

## MINI-REVIEW

# Biodiversity patterns in a macroinvertebrate community of a temporary pond network

MARGARITA FLORENCIO,<sup>1</sup> CARMEN DÍAZ-PANIAGUA,<sup>1</sup> CAROLA GÓMEZ-RODRÍGUEZ<sup>2</sup> and LAURA SERRANO<sup>3</sup> <sup>1</sup>Doñana Biological Station-CSIC, Seville, Spain, <sup>2</sup>Facultad de Biología, Universidad de Santiago de Compostela, Santiago de Compostela, Spain and <sup>3</sup>Department of Plant Biology and Ecology, University of Seville, Seville, Spain

**Abstract.** 1. Macroinvertebrate assemblages of temporary ponds are ideal model systems to explore biodiversity patterns and metacommunity ecology. In addition, the study of the environmental variables driving such biodiversity patterns is essential in establishing proper guidelines for the conservation of the singular fauna of temporary ponds, especially since such ponds are vulnerable systems.

2. We analysed the macroinvertebrate assemblages and environmental characteristics of 80 ponds spread across the Doñana National Park, SW Spain to (i) analyse macroinvertebrate  $\beta$ -diversity and metacommunity structure; and (ii) discern the main environmental and spatial drivers of these patterns.

3. The pond network was highly heterogeneous as temporary ponds were highly variable. Macroinvertebrate  $\beta$ -diversity partitioning showed that species replacement made the greatest contribution to total  $\beta$ -diversity while the contribution of nestedness was small. The macroinvertebrate community structure and  $\beta$ -diversity were similarly driven by: electrical conductivity (and co-variables alkalinity, pH, and ion concentrations), plant richness (and the co-variable pond surface area), maximum depth, marsh, and coastal proximity as well as two spatial descriptors extracted from Moran's eigenvector maps. The spatial descriptors indicated that large interpond distances were involved, suggesting that species dispersal limitations only take place over long distances in the area.

4. Those taxa that departed from the general nested pattern, termed idiosyncratic, significantly contributed to the maintenance of high pond network diversity through the species replacement and occurred within particular environmental conditions in the pond network.

5. These results reveal that environmental heterogeneity and connectivity are key factors in the preservation of high macroinvertebrate diversity in nested pond networks with high numbers of idiosyncratic species.

**Key words.** Aquatic insects, environmental heterogeneity, idiosyncratic species, Mediterranean temporary ponds, nestedness, pond conservation, spatial descriptors, species replacement, turnover.

## Introduction

The metacommunity is an emergent concept that considers the impact of the exchange of species in heterogeneous environments (Leibold *et al.*, 2004; Urban & Skelly, 2006).

Correspondence: Margarita Florencio, Doñana Biological Station-CSIC, Américo Vespucio s/n, 41092 Seville, Spain. E-mail: margarita@ebd.csic.es

Temporary ponds, which are characterised by annual inundation-desiccation cycles (Williams, 1997), are ideal model systems to study metacommunity ecology given their simple structure, local abundance, and occurrence in pond networks that demonstrate clear environmental gradients (Vanschoenwinkel *et al.*, 2007; Pandit *et al.*, 2009). Although temporary ponds are widely distributed worldwide (Williams *et al.*, 2001), their high biodiversity contrasts with their sensitivity and vulnerability to external perturbation, which has led to great interest in their con-

servation over the last few years (Williams *et al.*, 2001; Zacharias *et al.*, 2007; Céréghino *et al.*, 2008). In addition, temporary ponds harbour singular flora and fauna that are often exclusive or infrequently found in permanent ponds (Collinson *et al.*, 1995; Williams, 1997; Céréghino *et al.*, 2008). In particular, their singular macroinvertebrate species can adjust their life cycles to the annual period of pond inundation (hydroperiod), re-starting community assembly after each year's initial inundation (Bazzanti *et al.*, 1996; Boix *et al.*, 2004; Florencio *et al.*, 2009).

In metacommunity ecology,  $\beta$ -diversity, which is the variation in species composition among sites in a geographical area (Legendre *et al.*, 2005; but see e.g. Tuomisto, 2010; Anderson *et al.*, 2011), is a key concept for understanding ecosystem functionality from a management and conservation perspective. In pond networks, environmental heterogeneity has been revealed as crucial in supporting high biodiversity (Urban, 2004; Jeffries, 2005) and also in driving patterns of nested biodiversity, in which species-poor sites contain subsets of species-rich sites, particularly in those systems with good conservation status (Hylander *et al.*, 2005; Florencio *et al.*, 2011). Hence, the study of those species that depart from the expectations of nested biodiversity patterns, which occur more or less frequently than would be predicted in a nested system (termed idiosyncratic), is currently receiving great interest in applied ecology (e.g. Florencio *et al.*, 2011). To better understand the ecological processes maintaining high ecosystem diversity,  $\beta$ -diversity should be partitioned between (i) the  $\beta$ -diversity associated with non-random species loss in nested systems; and (ii) the  $\beta$ -diversity associated with true species replacement (Baselga, 2010). It is essential to disentangle the problem whether  $\beta$ -diversity is driven by species replacement or nestedness to make appropriate conservation decisions. If the former is the driver, it would prioritise the conservation of a large number of sites with variable richness and environmental conditions, while the latter would prioritise the conservation of the richest sites (Baselga, 2010).

One of the main debates in metacommunity ecology involves the relative importance of deterministic, niche-based process (e.g. environmental filters) versus stochastic ecological process (e.g. dispersal filters) in community assembly (Chase & Myers, 2011). Water chemistry and the physical characteristics of ponds each have an important influence on macroinvertebrate composition and abundance in wetlands (Wissinger, 1999; Williams, 2006). Conductivity is one of the most frequent chemical descriptors of macroinvertebrate communities (Garrido & Munilla, 2008; Waterkeyn *et al.*, 2008). In particular, acidic water has negative effects on macroinvertebrate species diversity (Radke *et al.*, 2003). Although nutrient concentrations have controversial effects, they usually negatively impact species occurrences at high levels (Declerck *et al.*, 2005). Applying the theory of island biogeography (MacArthur & Wilson, 1967) to lakes and ponds, high macroinvertebrate and plant species richness is harboured in large ponds (Friday, 1987; Nicolet *et al.*, 2004). Interpond

distances can also affect the incidence of species in particular pond assemblages as a result of species dispersal limitations (Briers & Biggs, 2005; Sanderson *et al.*, 2005).

We explored the main drivers of  $\beta$ -diversity and community structure in a macroinvertebrate metacommunity in a pond network of excellent conservation status. This is a highly dynamic system in which thousands of ponds fill and desiccate annually, with only a few ponds retaining water during the summer. The novelty of our study resides in the fact that we obtained comparable data on macroinvertebrates in 80 ponds distributed across an extensive area. We hypothesised that (i) there is high biodiversity in the macroinvertebrate metacommunity, with species replacement and nestedness being the main contributors to  $\beta$ -diversity; (ii) environmental variability is key in maintaining such high macroinvertebrate diversity in the pond network; and (iii) both random (i.e. dispersal) and deterministic processes (i.e. environment) are operating together in the macroinvertebrate assembly. To evaluate these hypotheses, we used data from 80 ponds, collected over a single season, to analyse (i) if  $\beta$ -diversity was mainly sustained by nestedness or by species replacement, and (ii) if spatial connectivity and environmental variability had an important influence on macroinvertebrate structure and  $\beta$ -diversity.

## Methods

### Study area

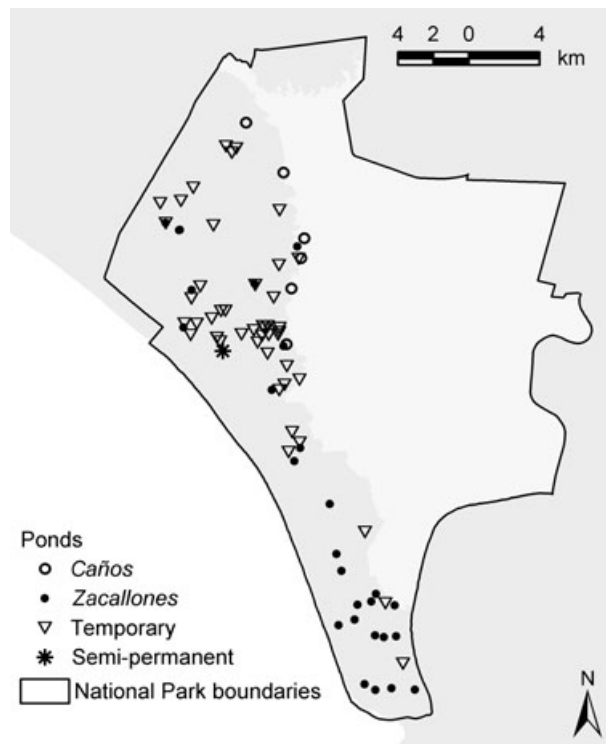
Doñana National Park (SW Spain) is one of the most pristine wetlands in Europe; it was included in the RAMSAR convention in 1982 and was later designated as a World Heritage Site by UNESCO in 1995. This area is located between the mouth of Guadalquivir River and the Atlantic Ocean. In the park, there is a clear geomorphological distinction between the ancient northern area and the southern area, locally known as 'Marismillas', which has a more recent marine origin (Siljeström *et al.*, 1994). The three main types of landscapes are as follows: a sandy area with stabilised dunes, a mobile dune system, and an extensive marsh area (see Siljeström *et al.*, 1994 for a detailed geomorphological description of the area). The climate is Mediterranean sub-humid, with mild winters, hot and dry summers, and heavy rains falling mainly in autumn or winter (mean annual rainfall = 544.6 (SD 211.3) mm with significant interannual variability, see Díaz-Paniagua *et al.*, 2010).

This area contains a pond network that is comprised of more than 3000 water bodies in wet years and that is mainly composed of temporary ponds spanning a wide range of hydroperiods (Díaz-Paniagua *et al.*, 2010). These ponds are fed by annual rainfall and a shallow water table that rises above the surface after heavy autumn or winter rainfall and they generally dry out during summer (Díaz-Paniagua *et al.*, 2010). The ponds are heterogeneous in surface area, depth, and hydroperiod and are very abundant in the stabilised dunes and areas of contact between the three types of

landscapes (Díaz-Paniagua *et al.*, 2010). In Doñana, there are only two large permanent (or semi-permanent) ponds, which only occasionally dry out after successive years of severe drought. There are also artificially deepened ponds (hereafter referred to as *zacallones*, the local name) that supply water for cattle and wild fauna during summer. They are present across the whole park but are the main water bodies present in the southern areas. In the contact area between the stable dunes and the freshwater marsh, there are ponds filled by the running water of intermittent streams that mainly flow towards the marsh after heavy rains (hereafter referred to as *caños*, the local name). This study included ponds that are representative of those in the study area and that were randomly selected across the entirety of the park: 46 temporary ponds, one of the two semi-permanent ponds, 27 *zacallones*, and 6 *caños*; we have grouped them according to their location in the northern or southern areas of the park (Fig. 1).

#### Macroinvertebrate sampling and taxon identification

We carried out a single survey of 80 ponds (late March–middle June of 2007) spread across the whole of Doñana National Park (SW Spain) to analyse the environmental and spatial effects operating over the minimum time win-



**Fig. 1.** Locations of the 80 study ponds in Doñana National Park: 46 temporary ponds, which were mainly located in the northern part of the park, 27 *zacallones*, which were mainly located in the southern part of the park, 6 *caños*, and 1 semi-permanent pond are indicated.

dow in which all sites could be visited. We determined the presence or absence of macroinvertebrates using a dip net (39 × 21 cm, 1 mm mesh size) and netting across a stretch of water of approximately 1.5 m length in each sampling unit. In each pond, we sampled all different available microhabitats, based largely on differences in aquatic plant cover and depth (Heyer *et al.*, 1994). As the efficiency of dip netting increases in small ponds (Heyer *et al.*, 1994), we took more samples in larger ponds, which also typically contained a higher number of microhabitats, to achieve a comparable effort in detecting rare species (samples per pond ranged from 3 to 13). Sampling appropriateness was supported by a previous study in which similar results were obtained for sample-based rarefaction and raw data (see Florencio *et al.*, 2011 for details). Most macroinvertebrates were identified *in situ* and then released again into the pond. Only unidentified individuals were preserved in 70% ethanol for later identification in the laboratory. We identified individuals to the species or genus level, except for Basomatophora, Diptera, Oligochaeta, and saldid bugs, which were identified to the family level (see Appendix 1 for the detailed taxonomic list). For those species for which we identified larvae and adults, we considered both stages separately in our analyses because of their different environmental requirements; they are thus referred to as taxa stages in our data.

#### Environmental variables in the extensive macroinvertebrate survey

To characterise the environmental gradients in Doñana ponds, we considered different groups of variables.

**Environmental variables.** In the field, we visually identified all the different plant taxa (species or genus level) per pond to estimate plant richness ( $R_{\text{plant}}$ ). Maximum water depth (Max depth) was measured at the deepest point of the pond with a graduated pole. Pond surface area, the total number of ponds with an extension >150 m<sup>2</sup> into a 200 m buffer area around each pond, and the total flooded surface area in a 200 m buffer area around each pond were extracted from a GIS-based map of ponds obtained from a hyperspectral image taken at a moment of high inundation of the area (see Gómez-Rodríguez *et al.*, 2008 for details). We recorded *in situ* pH (near the bed using pH meter HI 991000, HANNA instruments, Portugal), dissolved oxygen concentration (near the bed using YSI 550A Handheld Dissolved Oxygen and Temperature System, YSI Incorporated, Yellow Springs, OH, USA), electrical conductivity (EC) at 20 °C (near the bed using Multi-range Conductivity Meter HI 9033, HANNA instruments, Romania), and turbidity (in the water column using Loggin Microprocessor turbidity meter HI 93703-11, HANNA instruments, Hungary). Surface water (500 ml) was collected to determine nutrient concentrations (dissolved inorganic phosphate, nitrate, nitrite, and ammonium), and main cation and anion concentrations ( $\text{Cl}^-$ ,  $\text{Na}^+$ ,  $\text{Ca}^{2+}$ ,

$K^+$  and  $Mg^{2+}$ ). Ion concentrations were analysed using a Trace Inductively Coupled Plasma Mass Spectrometer, while nutrient concentrations were measured colourimetrically using an Auto Analyser (Bran+Luebbe). Alkalinity was analysed according to the titration method described in APHA (1998). Surface sediment samples (5 cm depth) were collected and the following variables were measured in the laboratory: organic matter (three replicates; lost on ignition, 450 °C, 5 h) and sediment total  $P$  (two replicates). Sediment total  $P$  was estimated using dissolved inorganic phosphate obtained following the method of Murphy and Riley (1962), in which the ignited sediment undergoes acid digestion with 0.5 M  $H_2SO_4$  and  $K_2S_2O_8$  (0.5–1 g) at 120 °C for 4 h (Golterman, 2004). The total Fe concentration in digested sediment (two replicates) was determined colourimetrically by means of o-phenantroline and using ascorbic acid as the reducing agent (Golterman, 2004). The  $Na^+/Ca^{2+}$  ratio was measured because of its biological implications in regulating processes associated with the acid-base balance of the organisms (Radke *et al.*, 2003). We did not use nitrite and nitrate concentrations in the analyses because most values were negligible (range <0.15–0.60 mg l<sup>-1</sup>).

*Marsh-coast distance variables.* To account for the influence of potential external sources of organisms (see e.g. Fahd *et al.*, 2007), we measured the minimum linear distances from each pond to the border of the marsh (Dmarsh) and the coast (Dcoast); these distances were also estimated using the GIS pond map (see Gómez-Rodríguez *et al.*, 2008 for details).

*Spatial variables.* Seventy-nine orthogonal spatial descriptors based on interpond distances were generated using Moran's eigenvector maps (MEMs) in R software 2.11.1 (R Development Core Team, 2010) ('spacemakeR' package, Dray, 2010; see Dray *et al.*, 2006), which provide a general framework of principal coordinates of neighbour matrices (see Borcard & Legendre, 2002). The spatial descriptors extracted from the MEMs were ordered from VI to V79, i.e. from the highest to the lowest eigenvalues. A selection of spatial descriptors that controlled for Type I error in the analyses was carried out according to Peres-Neto and Legendre (2010). The number of spatial descriptors was reduced using the 'ortho.AIC' command in R software 2.11.1 (R Development Core Team, 2010) ('spacemakeR' package, Dray, 2010). Only significant spatial descriptors with positive eigenvalues were considered in the analyses described below [redundancy analysis (RDA) and variation partitioning] to evaluate the effect of interpond distances on the structure of macroinvertebrate assemblages.

#### Statistical analyses

We constructed a pond-characteristic matrix with the values of the environmental and marsh-coast distance

variables. In addition, each group of variables (environmental, marsh-coast distance, and spatial) was considered in three individual matrices. Each variable had been previously transformed to approximate normality (Appendix 2). To obtain the pond-characteristic resemblance matrix, Euclidean distance was applied to the pond-characteristic matrix (Legendre & Legendre, 1998). Finally, we constructed a macroinvertebrate matrix that included the number of samples in which every taxa stage was present divided by the total number of samples taken in a pond. The Bray-Curtis index was applied to the macroinvertebrate matrix to obtain the macroinvertebrate resemblance matrix (Legendre & Legendre, 1998). Subsets of the macroinvertebrate matrix were extracted for the main taxonomical orders Coleoptera, Heteroptera, and Odonata.

To visualise the environmental variability in pond characteristics, we represented the pond dissimilarities by performing non-metric multidimensional scaling (NMDS) in PRIMER version 6 (Clarke & Warwick, 2001) on the pond-characteristic matrix.

We calculated the mean pair-wise macroinvertebrate  $\beta$ -diversity ( $\beta_{sor}$ ) in our extensive sampling survey data to analyse macroinvertebrate  $\beta$ -diversity in the study area. The Sørensen index was applied to the presence-absence data (Legendre & Legendre, 1998). Using R software 2.11.1 (R Development Core Team, 2010), we partitioned  $\beta_{sor}$  into  $\beta$ -diversity associated with species replacement ( $\beta_{sim}$ ) and  $\beta$ -diversity associated with nestedness ( $\beta_{nes}$ ) using the pair-wise measure approach described in Baselga (2010). In short, the total dissimilarity between each pair of ponds ( $\beta_{sor}$ ) was partitioned into two additive components accounting for dissimilarity due to species replacement ( $\beta_{sim}$ ) and dissimilarity due to nestedness ( $\beta_{nes}$ ), respectively, following the formula  $\beta_{sor} = \beta_{sim} + \beta_{nes}$  (Baselga, 2010). We also performed  $\beta$ -diversity partitioning using monthly macroinvertebrate assemblages of 22 of the temporary ponds for 2 years with different rainfalls (see Florencio *et al.*, 2009, 2011 for a detailed description of macroinvertebrate sampling). As we obtained similar results, these data are not presented here for the sake of simplicity.

To detect which environmental variables influenced the macroinvertebrate assemblage structure of ponds, we performed constrained ordination using RDA in R software 2.11.1 (R Development Core Team, 2010) ('vegan' package, Oksanen *et al.*, 2010) on each of the environmental, marsh-coast distance, and spatial variable matrices and the macroinvertebrate matrix and, independently, on the Coleoptera, Odonata and Heteroptera matrices. In the RDA, we excluded taxa stages that occurred in less than five ponds (30% of total species number) to avoid the disrupting effect of rare species (Leps & Smilauer, 2003). To exclude co-variables found to have poor explanatory power in RDA, we performed Spearman rank correlations ( $r_s$ ) between each pair of environmental variables (Appendix 2). We used a forward stepwise procedure to select environmental variables, as described in Blanchet *et al.* (2008). Variation partitioning was performed in R soft-

ware 2.11.1 (R Development Core Team, 2010) ('vegan' package, Oksanen *et al.*, 2010) to measure the independent effects of environmental, marsh-coast distance, and spatial variables (see Borcard *et al.*, 1992); only explanatory variables found to be significant were extracted from RDA and included. In our variation partitioning, we used the adjusted multiple coefficient of determination (Adj.  $r^2$ ), as required when matrices have different numbers of variables (Peres-Neto *et al.*, 2006). Significances were tested using Monte Carlo permutation tests (999 permutations).

After the RDA were performed, the influence of the significant explanatory variables on particular taxa stages and assemblages was analysed by performing a LINKTREE analysis in PRIMER version 6 (Clarke & Warwick, 2001) on the macroinvertebrate matrix (our parameterisation used three as the minimum group size and four as the minimum split size). SIMPROF analyses retained divisions significant at the 0.05 level and yielded a dendrogram of the results, otherwise known as a linkage tree (Clarke *et al.*, 2008). The pair-wise differences between each group of macroinvertebrate assemblages detected by the linkage tree were assessed using one-way ANOSIM analysis (ANOSIM statistic R is close to one when groups are completely different). We determined which taxa stages contributed the most to these pair-wise differences (>10% of contribution) using one-way simpler analysis in PRIMER version 6 (Clarke & Warwick, 2001).

To explore the relative influence of environmental variables on the partitioning of  $\beta$ -diversity, we used multiple regression on distance matrices (MRM), an extension of Mantel test (Legendre *et al.*, 1994). Spearman correlations ( $r_s$ ) were used in the MRM analyses. Significant explanatory variables were identified using a forward-selection procedure (Legendre *et al.*, 1994). The significance of MRM models was assessed using 1000 permutations and only the most significant non-correlated variables were retained within each group of variables (spatial descriptors, environmental and marsh-coast distance variables). We constructed three successive models: (i) *the spatial model*, which used significant spatial descriptors to measure spatial influences on  $\beta$ -diversity; (ii) *the spatial/envi-*

*ronmental model*, which used significant environmental variables in addition to spatial descriptors to obtain partial effects; (iii) *the spatial/environmental/marsh-coast distance model*, which added significant marsh-coast distance variables to the previous model. All these calculations were performed using R software 2.11.1 (R Development Core Team, 2010; 'ecodist' package, Goslee & Urban, 2007).

## Results

### Variability in pond characteristics

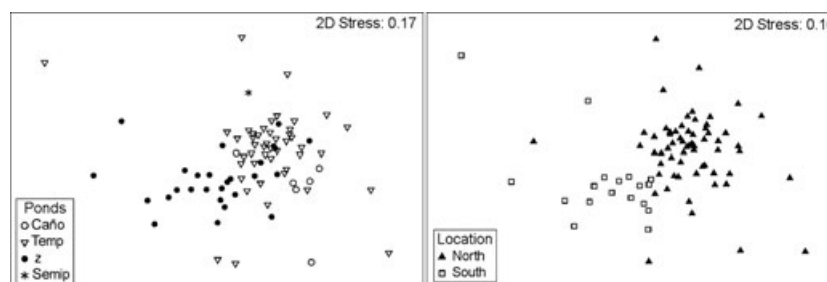
The NMDS representation of the environmental variables of the sampled ponds revealed a heterogeneous pond network (Fig. 2). Northern ponds, which were mainly temporary, evidenced their high environmental variability when compared with southern ponds, which were mainly *zacallones* (Fig. 2).

### Macroinvertebrate $\beta$ -diversity partitioning

We recorded 135 taxa stages across the 80 study ponds, with an average of 23.5 (SD 8.5) taxa stages per pond. Using our extensive macroinvertebrate survey, we found that  $\beta$ -diversity was important in the study area [pond average of  $\beta_{sor} = 0.65$  (SD 0.11)]. In  $\beta$ -diversity partitioning, species replacement contributed more to  $\beta$ -diversity [pond average of  $\beta_{sim} = 0.52$  (SD 0.14)] than nestedness [pond average of  $\beta_{nes} = 0.13$  (SD 0.10)].

### Pond environmental variables influencing macroinvertebrate community structure

The significant explanatory variables influencing pond macroinvertebrate compositions detected by RDA were EC, Rplant, and Max depth among the environmental variables; both Dmarsh and Dcoast; and two spatial



**Fig. 2.** Non-metric multidimensional scaling ordination of the 80 study ponds according to the pond-characteristic resemblance matrix (Euclidean distance). Temporary ponds (Temp), *zacallones* (z), *caños* (Caño), and the semi-permanent pond (Semip) are highlighted as well as the location of ponds in southern (South) and northern (North) areas of the park.

**Table 1.** Significant explanatory variables emerging from redundancy analyses (on the whole macroinvertebrate community and Coleoptera, Odonata, and Heteroptera matrices) performed independently on environmental, marsh-coast distance, and spatial variables<sup>†</sup>.

Explanatory variables	Community	Coleoptera	Odonata	Heteroptera
Environmental	<i>F</i> -ratio = 3.347**	<i>F</i> -ratio = 3.23**	<i>F</i> -ratio = 4.45*	<i>F</i> -ratio = 4.85**
EC	0.34*	0.02*	–	0.25**
Rplant	0.18*	–	–	0.15**
Max depth	0.17*	0.02**	n.s.	0.10*
Pond area	–	0.03**	n.s.	–
Na <sup>+</sup> /Ca <sup>2+</sup> ratio	n.s.	n.s.	n.s.	0.08*
Pond number	–	–	–	0.08*
Alkalinity	–	–	0.05*	–
Marsh-coast distance	<i>F</i> -ratio = 2.898**	<i>F</i> -ratio = 2.75**	<i>F</i> -ratio = 3.64*	n.s.
Dmarsh	0.26**	0.02**	0.04*	n.s.
Dcoast	0.17*	0.03**	–	n.s.
Spatial	<i>F</i> -ratio = 2.423**	<i>F</i> -ratio = 1.89*	n.s.	n.s.
V5	0.17*	0.02*	n.s.	n.s.
V2	0.15*	n.s.	n.s.	n.s.

n.s., non-significant variables; –, excluded variables; EC, electrical conductivity; Rplant, plant richness; Max depth, maximum water depth; Pond area, pond surface area; Pond number, total number of ponds with an extension > 150 m<sup>2</sup> into a 200 m buffer area around each pond; Dmarsh, minimum linear distances from each pond to the border of the marsh; Dcoast, minimum linear distances from each pond to the coast; V5, V2, eigenvectors extracted from the inter-pond distance based on the Moran's eigenvector maps.

<sup>†</sup>Values are the explained variance, indicating the magnitude of the effects of each significant explanatory variable, and global *F*-ratios.

\**P* < 0.05.

\*\**P* < 0.01.

descriptors with high eigenvalues, V2 and V5. These high eigenvalues implied large interpond distances were involved (Table 1). EC had the greatest effect on the macroinvertebrate community (Table 1).

Coleopterans averaged 10.8 (SD 5.2) taxa stages per pond. We found that three groups of environmental variables had important effects on the structure of coleopteran assemblages. EC, Max depth, and Pond surface area were the significant environmental explanatory variables; both marsh-coast distance variables, Dmarsh and Dcoast, were significant; and only the spatial descriptor V5 had a significant effect among the spatial variables (Table 1). Odonatan assemblages [average = 2.4 (SD 2.1) taxa per pond] were significantly explained by Alkalinity and Dmarsh; no spatial descriptors were significant explanatory variables (all *P* > 0.36, Table 1). For heteropteran assemblages [average = 7.1 (SD 2.8) taxa stages per pond], EC, Rplant, Max depth, Na<sup>+</sup>/Ca<sup>2+</sup> ratio, and the total number of ponds with an extension >150 m<sup>2</sup> into a 200 m buffer area around each pond were significant environmental explanatory variables; no marsh-coast distance variables or spatial descriptors were significant explanatory variables (all *P* > 0.09, Table 1).

Variation partitioning analyses revealed that environmental variables (EC, Rplant and Max depth) had a more important effect on macroinvertebrate assemblage structures than marsh-coast distance and spatial variables (Table 2). Environmental variables were also the most important explanatory variables in coleopteran (EC, Max depth and Pond surface area), odonatan (Alkalinity), and heteropteran assemblages (EC, Rplant, Max depth, Na<sup>+</sup>/

**Table 2.** Independent effects of environmental, marsh-coast distance, and spatial variables on macroinvertebrate community structure and Coleoptera, Odonata, and Heteroptera matrices as indicated by variation partitioning analyses.

Adj. <i>r</i> <sup>2†</sup>	Community	Coleoptera	Odonata	Heteroptera
Environmental	0.10**	0.07**	0.04**	0.20**
Marsh-coast distance	0.05**	0.03**	n.s.	–
Spatial	0.02**	0.01*	–	–

<sup>†</sup>Adjusted *r*<sup>2</sup> (ranged 0–1).

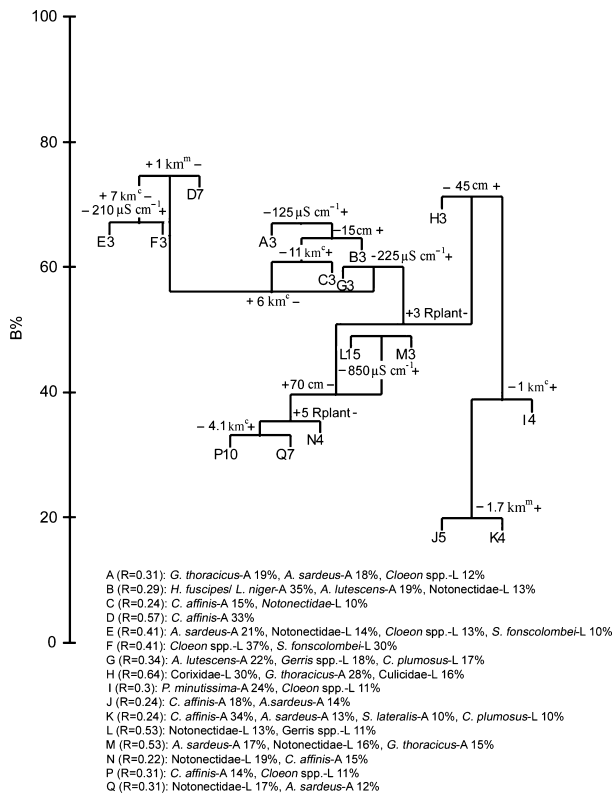
\**P* < 0.05.

\*\**P* < 0.01.

Ca<sup>2+</sup> ratio in water column, and the total number of ponds with an extension >150 m<sup>2</sup> into a 200 m buffer area around each pond) (Table 2). There were no significant independent effects of marsh-coast distance variables and spatial descriptors on the structure of odonatan and heteropteran assemblages (Table 2).

*Pond macroinvertebrate assemblages and environmental thresholds*

The linkage tree differentiated 16 pond groups based on differences in EC, Max depth, Dcoast, Dmarsh, Rplant, and pond macroinvertebrate assemblages. Macroinvertebrate assemblages associated with these pond



**Fig. 3.** Linkage tree representation showing significant divisive clustering of pond macroinvertebrate assemblages constrained by the significant environmental and marsh-coast distance variables detected by redundancy analyses: electrical conductivity ( $\mu\text{S cm}^{-1}$ ), maximum depth (cm), distance to the coast ( $\text{Km}^c$ ), distance to the marsh ( $\text{Km}^m$ ), and plant richness (Rplant). Pond number is indicated in each split group. Each successive split is conditioned by the indicated environmental thresholds of previous splits. B% is the contribution of each binary partition to global dissimilarity (ranged 0–100%). Capital letters indicate main taxa-stage contributors (>10% of contribution) to each split group (-A is adults, -L is larvae). R is the Spearman coefficient giving the dissimilarity value in every split.

groups differed in their contribution to the global dissimilarity of the whole macroinvertebrate community (Fig. 3). Fourteen taxa stages were the main contributors to pond assemblage differences along a generalist-specialist gradient; species ranged from occurring in several different types of environments to only being recorded under specialised conditions (Fig. 3). Four generalist taxa stages occurred under multiple environments (adults of *Corixa affinis* Leach, 1817; adults of *Anisops sardeus* Herich-Schäffer, 1849; larvae of *Cloeon* Leach, 1815 spp.; and larvae of Notonectidae); another five taxa stages were favoured by narrower environmental conditions [*Sympetrum fonscolombei* (Selys, 1841) larvae; *Chironomus plumosus* (Linne, 1758) larvae; *Anacaena lutescens* (Stephens, 1829) adults; *Gerris thoracicus* Schummel, 1832 adults; and *Gerris* spp. larvae]. Five further specialist taxa stages

were the main species contributing to the differentiation of ponds with particular characteristics: adults of *Hydrobius fuscipes* (Linnaeus, 1758) and *Limnoxenus niger* (Zschach, 1788) as well as Corixidae larvae and Culicidae larvae mainly occurred in shallow waters; *Plea minutissima* Leach, 1817 adults mainly occurred in deep ponds far from the coast with poor Rplant; and *Sigara lateralis* (Leach, 1817) adults were also common in deep waters with poor Rplant but that were close to the coast and far from the marsh (Fig. 3). *Sympetrum fonscolombei* larvae, *Gerris* spp. larvae, *G. thoracicus* adults, *A. lutescens* adults, *H. fuscipes*/L. *niger* adults, Corixidae larvae, *C. plumosus* larvae, Culicidae larvae, and *P. minutissima* adults made the greatest contributions to the global dissimilarity of the community, whilst *S. lateralis* adults contributed the least (Fig. 3).

#### Environmental variables driving the macroinvertebrate $\beta$ -diversity pattern

Among the variables included in the MRM analyses, only  $\text{NH}_4$  influenced the  $\beta$ nes pattern observed in the pond network ( $r_s = 0.13$ ,  $r^2 = 0.017$ ,  $P < 0.05$ ). With

**Table 3.** Different multiple regression models associating macroinvertebrate  $\beta$ -diversity to the species replacement and including only spatial variables; spatial and environmental variables; and spatial, environmental, and marsh-coast distance variables.

Variable	$r_s^\dagger$
Spatial model	$r^2 = 0.043^{**}$
V1 <sup>‡</sup>	0.153 <sup>**</sup>
V5 <sup>‡</sup>	0.140 <sup>**</sup>
Spatial/environmental model	$r^2 = 0.074^{**}$
V1	0.077 m.s.
V5	0.139 <sup>**</sup>
Alkalinity	0.141 <sup>**</sup>
Rplant	0.0949 <sup>**</sup>
Max depth	0.069 <sup>*</sup>
Spatial/environmental/marsh-coast distance model	$r^2 = 0.090^{**}$
V1	0.080 <sup>*</sup>
V5	0.130 <sup>**</sup>
Alk	0.136 <sup>**</sup>
Rplant	0.086 <sup>*</sup>
Max depth	0.063 <sup>*</sup>
Dcoast	0.094 <sup>*</sup>
Dmarsh	0.084 <sup>*</sup>

m.s., marginally significant ( $P = 0.057$ ); Rplant, plant richness; Max depth, maximum water depth; Dcoast, minimum linear distances from each pond to the coast; Dmarsh, minimum linear distances from each pond to the border of the marsh.

<sup>†</sup>Coefficients of Spearman correlations,  $r^2$  (ranged 0–1), 1000 permutations.

<sup>‡</sup>Eigenvectors extracted from the interpond distance based on the Moran's eigenvector maps.

<sup>\*</sup> $P < 0.05$ .

<sup>\*\*</sup> $P < 0.01$ .

respect to the explanatory variables of  $\beta sim$  involved in  $\beta$ -diversity, two spatial descriptors with high eigenvalues (V1 and V5) were found to be significant variables in the spatial model (Table 3). In the spatial/environmental model, V5 and Alkalinity had the highest coefficients and thus best explained the  $\beta sim$  values (Table 3). In the spatial/environmental/marsh-coast distance model, V5 and Alkalinity were retained and shared similar, high coefficients that revealed their influence on  $\beta sim$  (Table 3). The spatial/environmental/marsh-coast distance model, which included the highest number of significant variables, explained 9% of variation in  $\beta sim$  ( $r^2 = 0.09$ , Table 3).

## Discussion

### *Environmental variability*

The high dissimilarity detected in the environmental characteristics of Doñana ponds reveals this system to be highly heterogeneous; this pattern is particularly due to the wide variability observed among temporary ponds, which are the most abundant aquatic habitats in this area. Although the artificially deepened ponds (*zacallones*) in the southern area of the park were more similar in their environmental characteristics, they widely differed from northern water bodies, thus increasing the heterogeneity of the total pond network. The long hydroperiod of these *zacallones* extends the temporal availability of aquatic habitats in the area and thus they act as reservoirs for species typical of temporary ponds, mainly macroinvertebrate dispersers that are forced to leave drying ponds in summer (see e.g. Garrido & Munilla, 2008; Florencio *et al.*, 2009).

### *Macroinvertebrate $\beta$ -diversity in a heterogeneous pond network*

The macroinvertebrate  $\beta$ -diversity pattern reveals a diverse system mainly driven by species replacement in the pond network. Although the macroinvertebrate community of the Doñana pond network has been described as having a clear nested pattern (Florencio *et al.*, 2011),  $\beta$ -diversity partitioning indicated that nestedness hardly contributed to macroinvertebrate  $\beta$ -diversity. The relative importance of species replacement to  $\beta$ -diversity described in this study is concordant with the high number of idiosyncratic taxa stages (59) and ponds (34) found in the area that departed from the general nested pattern (Florencio *et al.*, 2011).

We detected some species whose occurrence was associated with particular environmental conditions, supporting the role of pond environmental heterogeneity in driving species replacement. In the linkage tree, we detected 10 taxa that were specialists occurring in a narrow range of environmental variability. These 10 specialists, with the exception of *Gerris* spp. larvae, were all

included in the 59 idiosyncratic taxa stages listed for the Doñana pond network (see Florencio *et al.*, 2011). Except for *S. lateralis*, these taxa stages significantly contributed to the global dissimilarity of the whole macroinvertebrate community.

### *Relationships between macroinvertebrate assemblages and pond characteristics*

We found similar explanatory variables influencing the macroinvertebrate community structure and the  $\beta$ -diversity associated with species replacement: EC (and alkalinity as a co-variable), maximum depth, aquatic plant richness, and distance from the ponds to the marsh and the coast, and two spatial descriptors. In metacommunity ecology, patterns of  $\beta$ -diversity are usually driven by biogeographical conditions (i.e. closer ponds should be more similar than more distant ponds as a result of species dispersal capabilities) as well as by environmental heterogeneity associated with complex processes (Leibold *et al.*, 2004; Legendre *et al.*, 2005). In this study, we found that one spatial descriptor as well as pond variability in alkalinity (and the co-variables EC, pH, and ion concentration) drove the macroinvertebrate  $\beta$ -diversity pattern via species replacement. Therefore, spatial and environmental filters are operating in community assembly via dispersal and species-sorting respectively (Patrick & Swam, 2011). These results are concordant with Chase and Myers (2011)'s predictions:  $\beta$ -diversity increases across spatial gradients in accordance with stochastic dispersal processes and  $\beta$ -diversity increases across environmental gradients in accordance with the niche-based theory.

In this study, EC (and co-variables) was correlated with the distance of ponds from the coast, revealing a gradual increase in water conductivity values from the north to the south of the park (82–8800  $\mu S cm^{-1}$ ). The study ponds have no surface or groundwater connection to the sea though they have some oceanic influence due to airborne sea salt deposition and so the closer to the coast the higher the electrical conductivity. This conductivity gradient thus influences both the macroinvertebrate community structure and the  $\beta$ -diversity pattern. We also found that some species typically occurred under low conductivity conditions, for example *A. lutescens* occurred in waters with values lower than 225  $\mu S cm^{-1}$ . Similarly, in other temporary water systems, different species can occur across wide conductivity gradients (see e.g. Gutiérrez-Estrada & Bilton, 2010). The occurrence of different species can be favoured at different values of the conductivity gradient. For example we observed that Heteropterans, for example the corixid *S. lateralis*, preferred southern *zacallones*, which exhibited the highest conductivity in the study area. In contrast, Odonatans preferred northern temporary ponds with the lowest conductivity values; for example *S. fonscolombi* was observed almost exclusively in these ponds.

When exploring the influence of interpond distances on macroinvertebrate assemblage structure and macroinverte-



brate  $\beta$ -diversity, we only obtained spatial descriptors with high eigenvalues, a result that, in natural systems, signifies the involvement of broad spatial scales (Borcard & Legendre, 2002; Diniz-Filho & Bini, 2005; Griffith & Peres-Neto, 2006). Therefore, in this study, only the largest interpond distances had an effect on the macroinvertebrate assemblages and thus also on macroinvertebrate  $\beta$ -diversity, resulting in a system with high connectivity where species demonstrated weak dispersal limitations. The excellent dispersal abilities that usually characterise species of temporary ponds and let them cope with pond desiccation (Williams, 2006) largely contributed to the weak dispersal limitations in the study area. The Doñana pond network has already been determined to be a robust network for amphibian species, allowing them to encounter reproduction habitats even in extremely dry years (Fortuna *et al.*, 2006); we confirm in this study that this assessment also applies to macroinvertebrate species.

We identified aquatic vegetation as an important variable structuring the macroinvertebrate community and its diversity, which is concordant with other studies carried out in temporary waters (e.g. Nicolet *et al.*, 2004; Bilton *et al.*, 2009). Diverse vegetation offers a wide range of niches for macroinvertebrate species, with a high number of refuges for species under predation and food availability for grazers. Plant species' architecture can influence biological processes, for example predator–prey interactions and the presence of oviposition sites. Hence, in this study, ponds with high aquatic plant richness harboured distinct macroinvertebrate assemblages that contributed significantly to macroinvertebrate diversity as a whole. In addition to aquatic vegetation, other biotic factors can affect the macroinvertebrate communities of temporary ponds; for instance, predators may have a seasonal effect, which could constitute an important focus for further research.

#### *Implications for conservation*

We demonstrate that both stochastic and deterministic ecological processes can operate together to assemble macroinvertebrates in a pond network. Stochastic processes such as dispersal only influenced the macroinvertebrate community and  $\beta$ -diversity at large spatial scales, which reveal the high connectivity of the system. Environmental variability was consequently key in maintaining high biodiversity in this system. The macroinvertebrate  $\beta$ -diversity pattern was mainly driven by species replacement, with different species occurring in different environments; in contrast, the contribution of nestedness to  $\beta$ -diversity was low. Although the Doñana pond network has been described as having a clear nested pattern, the species that most contributed to  $\beta$ -diversity were largely idiosyncratic species and thus departed from the general nested pattern. We found that these idiosyncratic species occurred in specialised environments and were predominantly responsible for maintaining the system's high

biodiversity. In this study, we demonstrate the importance of idiosyncratic species in sustaining diversity in nested systems that contain high numbers of idiosyncratic species. Therefore, the best strategy for conservation is to preserve diverse environments across a non-fragmented habitat where species are not limited by dispersal. In other words, it is preferable to protect a wide range of diverse and interconnected ponds rather than the richest ones, which would be the conservation priority in a strictly nested system.

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#### **References**

- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C. & Swenson, N.G. (2011) Navigating the multiple meanings of  $\beta$  diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19–28.
- APHA (1998) *Standard Methods for the Examination of Water and Wastewater*, 20th edn. American Public Health Association, Washington, District of Columbia.
- Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.
- Bazzanti, M., Baldoni, S. & Seminara, M. (1996) Invertebrate macrofauna of a temporary pond in Central Italy: composition, community parameters and temporal succession. *Archiv für Hydrobiologie*, **137**, 77–94.
- Bilton, D.T., McAbendroth, L., Nicolet, P., Bedford, A., Rundle, S.D., Foggo, A. & Ramsay, P.M. (2009) Ecology and conservation status of temporary and fluctuating ponds in two areas of Southern England. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **19**, 134–146.
- Blanchet, F.G., Legendre, P. & Borcard, D. (2008) Forward selection of explanatory variables. *Ecology*, **89**, 2623–2632.
- Boix, D., Sala, J., Quintana, X.D. & Moreno-Amichi, R. (2004) Succession of the animal community in a Mediterranean temporary pond. *Journal of the North American Benthological Society*, **23**, 29–49.

- Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, **153**, 51–68.
- Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.
- Briers, R.S. & Biggs, J. (2005) Spatial patterns in pond invertebrate communities: separating environmental and distance effects. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**, 549–557.
- Cérégino, R., Biggs, J., Oertli, B. & Declerck, S. (2008) The ecology of European ponds: defining the characteristics of a neglected freshwater habitat. *Hydrobiologia*, **597**, 1–6.
- Chase, J.M. & Myers, J.A. (2011) Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B*, **366**, 2351–2363.
- Clarke, K.R., Somerfield, P.J. & Gorley, R.N. (2008) Testing of null hypotheses in explanatory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology*, **366**, 56–69.
- Clarke, K.R. & Warwick, R.M. (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd edn. PRIMER-E, Plymouth, UK.
- Collinson, N.H., Biggs, J., Corfield, A., Hodson, M.J., Walker, D., Whitfield, M. & Williams, P.J. (1995) Temporary and permanent ponds: an assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. *Biological Conservation*, **74**, 125–133.
- Declerck, S., Vandekerckhove, J., Johansson, L., Muylaert, K., Conde-Porcuna, J.M., Van Der Gucht, K., Pérez-Martínez, C., Lauridsen, T., Schwenk, K., Zwart, G., Rommens, W., López-Ramos, J., Jeppesen, E., Vyverman, W., Brendonck, L. & De Meester, L. (2005) Multi-group biodiversity in shallow lakes along gradients of phosphorus and water plant cover. *Ecology*, **86**, 1905–1915.
- Díaz-Paniagua, C., Fernández-Zamudio, R., Florencio, M., García-Murillo, P., Gómez-Rodríguez, C., Siljeström, P. & Serrano, L. (2010) Temporary ponds from the Doñana National Park: a system of natural habitats for the preservation of aquatic flora and fauna. *Limnetica*, **29**, 1–18.
- Diniz-Filho, J.A.F. & Bini, L.M. (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography*, **14**, 177–185.
- Dray, S. (2010) *spacemakeR: spatial modelling*. R package version 0.0-5/r83. <<http://R-Forge.R-project.org/projects/sedar/>> 7th March 2011.
- Dray, S., Legendre, P. & Peres-Neto, P.R. (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, **196**, 483–493.
- Fahd, K., Florencio, M., Keller, C. & Serrano, L. (2007) The effect of the sampling scale on zooplankton community assessment and its implications for the conservation of temporary ponds in south-west Spain. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **17**, 175–193.
- Florencio, M., Díaz-Paniagua, C., Serrano, L. & Bilton, D.T. (2011) Spatio-temporal nested patterns in macroinvertebrate assemblages across a pond network with a wide hydroperiod range. *Oecologia*, **166**, 469–483.
- Florencio, M., Serrano, L., Gómez-Rodríguez, C., Millán, A. & Díaz-Paniagua, C. (2009) Inter and intra-annual variations of macroinvertebrate assemblages are related to the hydroperiod in Mediterranean temporary ponds. *Hydrobiologia*, **634**, 167–183.
- Fortuna, M.A., Gómez-Rodríguez, C. & Bascompte, J. (2006) Spatial network structure and amphibian persistence in stochastic environments. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1429–1434.
- Friday, L.E. (1987) The diversity of macroinvertebrate and macrophyte communities in ponds. *Freshwater Biology*, **18**, 87–104.
- Garrido, J. & Munilla, I. (2008) Aquatic Coleoptera and Hemiptera assemblages in three coastal lagoons of the NW Iberian Peninsula: assessment of conservation value and response to environmental factors. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **18**, 557–569.
- Golterman, H.L. (2004) *The Chemistry of Phosphate and Nitrogen Compounds in Sediments*. Kluwer Academic Publisher, Dordrecht.
- Gómez-Rodríguez, C., Bustamante, J., Koponen, S. & Díaz-Paniagua, C. (2008) High-resolution remote-sensing data in amphibian studies: identification of breeding sites and contribution to habitat models. *Herpetological Journal*, **18**, 103–113.
- Goslee, S.C. & Urban, D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, **22**, 1–19. <<http://cran.r-project.org/>> 14th October 2011.
- Griffith, D.A. & Peres-Neto, P.R. (2006) Spatial modelling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology*, **87**, 2603–2613.
- Gutiérrez-Estrada, J.C. & Bilton, D.T. (2010) A heuristic approach to predicting water beetle diversity in temporary and fluctuating waters. *Ecological Modelling*, **221**, 1451–1462.
- Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C. & Foster, M.S. (1994) *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, District of Columbia.
- Hylander, K., Nilsson, C., Jonsson, B.G. & Göthner, T. (2005) Differences in habitat quality explain nestedness in a land snail meta-community. *Oikos*, **108**, 351–361.
- Jeffries, M. (2005) Small ponds and big landscapes: the challenge of invertebrate spatial and temporal dynamics for European pond conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**, 541–547.
- Legendre, P., Lapointe, F.-J. & Casgrain, P. (1994) Modelling brain evolution from behavior: a permutational regression approach. *Evolution*, **48**, 1487–1499.
- Legendre, P., Lapointe, F.-J. & Casgrain, P. (2005) Analyzing beta diversity: Partitioning the spatial variation of community composition data. *Ecological Monographs*, **75**, 435–450.
- Legendre, P. & Legendre, L. (1998) Chapter 7: ecological resemblance. *Numerical Ecology: Developments in Environmental Modelling 20* (ed. by P. Legendre and L. Legendre), 2nd edn., pp. 247–302. Elsevier, Amsterdam, the Netherlands & New York City, New York.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.
- Leps, J. & Smilauer, P. (2003) *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, New York City, New York.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

- Murphy, J. & Riley, J.P. (1962) A modified single solution method for the determination of soluble phosphate in natural waters. *Analytica Chimica Acta*, **37**, 31–36.
- Nicolet, P., Biggs, J., Fox, G., Hodson, M.J., Reynolds, C., Whitfield, M. & Williams, P. (2004) The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. *Biological Conservation*, **120**, 261–278.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2010) *vegan: community ecology package*. R package version 1.18-13/r1328. <<http://R-Forge.R-project.org/projects/vegan/>> 7th March 2011.
- Pandit, S.N., Kolasa, J. & Cottenie, K. (2009) Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology*, **90**, 2253–2262.
- Patrick, C.J. & Swam, C.M. (2011) Reconstructing the assembly of a stream-insect metacommunity. *Journal of the North American Benthological Society*, **30**, 259–272.
- Peres-Neto, P.R. & Legendre, P. (2010) Estimating and controlling for spatial structure in the study of ecological communities. *Global Ecology and Biogeography*, **19**, 174–184.
- Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, **87**, 2614–2625.
- R Development Core Team (2010). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. <<http://www.R-project.org>> 14 October 2011.
- Radke, L.C., Juggins, S., Halse, S.A., De Deckker, P. & Finston, T. (2003) Chemical diversity in south-eastern Australia saline lakes II: biotic implications. *Marine and Freshwater Research*, **54**, 895–912.
- Sanderson, R.A., Eyre, M.D. & Rushton, S.P. (2005) Distribution of selected macroinvertebrates in a mosaic of temporary and permanent freshwater ponds as explained by autologist models. *Ecography*, **28**, 355–362.
- Siljeström, P.A., Moreno, A., García, L.V. & Clemente, L.E. (1994) Doñana National Park (south-west Spain): geomorphological characterization through a soil-vegetation study. *Journal of Arid Environments*, **26**, 315–323.
- Tuomisto, H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, **33**, 2–22.
- Urban, M.C. (2004) Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology*, **85**, 2971–2978.
- Urban, M.C. & Skelly, D.K. (2006) Evolving metacommunities: toward an evolutionary perspective on metacommunities (Concepts & Synthesis). *Ecology*, **87**, 1616–1626.
- Vanschoenwinkel, B., De Vries, C., Seaman, M. & Brendonck, L. (2007) The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos*, **116**, 1255–1266.
- Waterkeyn, A., Grillas, P., Vanschoenwinkel, B. & Brendonck, L. (2008) Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. *Freshwater Biology*, **53**, 1808–1822.
- Williams, D.D. (1997) Temporary ponds and their invertebrate communities. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **7**, 105–117.
- Williams, D.D. (2006) *The Biology of Temporary Waters*. Oxford University Press, Oxford, UK.
- Williams, P., Biggs, J., Fox, G., Nicolet, P. & Whitfield, M. (2001) History, origins and importance of temporary ponds. *European Temporary Ponds: A Threatened Habitat* (ed. by K. Rouen), pp. 7–15. Freshwater Biological Association, Birmingham.
- Wissinger, S.A. (1999) Ecology of wetland invertebrates. Synthesis and applications for conservation and management. *Invertebrates in Freshwater Wetlands of North America* (ed. by D. Batzer, R.B. Rader and S.A. Wissinger), pp. 1043–1086. Wiley, New York City, New York.
- Zacharias, I., Dimitrou, E., Dekker, A. & Dorsman, E. (2007) Overview of temporary ponds in the Mediterranean region: threats, management and conservation issues. *Journal of Environmental Biology*, **28**, 1–9.

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APPENDICES

Appendix 1. List showing the taxa captured in the study ponds (A is for adults, L is for larvae, N is for nymphs). The percent occurrence across all ponds (total), as well as in temporary ponds, zacallones, caños, and the semi-permanent pond is provided. Percentages for ponds located in the northern and southern areas of the park are given separately

Taxa	Family	Total		Temporary		Zacallones		Caños		Semi-permanent		Northern park		Southern park	
		A	L	A	L	A	L	A	L	A	L	A	L	A	L
Acari															
Hydrachnellae		3		0		7		0		0		2		6	
Bassomatophora															
Physa spp.	Physidae	33		28		30		67		100		37		17	
Planorbidae	Planorbidae	14		9		19		17		100		8		33	
Neotaenioglossa															
Potamopyrgus antipodarum (Gray 1843)	Hydrobiidae	3		0		7		0		0		0		11	
Coleoptera															
Bagous spp.	Curculionidae	16				7		0		100		21		0	
Dryops spp.	Dryopidae	34	1	39	2	30	0	0	0	100	0	40	2	11	0
Agabus conspersus (Marsham 1802)	Dytiscidae	39				59		17		100		34		56	
Agabus didymus (Olivier, 1795)	Dytiscidae	13		11		19		0		0		6		33	
Agabus nebulosus (Forster, 1771)	Dytiscidae	21				22		33		100		24		11	
Agabus spp.	Dytiscidae	10		13		4		4		100		13		0	
Cybisiter lateralmarginalis (De Geer, 1774)	Dytiscidae	3	24	2	26	4	19	0	17	0	100	2	24	6	22
Dytiscus circumflexus Fabricius, 1801	Dytiscidae	4	9	4	11	4	7	0	0	0	0	3	10	6	6
Eretes griseus (Fabricius, 1781)	Dytiscidae	3		4		0		0		0		3		0	
Graptodytes flavipes (Olivier, 1795)	Dytiscidae	3		2		4		0		0		2		6	
Hydatiticus leander (Rossi, 1790)	Dytiscidae		3		4		0	0		0			3		0
Hydroglyphus geminus (Fabricius, 1792)	Dytiscidae	33		24		48		17		100		23		67	
Hydroporus gyllenhali Schiödte, 1841	Dytiscidae	10		13		4		17		0		13		0	
Hydroporus lucasi Reiche, 1866	Dytiscidae	45		46		48		17		100		45		44	
	Dytiscidae	26		13		56		0		0		11		78	

Appendix 1. (Continued).

Taxa	Family	Total		Temporary		Zacallones		Cantos		Semi-permanent		Northern park		Southern park	
		A	L	A	L	A	L	A	L	A	L	A	L	A	L
<i>Hygrotus confluens</i> (Fabricius, 1787)	Dytiscidae	3		0		7		0		0		0		11	
<i>Hygrotus inaequalis</i> (Fabricius, 1777)	Dytiscidae	41		30		59		50		0		32		72	
<i>Hygrotus lagari</i> (Fery, 1992)	Dytiscidae		21		26		15		0		100		19		28
<i>Hydroporus</i> spp. or <i>Hygrotus</i> spp.	Dytiscidae	20	20	13	13	33	37	17	0	0	0	13	15	44	39
<i>Hyphydrus aubei</i> Ganglbauer, 1892	Dytiscidae	14		11		22		0		0		8		33	
<i>Ilybius montanus</i> (Stephens, 1828)/ <i>Agabus bipustulatus</i> (Linnaeus, 1767)	Dytiscidae	35	51	33	50	41	56	33	33	0	100	34	50	39	56
<i>Laccophilus minutus</i> (Linnaeus, 1758)	Dytiscidae	10		11		4		33		0		13		0	
<i>Liopterus atriceps</i> (Sharp, 1882)	Dytiscidae	36		39		30		33		100		44		11	
<i>Rhantus hispanicus</i> Sharp, 1882	Dytiscidae	16		15		22		0		0		15		22	
<i>Rhantus suturalis</i> (McLeay, 1825)	Dytiscidae	41		39		52		17		0		37		56	
<i>Colymbetes fuscus</i> (Linnaeus, 1758)	Dytiscidae		20		30		4		0		100		26		0
<i>Rhantus</i> spp. or <i>Colymbetes fuscus</i>	Dytiscidae	6		0		19		0		0		0		28	
<i>Yola bicarinata</i> (Latreille, 1804)	Dytiscidae	19		15		30		0		0		11		44	
<i>Gyrinus dejeani</i> Brullé, 1832	Gyrinidae	3		2		4		0		0		2		6	
<i>Gyrinus urinator</i> Illiger, 1807	Gyrinidae		3		4		0		0		0		3		0
<i>Gyrinus</i> spp.	Gyrinidae	6		7		7		0		0		3		17	
<i>Halipilus andalusicus</i> Wehncke, 1874	Halplidae	5		2		11		0		0		3		11	
<i>Halipilus guttatus</i> Aubé, 1836	Halplidae	5		2		11		0		0		3		11	
<i>Halipilus lineatocollis</i> (Marsham, 1802)	Halplidae		6		9		4		0		0		6		6
<i>Halipilus</i> spp.	Halplidae	45		46		41		50		100		48		33	
<i>Helophorus</i> spp.	Helophoridae	1		0		4		0		0		0		6	
<i>Limnebius fuscatus</i> Baudi, 1872	Hydraenidae	3		4		0		0		0		3		0	
<i>Ochthebius dilatatus</i> Stephens, 1829	Hydraenidae														

Appendix 1. (Continued).

Taxa	Family	Total		Temporary		Zacallones		Carios		Semi-permanent		Northern park		Southern park	
		A	L	A	L	A	L	A	L	A	L	A	L	A	L
<i>Ochthebius europallens</i> Fairmaire, 1879	Hydraenidae	5		7		4		0		0		3		11	
<i>Hydrochus flavipennis</i> Küster, 1852	Hydrochidae	4		2		7		0		0		3		6	
<i>Anacaena lutescens</i> (Stephens, 1829)	Hydrophilidae	54		61		37		67		100		60		33	
<i>Berosus affinis</i> Brullé, 1835	Hydrophilidae	21		22		22		17		0		19		28	
<i>Berosus guttalis</i> Rey, 1883	Hydrophilidae	15		17		11		17		0		18		6	
<i>Berosus signaticollis</i> (Charpentier, 1825)	Hydrophilidae	16		24		7		0		0		19		6	
<i>Berosus</i> spp.	Hydrophilidae		26		35		11		17		100		32		6
<i>Enochrus bicolor</i> (Fabricius, 1792)	Hydrophilidae	23		22		26		0		100		21		28	
<i>Enochrus fuscipennis</i> (C.G. Thomsom, 1884)	Hydrophilidae	40		46		33		33		0		45		22	
<i>Enochrus</i> spp.	Hydrophilidae		8		13		0		0		0		10		0
<i>Helochaetes lividus</i> (Forster, 1771)	Hydrophilidae	11		9		11		33		0		8		22	
<i>Hydrobius convexus</i> Brullé, 1835	Hydrophilidae	†		†											
<i>Hydrobius fuscipes</i> (Linnaeus, 1758) & <i>Linnoxenus niger</i> (Zschach, 1788)	Hydrophilidae	41		52		19		50		100		48		17	
<i>Hydrobius</i> spp. or <i>Linnoxenus niger</i>	Hydrophilidae		28		37		19		0		0		35		0
<i>Hydrochlara flavipes</i> (Steven, 1808)	Hydrophilidae	5		4		0		17		100		6		0	
<i>Hydrophilus pistaceus</i> (Laporte, 1840)	Hydrophilidae		4		0		7		17		0		5		0
<i>Laccobius revelierei</i> Perris, 1864	Hydrophilidae	1		2		0		0		0		2		0	
<i>Paracymus scutellaris</i> (Rosenhauer, 1856)	Hydrophilidae	20		24		11		33		0		26		0	
<i>Hygrobia hermanni</i> (Fabricius, 1775)	Paelobiidae	34		24		56		17		0		23		72	
<i>Noterus laevis</i> Sturm, 1834	Noteridae	8		4		7		17		100		8		6	
<i>Hydrocyphon</i> spp.	Scirtidae		3		4		0		0		0		3		0
Ephemeroptera															
<i>Cloeon</i> spp.	Baetidae		74		76		81		17		100		69		89

Appendix 1. (Continued).

Taxa	Family	Total		Temporary		Zacallones		Cariós		Semi-permanent		Northern park		Southern park	
		A	L	A	L	A	L	A	L	A	L	A	L	A	L
<i>Caenis</i> spp.	Caenidae	1		0		0		17		0		2		0	
Haplotoxida															
Tubificidae	Tubificidae	1		2		0		0		0		2		0	
Heteroptera															
<i>Corixa affinis</i> Leach, 1817	Corixidae	81		78		93		50		100		77		94	
<i>Micronecta scholzi</i> (Fieber, 1860)	Corixidae	8		2		19		0		0		2		28	
<i>Sigara lateralis</i> (Leach, 1817)	Corixidae	45		39		63		17		0		35		78	
<i>Sigara scripta</i> (Rambur, 1840)	Corixidae	14		9		26		0		0		6		39	
<i>Sigara selecta</i> (Fieber, 1848)	Corixidae	3		2		4		0		0		2		6	
<i>Sigara stagnalis</i> (Leach, 1817)	Corixidae	14		9		26		0		0		6		39	
<i>Trichocorixa verticalis</i> (Fieber, 1851)	Corixidae	15		17		15		0		0		13		22	
<i>Corixidae</i> spp.	Corixidae	10	56	11	59	7	59	17	17	0	100	11	53	6	67
<i>Gerris cf maculatus</i> Tamanini, 1946	Gerridae	65		72		52		67		100		69		50	
<i>Gerris thoracicus</i> Schummel, 1832	Gerridae	4	59	7	74	0	33	0	50	0	100	5	69	0	22
<i>Gerris</i> spp.	Gerridae	9	10	4	9	19	15	0	0	0	0	6	6	17	22
<i>Microvelia pygmaea</i> (Dufour, 1833)	Microveliidae	10	10	9	4	7	15	33	33	0	0	11	8	6	17
<i>Naucoris maculatus</i> Fabricius, 1798	Nauoridae	81		78		93		50		100		79		89	
<i>Nepa cinerea</i> Linnaeus, 1798	Nepidae	23		28		15		0		100		24		17	
<i>Anisops sardaeus</i> Herrich-Schäffer, 1849	Notonectidae	29		28		33		17		0		29		28	
<i>Notonecta glauca</i> Linnaeus, 1758 ssp. <i>glauca</i>	Notonectidae	14		13		19		0		0		13		17	
<i>Notonecta glauca</i> Linnaeus, 1758 ssp. <i>meridionalis</i> Poisson, 1926	Notonectidae	26		20		41		17		0		26		28	
<i>Notonecta maculata</i> Fabricius, 1794	Notonectidae	33	75	24	83	52	70	0	33	100	0	29	77	44	67
<i>Notonecta viridis</i> Delcourt, 1909	Pleidae	10	10	11	11	11	11	0	0	0	0	8	8	44	17
<i>Notonectidae</i> spp.	Notonectidae	33	10	24	11	52	11	0	0	100	0	29	8	44	17

Appendix 1. (Continued).

Taxa	Family	Total		Temporary		Zacallones		Cantos		Semi-permanent		Northern park		Southern park	
		A	L	A	L	A	L	A	L	A	L	A	L	A	L
<i>Plea minutissima</i> Leach, 1817															
Notostraca															
<i>Triops mauritanicus</i> (Ghigi, 1921)	Triopsidae	3		4		0		0		0		3		0	
Spinicaudata															
<i>Cyzicus grubei</i> Simon, 1886	Cyzicidae	1		2		0		0		0		0		6	
<i>Maghrebestheria maroccana</i> Thiéry, 1988	Leptestheriidae	3		4		0		0		0		3		0	
Anostraca															
<i>Branchipus cortesi</i> Alonso y Jaume, 1991	Branchipodidae	1		2		0		0		0		2		0	
<i>Branchipus schafferi</i> Fischer de Waldheim, 1834	Branchipodidae	1		2		0		0		0		2		0	
<i>Tanymanstix stagnalis</i> (Linnaeus, 1758)	Tanymanstigidae	1		2		0		0		0		2		0	
<i>Streptocephalus torvicornis</i> (Waga, 1842)	Chirocephalidae	3		4		0		0		0		2		6	
Odonata															
<i>Aeshna affinis</i> * Vander Linden, 1823	Aeshnidae	8		11		4		4		0		8		6	
<i>Aeshna mixta</i> Latreille, 1805	Aeshnidae	8		4		11		17		0		8		6	
<i>Coenagrion scitulum</i> (Rambur, 1842)	Coenagrionidae	6		7		7		0		0		8		0	
<i>Ischnura elegans</i> * (Vander Linden, 1820)	Coenagrionidae	28		30		26		0		100		31		17	
<i>Ischnura pumilio</i> * (Charp., 1825)	Coenagrionidae	38		41		30		33		100		44		17	
<i>Lestes barbarus</i> (Fabr., 1798)	Lestidae	13		15		11		0		0		16		0	
<i>Lestes dryas</i> Kirby, 1890	Lestidae	10		11		11		0		0		11		6	
<i>Lestes macrostigma</i> (Eversm., 1836)	Lestidae	1		2		0		0		0		2		0	
<i>Lestes virens</i> (Charpentier, 1825)	Lestidae	9		2		22		0		0		3		28	
<i>Crocothemis erythraea</i> (Brullé, 1832)	Libellulidae	4		4		4		0		0		3		6	
	Libellulidae	51		67		26		33		100		63		11	



Appendix 1. (Continued).

Taxa	Family	Total		Temporary		Zacallones		Cáños		Semi-permanent		Northern park		Southern park	
		A	L	A	L	A	L	A	L	A	L	A	L	A	L
<i>Sympetrum fonscolombei</i> (Selys, 1841)	Libellulidae	19	33	0	0	0	0	0	0	0	0	24	0		
<i>Sympetrum meridionale</i> (Selys, 1841)	Libellulidae	24	37	7	0	0	0	0	0	0	29	6			
<i>Sympetrum sanguineum</i> (Müller, 1764)	Libellulidae	26	37	7	33	0	0	0	0	0	34	0			
<i>Sympetrum stritotatum</i> (Charpentier, 1840)	Libellulidae	1	0	4	0	0	0	0	0	0	0	6			
<i>Orithetrum brunneum</i> * (Fonscolombe, 1837)	Libellulidae	1	0	4	0	0	0	0	0	0	0	6			
<i>Orithetrum cancellatum</i> (Linneo, 1758)	Libellulidae	1	0	4	0	0	0	0	0	0	2	0			
<i>Orithetrum nitidinerve</i> * (Selys, 1841)	Libellulidae	L	N	L	N	L	N	L	N	L	N	L	N	L	N
Diptera		6	11	0	0	0	0	0	0	0	8				
<i>Chaoborus</i> spp.	Chaoboridae	60	57	70	33	100	61								
<i>Chironomus plumosus</i> (Linneo, 1758)	Chironomidae	29	16	43	22	7	11	17	0	0	0	35	18	6	11
Culicidae	Culicidae	5	9	0	0	0	0	0	0	0	0	6	0		
<i>Dixa</i> spp.	Dixidae	1	2	0	0	0	0	0	0	0	2	0			
Dolichopodidae	Dolichopodidae	3	2	0	0	0	0	0	0	0	0	0			
Ephydriidae	Ephydriidae	11	11	11	17	0	0	0	0	0	0	11	11		
Orthocladinae	Chironomidae	5	9	0	0	0	0	0	0	0	6	0			
Rhagionidae	Rhagionidae	1	2	0	0	0	0	0	0	0	2	0			
Sciomyzidae	Sciomyzidae	3	4	0	0	0	0	0	0	0	3	0			
Tabanidae	Tabanidae	9	7	7	33	0	0	0	0	0	8	11			
Tanypodinae	Chironomidae	5	9	0	0	0	0	0	0	0	6	0			
Tipulidae	Tipulidae														

\*Confirmation of the identity of these species is required because species identification keys based on larval morphology are difficult to use and these species have not been previously cited as being in the study area.

†Only occasional presence of this species was detected.

**Appendix 2.** Mean and standard deviation (SD) are shown for the pond characteristics (environmental and marsh-coast distance variables) of sampled ponds

Environmental	Temporary ( <i>N</i> = 46)		<i>Zacallones</i> ( <i>N</i> = 27)		<i>Caños</i> ( <i>N</i> = 6)		Transf.	<i>r<sub>s</sub></i> > 0.6 <sup>†</sup>
	Mean	SD	Mean	SD	Mean	SD		
Rplant	7.4	3.7	3.9	3.0	6.2	3.5	-	Pond area (+)
Max depth (cm)	59.8	31.8	103.8	13.2	52.2	34.2	-	
Pond area (m <sup>2</sup> )	3390	5586	119	329	538	408	Log	Aq plant R (+)
Pond number	5.1	4.0	3.1	3.4	2.8	2.2	-	Flooded area (+)
Flooded area (m <sup>2</sup> )	3814	6268	1649	3397	1227	1993	Log	Pond number (+)
NH <sub>4</sub> <sup>+</sup> (mg l <sup>-1</sup> )	0.17	0.54	0.12	0.15	0.14	0.12	Log	
i-P (mg l <sup>-1</sup> )	0.11	0.13	0.08	0.10	0.21	0.28	Log	
TP-s (µg g <sup>-1</sup> d.w.)	258.36	314.59	105.29	121.80	328.40	333.52	-	TFe-s (+), O.M. (+)
TFe-s (mg g <sup>-1</sup> d.w.)	3.30	3.18	2.36	2.61	4.57	4.41	-	TP-s (+), O.M. (+)
O <sub>2</sub> (mg l <sup>-1</sup> )	2.0	1.8	2.5	3.6	3.6	3.1	Log	
pH	6.5	0.7	7.7	1.1	6.9	0.6	Log	EC (+), Alk (+), Na <sup>+</sup> (+), Ca <sup>2+</sup> (+), K <sup>+</sup> (+), Mg <sup>2+</sup> (+)
EC (µS cm <sup>-1</sup> )	670.8	1270.6	1304.7	1226.4	479.2	356.3	Log	pH (+), Alk (+), Cl <sup>-</sup> (+), Na <sup>+</sup> (+), Ca <sup>2+</sup> (+), K <sup>+</sup> (+), Mg <sup>2+</sup> (+), coast (-)
Alkalinity (meq l <sup>-1</sup> )	1.99	2.72	4.96	4.22	1.47	0.82	Log	pH (+), EC (+), Cl <sup>-</sup> (+), Na <sup>+</sup> (+), Ca <sup>2+</sup> (+), K <sup>+</sup> (+), Mg <sup>2+</sup> (+)
Turbidity (NTU)	27	51	17	18	192	385	Log	
O.M. (%)	7.02	6.60	2.63	3.49	6.08	6.00	-	TP-s (+) and TFe-s (+)
Cl <sup>-</sup> (meq l <sup>-1</sup> )	4.20	7.81	8.65	11.83	3.79	2.91	Log	EC (+), Alk (+), Na <sup>+</sup> (+), Ca <sup>2+</sup> (+), K <sup>+</sup> (+), Mg <sup>2+</sup> (+)
Na <sup>+</sup> (meq l <sup>-1</sup> )	3.88	6.47	7.28	7.87	3.19	2.41	Log	EC (+), Alk (+), Cl <sup>-</sup> (+), Ca <sup>2+</sup> (+), K <sup>+</sup> (+), Mg <sup>2+</sup> (+)
Ca <sup>2+</sup> (meq l <sup>-1</sup> )	0.85	1.15	2.19	2.41	0.59	0.47	Log	EC (+), Alk (+), pH (+), Cl <sup>-</sup> (+), Na <sup>+</sup> (+), K <sup>+</sup> (+), Mg <sup>2+</sup> (+)
K <sup>+</sup> (meq l <sup>-1</sup> )	0.16	0.32	0.33	0.38	0.03	0.06	Log	EC (+), Alk (+), pH (+), Cl <sup>-</sup> (+), Na <sup>+</sup> (+), Ca <sup>2+</sup> (+), Mg <sup>2+</sup> (+)
Mg <sup>2+</sup> (meq l <sup>-1</sup> )	0.92	1.34	3.34	3.86	0.71	0.63	Log	EC (+), Alk (+), pH (+), Cl <sup>-</sup> (+), Na <sup>+</sup> (+), Ca <sup>2+</sup> (+), K <sup>+</sup> (+), Mg <sup>2+</sup> (+)
Na <sup>+</sup> /Ca <sup>2+</sup> ratio	14.49	58.08	4.92	4.80	4.93	1.24	Log	
Marsh-coast distance								
Dmarsh (m)	2293	1798	2180	1450	234	410	-	
Dcoast (m)	5097	2529	3085	2099	9523	2806	-	EC (-)

Temporary, temporary ponds; *Zacallones*, artificially deepened ponds; Semip, the semi-permanent pond; *Caños*, ponds filled by the running water of intermittent streams which mainly flow towards the marsh after heavy rains (*N* = number of ponds); Transf., independent transformations to approximate normality (Sqr is square root transformation; Log is Log(*X* + 1) transformation; -, is no transformation required); Rplant, plant richness; Max depth, maximum water depth; Pond area, pond surface area; Pond number, total number of ponds with an extension > 150 m<sup>2</sup> into a 200 m buffer area around each pond; Flooded area, total flooded surface area in a 200 m buffer area around each pond; i-P, dissolved inorganic phosphate; TP-s, sediment total P; TFe-s, total Fe concentration in the sediment; O<sub>2</sub>, dissolved oxygen concentration; EC, electrical conductivity; O.M., organic matter; Dmarsh, the minimum linear distances from each pond to the border of the marsh; Dcoast, the minimum linear distances from each pond to the coast.

<sup>†</sup>Significant Spearman coefficient higher than 0.6 (all *P* < 0.01) indicating variables with positive (+) and negative (-) correlations.