, in the case of nonmanaged saltpans Vau and Atalaia, which revealed abundance peaks for coleopteran larvae and adults. Diptera (e.g., Chironomidae) also revealed abundance peaks for larvae stages. Insect groups that have aquatic larvae and terrestrial adults provide this type of dispersion and a link between aquatic and terrestrial environments. Invertebrates with such life strategies seem to be adapted to high temporal variability for water depths and conductivity and a fragmentary spatial pattern for organic matter.

As observed in the present study, drastic changes in habitat resources at short temporal scales avoid the structuring of stable communities with species of large life span and large body size. However, spatial heterogeneity in the environment can also positively influence macroinvertebrate communities in disturbed environments [21, 24]. We suggest that macroinvertebrate communities in saltpans can be understood as a combination of spatial or temporal refuges. Patchy distributions can even occur in apparently homogeneous sediment, but it is usually a result of the heterogeneity in the habitat, the presence of organisms that promote or avoid new settlers, and a well-succeeded colonization of some areas by some opportunists [25]. According to [26], species richness in transects along saltmarsh areas were

not explained by area (habitat size) and it was caused by edge effects. Saltmarsh vegetation has an important role on the overall ecosystem [27]. Recolonization of flooded ponds could be influenced by edge effects related to narrow strips of water and saltmarsh vegetation. In small tidal marshes species richness could be inflated by immigration from nearby habitats, thus changing expected species-area relationship. According to [25] species richness was not altered in a predictable way by floods. That was explained by the patchy distribution and assemblage structure of macroinvertebrate communities related to habitat heterogeneity. Channel and coarse patches did not necessarily show lower species richness during the spate. Vaia pond seemed to be a good example of that, especially during 2000 when patchy distribution of *C. capitata* was clearly observed. *C. capitata* was mainly captured in parts of Vaia pond immediately after the channel of water reception. Another Polychaeta, *Hediste diversicolor*, was also found in those parts of Vaia pond but revealing lower abundances. Abundance Biomass Curves or the ABCmethod also used in other studies [13–15] suggested that the status of macrobenthic communities affected by disturbances could be assessed through the relation between abundance and biomass. The ABC-method confirmed that macroinvertebrate communities in salt pans were under stressful conditions, with abundance curve above the biomass curve during large part of species rank, revealing higher numerical dominance than biomass dominance, which means higher biomass diversity than numerical diversity. When the frequency of disturbance in communities is faster than its rate of recovery, conservative species are the first to be affected, while opportunistic species are benefited and they can even become the biomass dominants as well as the numerical dominants. *C. capitata* occurring in Vaia salt pan is a good example of that. Initially there is an increase in the diversity, but with further increase of disturbance the numbers of the less resilient opportunists start to diminish, and diversity again begins to decrease [13]. Under moderate disturbance the large competitive dominants are eliminated and the different sizes between numerical and biomass dominants are reduced thus approximating the biomass and abundance curves that can cross each other several times. This pattern was observed for Vasa-Sacos during 2000, also an abandoned salt pan. If disturbance becomes higher, then communities turn numerically dominated by few opportunist species.

According to the present results, macroinvertebrate communities in salt pans seem to be influenced by organic matter and salt concentration, which in turn are affected by water inputs. Organic matter in sediments is partly influenced by water inflows and also autochthonous sources; permanently closed salt pans also revealed increments of organic matter. We can consider that species biological cycles determine the availability of settlers, but the possibility to settle in the sediment is determined by these environmental conditions. Total abundance increased with water depth, and curiously diversity increased with organic content of sediments. According to [24] macroinvertebrate diversity decreased with increasing organic loads for large organic contents in the substrate. The positive relation

between macroinvertebrate diversity and organic matter in sediments as observed in the studied salt pans can result from the settlement of some particular macroinvertebrate groups and suggested that the salt pan ponds were only moderately organic polluted. This is typical of moderately polluted environments for organic matter. Organic matter can initially promote diversity through the colonization by opportunists, but diversity is reduced for increasing organic loads because only part of such opportunists remains in the sediment [13, 24].

The positive relation between water depth and total abundance is very interesting and may result from the presence of moderate flooding which promoted emergence of insect larvae. The conjugation between water depth increments and moderately organic enrichment seems to contribute in a complementary way to the emergence of insect larvae and also to the settlement of aquatic groups that depend on organic content of sediments, the detritivorous. Considering that salt pans are depuration areas and receive high organic loads, such median values for percentage of organic matter in sediments can result from the fact that abandoned salt pans which stay closed to tides will dry completely in early summer. Decomposition of organic loads can also occur before the drying period, and reductive conditions resulting from oxygen depletion in the water can also contribute to the reduction of the number of species establishing there and to the limitation of first stages numerically dominated. Water depth variation results from instable balance between water inputs and evaporation, and it can affect salt concentration as observed in 2002; negative correlation was observed between water depth and conductivity. The fact that most salt pans keep median salt concentration values can have different causes, for example, the flooding regime and evaporation rates, but the presence of water management could compensate others. Water depth was positively correlated with total abundance and negatively correlated with diversity and that may indicate that water inflow in the present salt pans contributes to the abundance of some particular groups. That seemed to be the case of Corixidae nymphs, since abundance was positively correlated with water depth. Several factors can modify locally the pattern for communities establishing after flooding, for example, the influence of saltmarsh edges and refuges on patchy distribution. According to [26] migration from adjacent areas and refuges is important. Communities after flooding can be very difficult to preview also because heterogeneity of habitat [25].

Chironomidae was the most constant group along all salt pans. Chironomids reveal a preference for shallow waters in estuarine or lagoon systems and has been referred as increasing immediately after moderate flooding [28, 29], but severe flooding seemed to be not much tolerated by these and other insect larvae [30]. Chironomidae larvae were observed in a higher number of replicates than other groups, including those in ponds with regular flooding (e.g., Vaia, Vau-Poente). Corixidae also seem not inhibited by flooding and instead it seems to benefit from re-establishment of water depth, as its abundance was positively correlated with water depth. Flooding usually represents nutrient enrichment and high

primary production and that represents a food source for grazers. Associated high organic enrichment and microbial activity represent food source for detritivorous. Chironomids can be predators or detritivorous. Corixidae are scavengers or grazers. The coexistence of species in benthic communities of small lentic systems with low water columns seems to be ensured by tolerance to physical gradients and also by resource partitioning for food and space. According to [31] the confined niche potentiality results in a different spatial/temporal utilization of habitat resources by each species. This explains species coexistence in small and confined lentic systems like saltpan ponds, since they minimize interaction by temporal avoidance of each other, as observed in the study through abundance peaks of different species for different short temporal periods. The presence of water management clearly benefited the coexistence of a wide range of taxonomic groups, and it was possible due to the potential of resource partitioning.

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