POND CONSERVATION

Inter- and intra-annual variations of macroinvertebrate assemblages are related to the hydroperiod in Mediterranean temporary ponds

**Margarita Florencio · Laura Serrano ·
Carola Gómez-Rodríguez · Andrés Millán ·
Carmen Díaz-Paniagua**

Abstract Macroinvertebrate assemblages of 22 temporary ponds with different hydroperiod were sampled monthly during a dry year (2005–2006) and a wet year (2006–2007). Coleopteran and Heteropteran adults were most abundant at the end of the hydroperiod, while Coleopteran larvae, mainly Dytiscidae, were mostly recorded in spring. Macroinvertebrate assemblages differed between study years. The shorter hydroperiod of ponds in the dry year constrained the length of the aquatic period for macroinvertebrates, and three distinct wet phases of community composition could be distinguished: filling phase, aquatic phase and drying phase. In the wet year, with a longer pond hydroperiod, five phases could be identified, with the aquatic phase differentiated into winter, early spring and late spring phases. Dispersers such as *Anisops sardeus*, *Berosus guttalis* or *Anacaena lutescens* were typical during the filling phase and *Corixa affinis* or *Enochrus fuscipennis* during the drying phase. The ponds with intermediate hydroperiod showed a similar composition (mainly dispersers) at the beginning and end of their wet period; this is not being seen in early drying or long hydroperiod ponds. A general pattern was detected, with similar variation between both years, which may be associated with the life histories of the macroinvertebrate taxa recorded.

Keywords Aquatic macroinvertebrates · Temporal variation · Wet phases · Hydroperiod · Community composition · Life cycle

M. Florencio (✉) · C. Gómez-Rodríguez ·
C. Díaz-Paniagua
Doñana Biological Station-CSIC, P.O. Box 1056,
41080 Seville, Spain
e-mail: margarita@ebd.csic.es

C. Gómez-Rodríguez
e-mail: carola@ebd.csic.es

C. Díaz-Paniagua
e-mail: poli@ebd.csic.es

L. Serrano
Department of Plant Biology and Ecology, University of Seville, P.O. Box 1095, 41080 Seville, Spain
e-mail: serrano@us.es

A. Millán
Department of Ecology and Hydrology, University of Murcia, Campus Espinardo, 30100 Murcia, Spain
e-mail: acmillan@um.es

Introduction

Temporary ponds are optimal habitats for many macroinvertebrate species, being important for the conservation of their specialized fauna (Strayer, 2006). However, these ponds have been frequently neglected in conservation programmes that have traditionally considered protection of extensive wetlands but not of

small water bodies, despite their high biodiversity (Collinson et al., 1995; Céréghino et al., 2008). Moreover, temporary ponds are highly suitable for ecological studies due to their wide environmental gradients of salinity, temperature, vegetation, pH or hydroperiod (Herbst, 2001; Batzer et al., 2004; Waterkeyn et al., 2008; Bilton et al., 2009).

Despite the fact that permanent ponds may contain many aquatic species (Bazzanti et al., 1996; Brooks, 2000; Serrano & Fahd, 2005; Della Bella et al., 2005), temporary ponds usually harbour exclusive species or large populations of species which are scarce in or absent from permanent waters (Collinson et al., 1995; Williams, 1997; Boix et al., 2001; Della Bella et al., 2005; Céréghino et al., 2008). While the dry period may exclude many aquatic organisms from temporary ponds, the absence of large predators, such as fish, is a critical factor that determines the presence of specialist taxa (Wellborn et al., 1996).

Many macroinvertebrate species require an aquatic phase to complete their complex life cycles for which different life history strategies have been reported. Among the most important challenges for the macroinvertebrates of temporary ponds is survival during the dry period. Some adaptations for living in temporary ponds are dispersal to more permanent waters, or resistance of eggs, larvae, or adults to desiccation (Wiggins et al., 1980). Physiological and behavioural mechanisms to survive desiccation have also been described in different aquatic invertebrates (Williams, 2006). Wiggins et al. (1980) segregated groups of macroinvertebrates according to their life history strategies, justifying the presence of specific fauna in different ponds. Differences in the life history strategies of species allow the identification of functional groups which appear at different times in the ponds (Gascón et al., 2008) or to differences in optimal habitats, being able to only complete their life cycles in ponds with a long hydroperiod, but not in ephemeral ponds (Schneider & Frost, 1996).

Annual and seasonal variations of macroinvertebrate assemblages have been reported in temporary ponds (Brooks, 2000) and have been associated with seasonal changes in environmental conditions during the wet phase (Boulton & Lake, 1992). Jeffries (1994) found differences in the macroinvertebrate assemblages of the same ponds in three different years, including a low rainfall year in which ponds did not fill. Different macroinvertebrate groups have

been described as characteristics of different pond phases; usually classified as filling, aquatic and drying phases, out of which the aquatic phase could be further differentiated into three additional phases (Boulton & Lake, 1992; Bazzanti et al., 1996; Boix et al., 2004).

Our study has been carried out in an area in which more than 3000 water bodies support a robust network of aquatic habitats (Fortuna et al., 2006) that exhibit high conservation values and encompass a wide range of hydroperiod and environmental conditions (Gómez-Rodríguez et al., 2009). Several studies have focused on the limnology of these ponds (García Novo et al., 1991; Serrano & Toja, 1995; Serrano et al., 2006) and their use as amphibian breeding sites (Díaz-Paniagua, 1990; Díaz-Paniagua et al., 2005). In contrast, only preliminary data on macroinvertebrates (Agüesse, 1962; Bigot & Marazanof, 1966; Marazanof, 1967; Millán et al., 2005) and studies on abundance of Coleoptera, Heteroptera and Odonata (Montes et al., 1982) have been reported.

In this research, we have studied temporal variation in macroinvertebrate abundance and composition in temporary ponds, with the following specific aims: (1) detecting inter-annual variation; (2) detecting seasonal variation in relation to different phases of the wet period of ponds; (3) comparing monthly variation within ponds of different hydroperiod and (4) determining if there is a general pattern of temporal variation for all ponds in the study area.

Methods

The study was carried out in 22 ponds located in the Doñana Biological Reserve (Doñana National Park, Southwestern Spain, Fig. 1). This area is located between the Atlantic coast and the mouth of the Guadalalquivir River. It includes a high number of temporary ponds, appearing during autumn or winter, and two permanent ponds. The type of climate is Mediterranean sub-humid, with hot and dry summers, mild winters, and rainfall mainly falling in autumn and winter (see Siljeström et al., 1994, García-Novo & Marín, 2006 for a detailed description of the area).

Our study period was from October 2005 to July 2007. Annual rainfall was calculated as the amount of rainfall collected from 1st September to 31st August of the following year. This amounted to 468.3 mm in
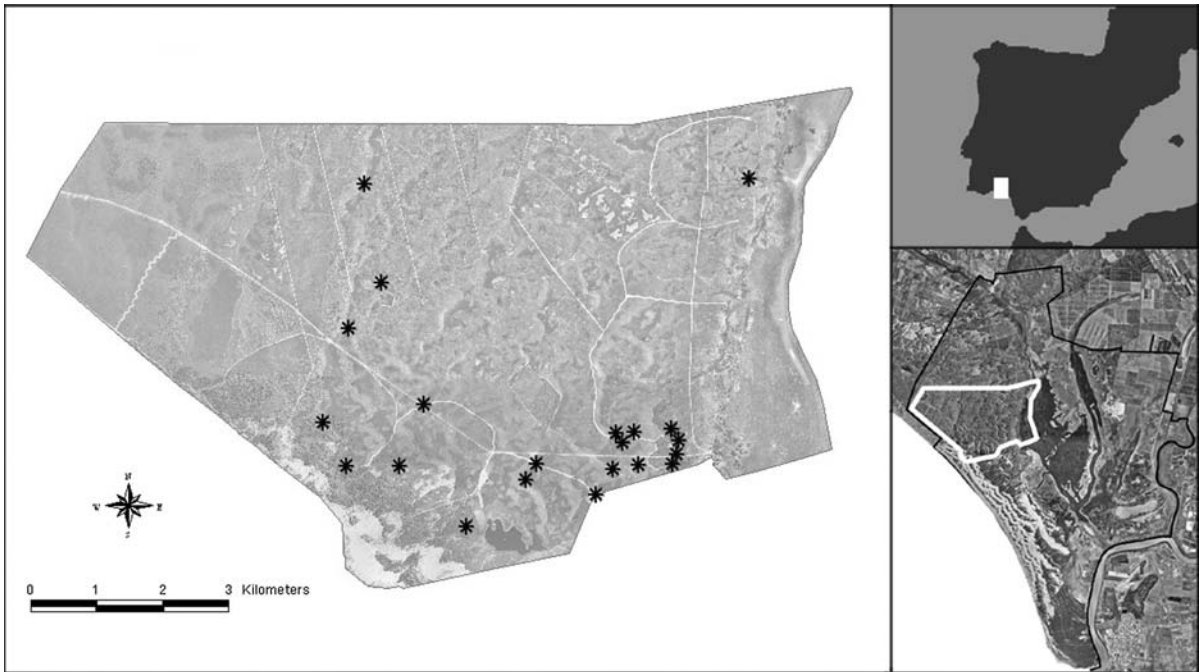
Fig. 1 Location of the 22 temporary ponds in the Doñana Biological Reserve, Doñana National Park (SW Spain)

the first year (hereafter referred to as the dry year), when we sampled 18 temporary ponds which usually dry out every summer and one semi permanent pond which only dries out in years of severe drought. As this pond was dry in 2005, prior to our study period, we considered it as a temporary pond. Ponds were selected to encompass the highest possible range of hydroperiods, being representative of the range of ponds found in the study area. In the second year, annual rainfall was 716.9 mm (hereafter referred to as the wet year) when a higher number of ponds with short hydroperiod were formed in the area. In order to assess the widest range of hydroperiod during the wet year, we sampled three of these new ponds, although the total number of ponds sampled was the same as the year before. In the dry year, most temporary ponds were wet from February to June and from October to July during the wet year, although the ponds with longest hydroperiod had water even during August in both years. A detailed description of the characteristics of Doñana temporary ponds, including most of our study ponds, is given by Gómez-Rodríguez et al. (2009). Hydroperiod and maximum depth of ponds during our study, as well as their basin areas, are shown in Table 1. Pond area was extracted from a pond cartography obtained in a

moment of large inundation (see Gómez-Rodríguez et al., 2008). Vegetation in the ponds was mainly composed of meadow plants as *Mentha pulegium* L., *Illecebrum verticillatum* L. or *Hypericum elodes* L., in the littoral zone, while aquatic macrophytes were common in deeper areas, such as *Juncus heterophyllus* Dufour, *Myriophyllum alterniflorum* DC. in Lam & DC., *Potamogeton pectinatus* L. and *Ranunculus peltatus* Schrank (García Murillo et al., 2006).

Macroinvertebrates were sampled monthly in each pond by using a dip-net with a 1 mm mesh, netting a stretch of water of ∼1.5 m length in each sampling unit. In the wet year, the four ponds with the shortest hydroperiod (including the three ponds only sampled during this year) were sampled every 15 days. In each pond, we sampled at different points along one or two transects from the littoral to the open water, the number of sampling points being proportional to pond size. We also took additional samples in microhabitats which were not represented in these transects. The maximum number of samples per pond ranged from 6 to 13 in the month of maximal inundation. As pond size decreased during the season, the number of samples taken was reduced accordingly. Most macroinvertebrates captured were identified in situ, being counted and released. Individuals of unidentified

Table 1 Hydroperiod and maximum depth of every pond (named with *three letters*) are shown for the dry year and wet year, and also the pond area calculated in a large inundation moment (hydroperiod is only given for the year in which each pond was sampled)

Pond	Hydroperiod (months)		Maximum depth (cm)		Pond area (m²)
	Dry year	Wet year	Dry year	Wet year	Maximum inundation
Pol	3.1	7.2	33	50	1,200
Acm	3.3	6.4	34	44	50
Rp	2.1	7.2	24	64	4,075
Pg	3.1	7.2	31	54	3,925
Jim	2.2	7.2	9.5	86	39,900
Cam	2.7	7.2	23	55	2,200
Zah	3.8	9.1	47	69	48,189
Lve	6.1	12	104	132	3,300
Dul	8.9	12	142	165	122,672
Abe	2.3	6.9	18	43	50
Bre	3.4	7.9	47	85	2,150
Pp	3.1	7.2	42	82	875
Tej	2.8	7.2	22	67	150
Orf	4.3	9	80	82	850
Ant	1.4	6.8	15	45	5,131
Wou	3.4	–	31.5	–	14,375
Mor	3.2	–	25	–	14,725
Tar	4.4	–	55	–	81,250
Arm	–	4.2	–	21	25
Vac	0.4	6.2	–	51	25
Len	–	5.5	–	24	650
Tps	–	6.1	–	39	6,375

species were preserved in 70% ethanol for identification in the laboratory. Whenever possible, individuals were identified to species level, except for Diptera, which were identified to family. For Chironomidae and Ceratopogonidae, only presence–absence data were recorded. All recorded taxa with only presence–absence data were not included in analyses.

For the analysis of the macroinvertebrate assemblage composition, we estimated the relative abundance of each taxon, as the total number of individuals captured across all samples taken in a pond, divided by the total number of samples taken in that pond. In these analyses, we differentiated adults from larvae or nymphs, and considered these as different taxa (hereafter referred to as "taxa" for simplicity) in our data matrix. Relative abundance was log transformed

$(X + 1)$ to calculate the similarity matrix with the Bray–Curtis similarity index (Clarke & Warwick, 2001).

For each pond, we computed the Spearman correlations between the corresponding taxa of each pair of similarity matrices of relative abundances in different months, using the RELATE program (Primer v.6, Clarke & Warwick, 2001) to assess *monthly variation in the macroinvertebrate assemblages within ponds*. The Spearman correlation coefficient (ρ) was close to one when the monthly similarity matrices were highly corresponding. These analyses detected if the similarity among the composition of macroinvertebrates was higher in subsequent months (Serial RELATE) than in more distant months, such as the beginning and the end of each hydroperiod (Cyclic RELATE). Similarity distances among months were represented using non-metric multidimensional scaling (NMDS). As pond hydroperiod was relatively short in the dry year, these analyses of monthly variation of macroinvertebrate assemblages were performed only for the wet year.

In order to assess *seasonal variation* in macroinvertebrate assemblages, we used a NMDS representation of the similarity matrices of relative abundances of all ponds and months except for the February matrix of one pond in the dry year which had been previously filled. The different groups observed in the NMDS were used as grouping factor including three or five levels depending on number of observed groups in every case. We then tested differences among observed groups using one-way ANOSIM analyses (performed with 9999 number of permutations). The ANOSIM test statistic, R, is close to 1 when the levels of grouping factor are different; that is to say, all dissimilarities between levels of grouping factor are larger than any dissimilarity among samples in every level of grouping factor (Clarke & Warwick, 2001). An exploratory analysis (SIMPER) was used to detect those taxa with the highest contribution to the dissimilarity of each level of grouping factor versus all other levels for the same factor (Primer v.6, Clarke & Warwick, 2001).

In order to explore particular questions about the temporal variation of macroinvertebrate assemblages, we averaged the relative abundances of macroinvertebrates in different ways. (1) To analyse *inter-annual variation* between the dry year and wet year, we averaged the relative abundance of macroinvertebrate taxa every year by dividing by the numbers of months that every pond was sampled. These averaged matrices were represented in NMDS to observe whether both

years corresponded to different groups. We tested if macroinvertebrate assemblages were different in two study years through one-way ANOSIM analysis, using the year as groping factor with two levels. SIMPER analysis detected those taxa making a higher contribution to dissimilarity between the two years (Primer v.6, Clarke & Warwick, 2001). We removed the macroinvertebrate assemblages of two ponds sampled in the dry year of these analyses and NMDS representation because they only were sample once, not being comparable with the rest of ponds in both years. (2) To analyse if *a general pattern of monthly variation* occurred in both study years, we averaged the relative abundance of individual taxa across all ponds every month by dividing by the number of sampled ponds per month. Then, we used only one averaged matrix of relative abundance of macroinvertebrates per month, representing a unique similarity value per month in a NMDS. The Spearman correlation between these monthly similarity values for the average matrix of relative abundance of macroinvertebrates across all ponds was calculated for each year through a Serial RELATE. The Spearman correlation coefficient value (ρ) would be 1 in case of maximum correlation. Prior to these analyses, we tested whether the variation among months was higher than among ponds within a month, using the complete relative abundance matrix of both study years through a one-way ANOSIM analysis where months in every year were the grouping factor with a total of 18 levels.

Monthly matrices of relative abundance of macroinvertebrates were not included in the analyses when any or very scarce abundances were detected in a pond (mainly during the initial stages of annual sampling). Some taxa had to be combined to compare between years, because some species were not identified during the first year (adults of all species of *Haliplus* were included in one taxon, as were adults of Corixidae, except for *Corixa affinis* Leach, 1817).

Results

Macroinvertebrate taxa and their monthly variation

The macroinvertebrates recorded in the Doñana ponds included 123 different taxa, including 97 species, and additionally unidentified species included in 6 genera,

16 families, 3 subfamilies and 1 order. The most abundant species were *C. affinis*, *Cloeon* spp. and *Anisops sardeus* Herrich-Schäffer, 1849, while other species such as *Coenagrion scitulum* (Rambur, 1842) appeared occasionally and with very low abundance (Table 2). Coleoptera, Heteroptera and Odonata were the orders that included the highest number of species and individuals during both years. The monthly variation of the average number of individuals caught in all the samples during both years is shown in Fig. 2. Adults of Coleoptera and Heteroptera showed the highest abundance both at the end of the wet period and at the beginning during the wet year. Dytiscidae and Hydrophilidae were the most abundant families of Coleoptera. Larvae of Coleoptera (mainly Dytiscidae) were found in the middle of the wet period, while the highest abundance of Coleoptera was reached by adults of Hydrophilidae at the end of the wet period, in July during the wet year and in May during the dry year, when ponds had shorter hydroperiod. Adults of Heteroptera (mainly Corixidae and Notonectidae) reached their highest abundance in ponds with longer hydroperiods in summer. *A. sardeus* and *C. affinis* were the most abundant heteropterans; *C. affinis* being much more abundant during the wet year than the dry year. Among Odonata, Libellulidae [mainly *Sympetrum fonscolombei* (Selys, 1841)] were found throughout the wet period, while Coenagrionidae [mainly *Ischnura pumilio* (Charp., 1825)] were especially abundant at the end of this.

Inter-annual variation

Macroinvertebrate compositions of every pond were segregated in two groups corresponding with both study years, although the dissimilarity between the dry year and the wet year was not very strong (ANOSIM: $R = 0.235$; $P = 0.02$) (Fig. 3). SIMPER analyses showed that adults of *Hydroglyphus geminus* (Fabricius, 1792) (13.67%), *Anacaena lutescens* (Stephens, 1829) (13.64%) and Notonectidae larvae (10.91%) mainly contributed to these differences in the dry year, while *Cloeon* spp. (11%) and adults of *A. sardeus* (10.81%) had a larger contribution in the wet year.

Seasonal variation

During the dry year, we observed three groups in the NMDS composed by different macroinvertebrate

Table 2 Taxa of macroinvertebrates recorded in the study ponds during both years

Taxa	Family	Average		Maximum	
		Adult	Larva	Adult	Larva
Acari					
Hydrachnellae	–	0.029		11	
Bassomatophora					
Physa spp.	Physidae	1.849		446	
Planorbidae	Planorbidae	1.486		259	
Coleoptera					
Donacia spp.	Chrysomelidae	[a]		[a]	
Bagous spp.	Curculionidae	0.017		3	
Bagous revelieri Tournier, 1884[b]	Curculionidae	[a]		[a]	
Bagous subcarinatus Gyllenhal, 1836[b]	Curculionidae	[a]		[a]	
Bagous vivesi González, 1967[b]	Curculionidae	[a]		[a]	
Dryops luridus (Erichson, 1847)	Dryopidae	[a]		[a]	
Dryops spp.	Dryopidae	0.602	0.01	54	2
Agabus bipustulatus (Linnaeus, 1767)	Dytiscidae	[a]		[a]	
Agabus conspersus (Marsham 1802)	Dytiscidae	0.026		5	
Agabus didymus (Olivier, 1795)	Dytiscidae	0.001		1	
Agabus nebulosus (Forster, 1771)	Dytiscidae	0.012		3	
Agabus spp.	Dytiscidae		0.397		19
Cybister (*Scaphinectes*) *lateralimarginalis* (De Geer, 1774)	Dytiscidae	0.014	0.025	3	2
Dytiscus circumflexus Fabricius, 1801	Dytiscidae	0.001	0.02	1	2
Eretes griseus (Fabricius, 1781)	Dytiscidae	0.001		1	
Graptodytes flavipes (Olivier, 1795)	Dytiscidae	0.004		1	
Hydaticus (*Guignotites*) *leander* (Rossi, 1790)	Dytiscidae	0.001	0.001	1	1
Hydroglyphus geminus (Fabricius, 1792)	Dytiscidae	0.516		92	
Hydroporus gyllenhali Schiödte, 1841	Dytiscidae	0.023		5	
Hydroporus lucasi Reiche, 1866	Dytiscidae	0.079		22	
Hygrotus confluens (Fabricius, 1787)	Dytiscidae	0.012		3	
Hygrotus lagari (Fery, 1992)	Dytiscidae	0.478		47	
Hydroporus spp. or *Hygrotus* spp.	Dytiscidae		0.151		12
Hyphydrus aubei Ganglbauer, 1892	Dytiscidae	0.009	0.033	2	5
Ilybius montanus (Stephens, 1828)	Dytiscidae	0.003		1	
Laccophiluis minutus (Linnaeus, 1758)	Dytiscidae	0.171	0.358	65	33
Liopterus atriceps (Sharp, 1882)	Dytiscidae	0.044		15	
Rhantus (*Rhantus*) *hispanicus* Sharp, 1882	Dytiscidae	0.063		5	
Rhantus (*Rhantus*) *suturalis* (McLeay, 1825)	Dytiscidae	0.02		6	
Colymbetes fuscus (Linnaeus, 1758)	Dytiscidae	0.063		19	
Rhantus spp. or *Colymbetes fuscus*	Dytiscidae		0.442		18
Gyrinus (*Gyrinus*) *dejeani* Brullé, 1832	Gyrinidae	0.007	0.007	1	1
Haliplus (*Liaphlus*) *andalusicus* Wehncke, 1874	Haliplidae	0.018		4	
Haliplus (*Liaphlus*) *guttatus* Aubé, 1836	Haliplidae	0.01		2	
Haliplus (*Neohaliplus*) *lineatocollis* (Marsham, 1802)	Haliplidae	0.008		2	
Haliplus spp.	Haliplidae		0.020		3
Helophorus spp.	Helophoridae	0.367	0.001	93	1

Table 2 continued

Taxa	Family	Average		Maximum	
		Adult	Larva	Adult	Larva
Helophorus (*Trichohelophorus*) *alternans* Gené, 1836	Helophoridae	a		a	
Helophorus (*Rhopalohelophorus*) *longitarsis* Wollaston, 1864	Helophoridae	a		a	
Hydraena (*Hydraena*) *rugosa* Mulsant, 1844	Hydraenidae	0.012		2	
Limnebius furcatus Baudi, 1872	Hydraenidae	0.001		1	
Ochthebius (*Asiobates*) *dilatatus* Stephens, 1829	Hydraenidae	0.018		9	
Ochthebius (*Ochthebius*) *punctatus* Stephens, 1829	Hydraenidae	0.004		1	
Ochthebius (*Ochthebius*) *auropallens* Fairmaire, 1879	Hydraenidae	0.060		17	
Hydrochus flavipennis Küster, 1852	Hydrochidae	0.029		12	
Anacaena (*Anacaena*) *lutescens* (Stephens, 1829)	Hydrophilidae	1.165		421	
Berosus (*Berosus*) *affinis* Brullé, 1835	Hydrophilidae	0.455		136	
Berosus (*Enoplurus*) *guttalis* Rey, 1883	Hydrophilidae	0.165		13	
Berosus (*Berosus*) *signaticollis* (Charpentier, 1825)	Hydrophilidae	0.201		12	
Berosus spp.	Hydrophilidae		0.084		5
Enochrus (*Lumetus*) *bicolor* (Fabricius, 1792)	Hydrophilidae	0.059		6	
Enochrus (*Lumetus*) *fuscipennis* (C.G. Thomsom, 1884)	Hydrophilidae	1.192		242	
Enochrus spp.	Hydrophilidae		0.007		1
Helochares (*Helochares*) *lividus* (Forster, 1771)	Hydrophilidae	0.029		14	
Hydrobius convexus Brullé, 1835	Hydrophilidae	a		a	
Hydrobius fuscipes (Linnaeus, 1758) & *Limnoxenus niger* (Zschach, 1788)	Hydrophilidae	0.369		40	
Hydrobius spp. or *Limnoxenus niger*	Hydrophilidae		0.084		21
Hydrochara flavipes (Steven, 1808)	Hydrophilidae	0.023	0.007	6	2
Hydrophilus (*Hydrophilus*) *pistaceus* (Laporte, 1840)	Hydrophilidae	0.001	0.007	1	2
Laccobius (*Hydroxenus*) *revelierei* Perris, 1864	Hydrophilidae	0.003		2	
Paracymus scutellaris (Rosenhauer, 1856)	Hydrophilidae	0.222		110	
Hygrobia hermanni (Fabricius, 1775)	Paelobiidae	0.029	0.107	12	8
Noterus laevis Sturm, 1834	Noteridae	0.019		11	
Hydrocyphon spp.	Scirtidae		0.019		4
Decapoda					
Procambarus clarkii (Girard, 1852)	Cambaridae		0.027		7
Ephemeroptera					
Cloeon spp.	Baetidae		6.179		394
Haplotaxida					
Lumbricidae & Sparganophilidae	Lumbricidae & Sparganophilidae		a		a
Tubificidae	Tubificidae		a		a
Heteroptera					
Corixa affinis Leach, 1817	Corixidae	8.879		2209	
Micronecta scholzi (Fieber, 1860)	Corixidae	0.001		1	
Paracorixa concinna (Fieber, 1848)	Corixidae	0.006		3	
Sigara (*Vermicorixa*) *lateralis* (Leach, 1817)	Corixidae	0.391		59	
Sigara (*Vermicorixa*) *scripta* (Rambur, 1840)	Corixidae	0.04		14	
Sigara (*Halicorixa*) *selecta* (Fieber, 1848)	Corixidae	0.003		1	

Table 2 continued

Taxa	Family	Average		Maximum	
		Adult	Larva	Adult	Larva
Sigara (*Halicorixa*) *stagnallis* (Leach, 1817)	Corixidae	0.037		6	
Trichocorixa verticalis (Fieber, 1851)	Corixidae	0.009		2	
Corixidae spp.	Corixidae		1.258		99
Gerris (*Gerris*) cf. *maculatus* Tamanini, 1946	Gerridae	0.002		1	
Gerris (*Gerris*) *thoracicus* Schummel, 1832	Gerridae	0.229		2	
Gerris spp.	Gerridae		0.282		12
Microvelia pygmaea (Dufour, 1833)	Microveliidae	0.011		2	
Naucoris maculatus Fabricius, 1798	Naucoridae	0.01	0.03	5	12
Nepa cinerea Linnaeus, 1798	Nepidae	0.008	0.009	5	6
Anisops sardeus Herrich-Schäffer, 1849	Notonectidae	3.704		272	
Notonecta glauca Linnaeus, 1758 ssp. *glauca*	Notonectidae	0.025		4	
Notonecta glauca Linnaeus, 1758 ssp. *meridionalis* Poisson, 1926	Notonectidae	0.039		4	
Notonecta maculata Fabricius, 1794	Notonectidae	0.011		3	
Notonecta viridis Delcourt, 1909	Notonectidae	0.029		6	
Notonectidae spp.	Notonectidae		1.219		91
Plea minutissima Leach, 1817	Pleidae	0.677	0.208	130	38
Saldidae	Saldidae	0.018		12	
Isopoda					
Asellus aquaticus (Linnaeus, 1758)	Asellidae	0.014		11	
Lumbriculida					
Lumbriculidae	Lumbriculidae	[a]		[a]	
Notostraca					
Triops mauritanicus (Ghigi, 1921)	Triopsidae	0.055		6	
Spinicaudata					
Cyzicus grubei Simon, 1886	Cyzicidae	[a]		[a]	
Maghrebestheria maroccana Thiéry, 1988	Leptestheriidae	[a]		[a]	
Anostraca					
Branchipus cortesi Alonso y Jaume, 1991	Branchipodidae	[a]		[a]	
Branchipus schafferi Fischer de Waldheim, 1834	Branchipodidae	[a]		[a]	
Tanymastix stagnalis (Linnaeus, 1758)	Tanymastigiidae	[a]		[a]	
Chirocephalus diaphanus Desmarest, 1823	Chirocephalidae	[a]		[a]	
Odonata					
Aeshna affinis Vander Linden, 1823	Aeshnidae		0.005		1
Aeshna mixta Latreille, 1805	Aeshnidae		0.012		2
Anax imperator Leach, 1815	Aeshnidae		[a]		[a]
Hemianax (*Anax*) *ephippiger* (Burmeister, 1839)	Aeshnidae		0.003		1
Coenagrion scitulum (Rambur, 1842)	Coenagrionidae		0.001		1
Ishnura elegans (Vander Linden, 1820)	Coenagrionidae		0.052		9
Ishnura pumilio (Charp., 1825)	Coenagrionidae		0.525		50
Lestes barbarus (Fabr., 1798)	Lestidae		0.028		16
Lestes dryas Kirby, 1890	Lestidae		0.008		2
Lestes macrostigma (Eversm., 1836)	Lestidae		0.001		1
Lestes virens (Charpentier, 1825)	Lestidae		0.002		1

Table 2 continued

Taxa	Family	Average		Maximum	
		Adult	Larva	Adult	Larva
Crocothemis erythrarea (Brullé, 1832)	Libellulidae		0.033		5
Sympetrum fonscolombei (Selys, 1841)	Libellulidae		0.252		9
Sympetrum meridionale (Selys, 1841)	Libellulidae		0.024		3
Sympetrum sanguineum (Müller, 1764)	Libellulidae		0.038		5
Sympetrum striotalum (Charpentier, 1840)	Libellulidae		0.048		4

Taxa	Family	Average		Maximum	
		Larva	Nymph	Larva	Nymph
Diptera					
Ceratopogoninae	Ceratopogonidae	[a]		[a]	
Chaoborus spp.	Chaoboridae	[a]		[a]	
Chironomidae sp.	Chironomidae	[a]	0.001	[a]	1
Chironomus plumosus	Chironomidae	[a]	0.001	[a]	1
Culicidae	Culicidae	0.567	0.132	253	8
Dixa spp.	Dixidae	0.01	0.004	2	2
Dolichopodidae	Dolichopodidae	0.016		11	
Ephydridae	Ephydridae	0.023	0.013	12	4
Orthocladiinae	Chironomidae	[a]		[a]	
Rhagionidae	Rhagionidae	0.009		2	
Scatophagidae	Scatophagidae	0.001		1	
Sciomyzidae	Sciomyzidae	0.001		1	
Syrphidae	Syrphidae	0.005	0.004	3	2
Tabanidae	Tabanidae	0.005		1	
Tanypodinae	Chironomidae	[a]	0.001	[a]	1
Thaumelidae	Thaumelidae		0.001		1
Tipulidae	Tipulidae	0.011	0.004	2	2

Average and maximum number of individuals per sample is shown for adults, larvae and nymphs

[a] Only presence was recorded

[b] New records for Doñana National Park

compositions detected in every pond and month, which corresponded to different wet phases of the ponds (Fig. 4): filling phase (February), aquatic phase (March and April) and drying phase (May–September) (ANOSIM, global $R = 0.615$, $P = 0.01$). In the aquatic phase, we also distinguished a weak segregation in two subgroups: early spring (March) and late spring (April) phases (ANOSIM, $R = 0.297$, $P = 0.02$). We identified the main taxa that contributed to the dissimilarity of the three phases with a SIMPER analysis: Adults of *Berosus affinis* Brullé, 1835 (17.32%), *Helophorus* spp. (17.24%), *A. lutescens* (15.74%), Corixidae (without *C. affinis*) (12.52%) and *Dryops* spp. (11.97%) in the filling phase; Notonectidae larvae (14.14%) and adults of *H. geminus* (13.69%) in the aquatic phase; adults of Corixidae (without *C. affinis*) (25.83%) and *A. sardeus* (19.18%) in the drying phase. During the wet year, we observed five consecutive groups of macroinvertebrates compositions of every pond and month in the NMDS that corresponded to different wet phases (Fig. 4): filling phase (November), winter (December and January), early spring (February and March), late spring (April) and drying phase (May–August). The wet phases presented different similarities according to an ANOSIM analysis (global $R = 0.538$, $P = 0.01$).
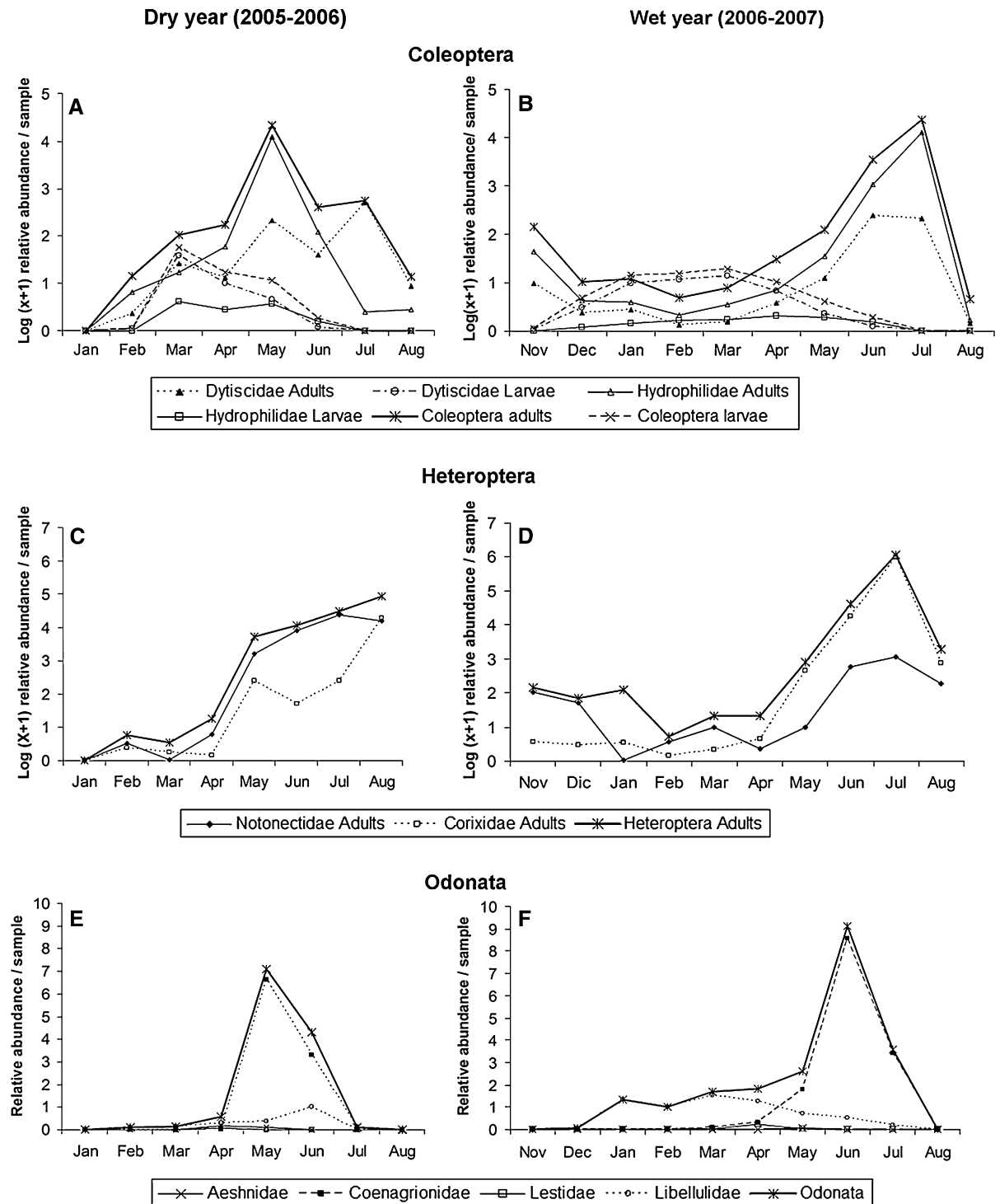
Fig. 2 Monthly variation in the relative abundance of individuals of different taxa of macroinvertebrates averaging data of all ponds in a dry year and a wet year: Coleoptera (**A**, **B**), Heteroptera (**C**, **D**) and Odonata (**E**, **F**)
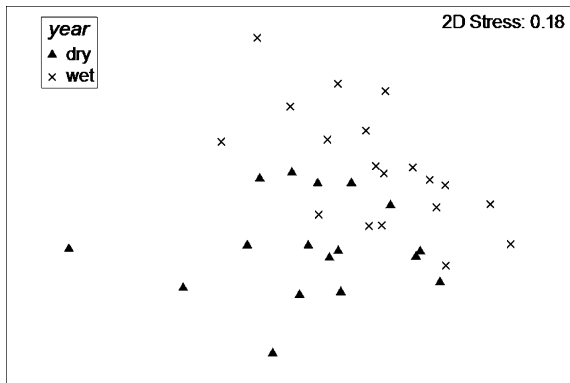
Fig. 3 NMDS ordination of the relative abundance of macroinvertebrates in every pond, showing their inter-annual variation. It is averaging the number of individuals per month in the dry year and the wet year
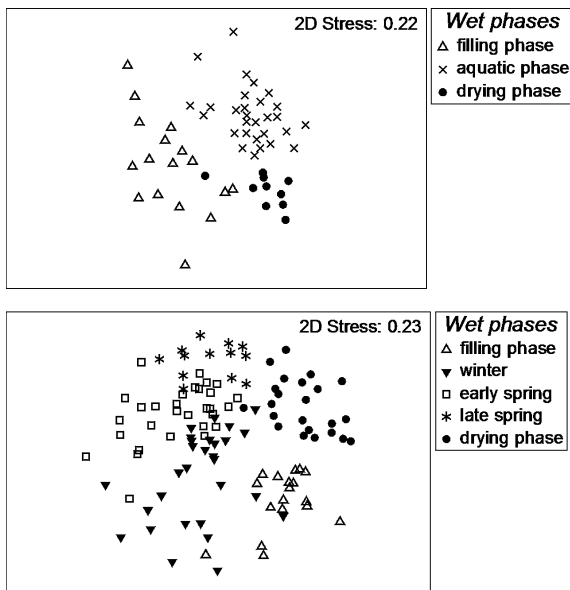

Fig. 4 NMDS ordination of the relative abundance of macroinvertebrates in different ponds and months during the dry year (top) and wet year (bottom). Different phases identified are indicated on the plot

The highest R value in the pairwise comparison of wet phases during the wet year was for filling phase versus early spring ($R = 0.826$; $P = 0.01$) and filling phase versus late spring ($R = 0.912$; $P = 0.01$). SIMPER analysis revealed that the taxa with highest contribution to global dissimilarity were: adults of *A. sardeus* (23.90%) and *Berosus guttalis* Rey, 1883 (12.30%) in the filling phase; *A. sardeus* (adults) (31.41%) and *Cloeon* spp. (19.34%) in the winter phase; *Cloeon* spp.

(39.79%) in the early spring phase; *Gerris* spp. larvae (14.04%), Notonectidae larvae (11.94%) and *Cloeon* spp. (11.93%) in the late spring phase; and adults of *C. affinis* (25.15%) and *Enochrus fuscipennis* (C.G. Thomsom, 1884) (10.44%) in the drying phase.

Monthly variation of macroinvertebrate assemblages within ponds

In the wet year, the Spearman correlations comparing the similarity matrices of monthly macroinvertebrate assemblages in each pond tended to present higher ρ values in serial than in cyclic correlations in 13 ponds (Table 3; Fig. 5A). In contrast, in five ponds they tended to present higher cyclic correlations (Table 3; Fig. 5B). In one pond, the ρ value for these similarity

Table 3 The Spearman correlation coefficients (ρ) calculated among monthly macroinvertebrate assemblages in each pond (Serial and Cyclic RELATE analyses) during the wet year

	Spearman's correlation (ρ)			
Pond	Monthly		Every 15 days	
	Serial	Cyclic	Serial	Cyclic
Pol	**0.732** (7)	0.491** (7)		
Acm	**0.627** (6)	0.466* (6)		
Rp	**0.618** (7)	0.472** (7)		
Pg	**0.736** (7)	0.616** (7)		
Jim	**0.757** (7)	0.478** (7)		
Cam	**0.641** (7)	0.287** (7)		
Zah	**0.881** (9)	0.658** (9)		
Lve	**0.653** (10)	0.614** (10)		
Dul	**0.724** (12)	0.665** (12)		
Abe	**0.593* (7)**	0.549** (7)		
Bre	0.241 (9)	**0.474** (9)		
Pp	0.511* (7)	**0.636** (7)		
Tej	0.555* (7)	**0.742** (7)		
Orf	0.391* (9)	**0.471** (9)		
Ant	0.35 (6)	0.086* (6)		
Arm	0.156 (6)	0.362 (6)	0.309 (8)	**0.428* (8)**
Vac	**0.724** (7)	0.684** (7)	**0.553** (11)	0.42** (11)
Len	0.736* (7)	0.736* (7)	**0.509** (10)	0.358** (10)
Tps	**0.583** (6)	0.265* (6)	**0.506** (10)	0.291* (10)

For ponds sampled every 15 days, both monthly and 15-day analyses are shown. Number of samples in each correlation analysis is given in *brackets*. * $P < 0.05$; ** $P < 0.01$. The highest significant ρ value (cyclic or serial correlations) for each pond is marked in *bold*
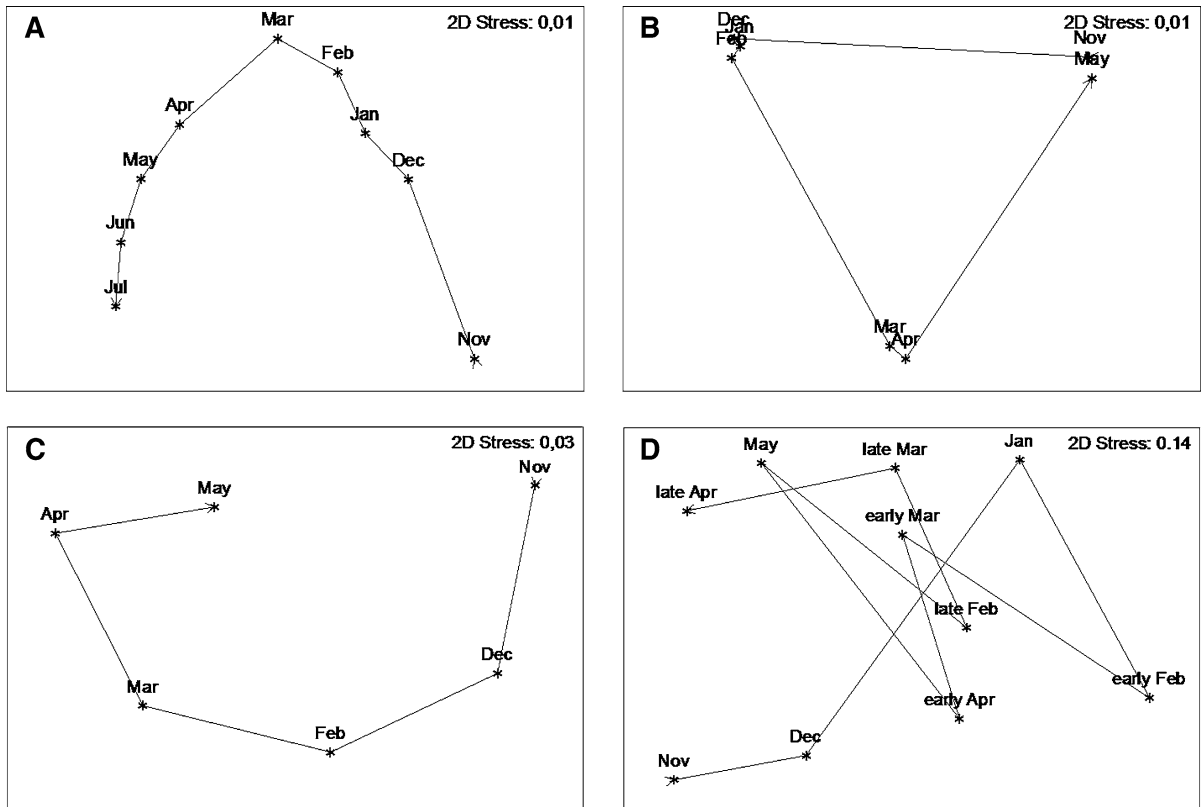
Fig. 5 Monthly variation of the macroinvertebrate assemblage in three different temporary ponds (**A**, **B**, **C**) represented in a NMDS during the wet year. Pond **A** (Zah) presented a higher serial correlation while **B** (Pp) presented a higher cyclic correlation. **C** and **D** show the same pond (Len) with monthly samples (**C**) and 15-day samples (**D**). Pond shown in **C** and **D** was occasionally dried in January when we could not record data for the monthly sample (**C**), but only for the 15-day samples (**D**)
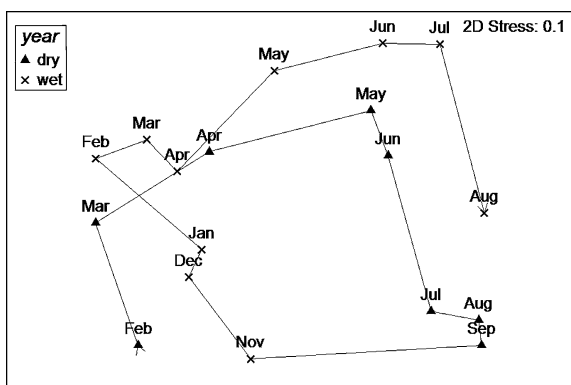
Fig. 6 NMDS ordination of the relative abundance of macroinvertebrates showing monthly variation after averaging across all the study ponds per month in the consecutive dry year and wet year

matrices was not significant in the case of serial correlation and was very low in the case of cyclic correlation (Table 3). The correlations were higher in

three of the four ponds sampled monthly compared to every 15-day sampled ponds. In these three ponds, monthly macroinvertebrate assemblages presented higher serial than cyclic correlations, while in one pond they only presented a significant cyclic correlation for 15-day samples (Table 3). These ponds exhibited a high variability among 15-day samples in the NMDS representation, pointing out their fluctuating trajectory which was not detected among monthly samples (Fig. 5D, C).

General pattern of monthly variation in the macroinvertebrate community

We detected differences in the macroinvertebrate assemblages of all ponds and months using the sampling month in both study years as grouping factor, with an ANOSIM analysis (global $R = 0.475$, $P = 0.01$). It showed that the variation among months

was higher than among ponds for each month. The monthly variation of the community showed a similar pattern in both years, observed in the NMDS representation. The highest similarity was found between the months of April of both years (Fig. 6). The monthly macroinvertebrate community presented a strong serial correlation (Serial RELATE) in both the dry year ($\rho = 0.916$; $P = 0.01$) and the wet year ($\rho = 0.788$; $P = 0.01$).

Discussion

Macroinvertebrate fauna of temporary ponds

Our temporary ponds had a rich macroinvertebrate fauna with similar or even higher richness than other temporary (Schneider & Frost, 1996; Bazzanti et al., 1996; Brooks, 2000; Boix et al., 2001) or permanent ponds (Heino, 2000; Della Bella et al., 2005). The high richness found in our study does not correspond to a single pond, but to a system of temporary ponds which allow movement and dispersal of individuals among ponds (Fortuna et al., 2006). In this kind of systems, the high connectivity and non-fragmentation area are very important factors to conserve their invertebrate biodiversity (Briers & Biggs, 2005; Van de Meutter et al., 2006). In the past, temporary ponds were usually excluded from conservation plans for wetlands, neglecting the diversity of their associated fauna due to their small size and temporal behaviour (Williams et al., 2001; Grillas et al., 2004; Williams, 2006; Zacharias et al., 2007). The high richness of macroinvertebrates in temporary ponds justifies the necessity of their conservation, this also being important since they include different fauna from permanent aquatic habitats, including many rare species (Collinson et al., 1995). These temporary habitats also allow the occurrence of many species which are vulnerable to predation and adapted to survive their characteristic dry phase (Wellborn et al., 1996; Williams, 2006).

Inter-annual variation

Temporary ponds are fluctuating habitats, and in this study we have detected significant changes in their macroinvertebrate composition. Many physical characteristics of temporary ponds are widely dependent on rainfall, with important variation from dry year to wet year. Consequently, macroinvertebrate assemblages may differ among wet year and dry year (Jeffries, 1994). Historical events, such as very dry years, may affect the macroinvertebrate community composition as much as site-specific abiotic differences among ponds (Boulton & Lake, 1992). Between our dry and wet study years, the same ponds differed in their hydroperiod, as well as in water depth and area, and accordingly we also found significant differences in the macroinvertebrate composition between years, despite these being consecutive. The shorter hydroperiod of the ponds in the dry year constrained the length of the aquatic period for macroinvertebrates. Thus, the occurrence of larvae of Coleoptera and Odonata was more concentrated and we detected differences in the peak of abundance of Coleoptera and Odonata that occurred in May in the dry year, 1 or 2 months earlier than in the wet year (June–July).

Seasonal variation

From filling to desiccation, temporary ponds experience large physicochemical variations (García Novo et al., 1991; Serrano & Toja, 1995; Gómez-Rodríguez et al., 2009), characterizing different phases according to the wet period (Bazzanti et al., 1996). Particular macroinvertebrate compositions have been described as characteristic of different wet phases of such ponds. They are explained as a consequence of the changes experienced in these aquatic habitats, which present optimal environmental conditions for different macroinvertebrates (Boulton & Lake, 1992; Boix et al., 2004; Culioli et al., 2006). In fact, different taxa of macroinvertebrates show wide differences in their life strategies, such as in reproduction, feeding, development or dispersal, and other particularities of their life cycle (Bilton et al., 2001; Williams, 2006; Verberk et al., 2008). The macroinvertebrate groups obtained in the NMDS representation of ponds and months also revealed this variation in macroinvertebrate assemblages (including adults, larvae and nymphs), changing through the different wet phases of the ponds. However, the shorter pond hydroperiod of the dry year also reduced the number of phases observed in this year relative to the wet year. During the dry year, only three distinct phases were identified: filling phase, aquatic phase and drying phase, while during the wet year, five phases were detected: filling phase, winter, early spring, late spring phases (aquatic phase) and

drying phase. The reduction of the number of phases in years of low rainfall causes macroinvertebrates to synchronize their life histories (Wiggins et al., 1980; Nilsson, 2005b) concentrating biological processes into the short hydroperiod available. In ponds with very short hydroperiods, the number of phases may be even lower than three (Boix et al., 2004). In dry years, organisms with long life cycles may be the taxa most affected by short hydroperiods, as they cannot successfully complete their aquatic development (Schneider & Frost, 1996; Taylor et al., 1999).

The filling phase, just after pond formation, is characterized by the arrival of coleopterans and heteropterans through dispersal from other (more permanent) ponds (Wiggins et al., 1980). The taxa most characteristic of this phase did not coincide in our two study years, probably because the date of filling occurred in different seasons in both years, affecting the activity cycles of the species. We also found other macroinvertebrates taxa that usually spend the dry period in the mud, such as adults of *Berosus signaticollis* (Charpentier, 1825) (Boix et al., 2001) or adults of some species of Hydrophilidae which have a period of flight to colonize new habitats in newly filled ponds (Wiggins et al., 1980; Hansen, 2005; Williams, 2006).

The aquatic phase was longer in the wet year, and also the species characteristic of this or these phases were different among years, except for Notonectidae larvae which mostly appeared in the late spring phase of the wet year, having their peak abundance in the same month of the dry year. The environmental conditions of the wet year appear to have favoured particular species, such as *Cloeon* spp., which was very abundant in the wet year, being the only taxon characteristic of the three phases, winter, early and late spring that constituted the aquatic phase of this year. In contrast, its abundance was not high during the dry year.

The taxa most characteristics of the drying phases of both years did not coincide either in both study years, although adult corixids were characteristic of this phase in both the dry year and wet year. In the drying phase, adult heteropterans and coleopterans were the most common taxa in our study ponds, as described in other studies (Boulton & Lake, 1992; Culioli et al., 2006; Garrido & Munilla, 2008). Some beetles and almost all hemipterans possess excellent dispersal capabilities (Wiggins et al., 1980; Bilton et al., 2001). The high abundance of these taxa may be explained by the arrival of dispersers, moving from dry ponds to other ponds while dispersing to more permanent habitats to survive during dry periods (Wiggins et al., 1980; Higgins & Merrit, 1999; Bilton et al., 2001, Williams, 2006). We observed some dispersing individuals landing in some of our study ponds during the drying phase, such as *Colymbetes fuscus* (Linnaeus, 1758), *Gerris thoracicus* Schummel, 1832, and *C. affinis*. In the dry phase, as well as in the filling phase, the increase in number of species recorded in particular ponds were mainly due to dispersers, as reported for summer and autumn seasons by Verberk et al. (2005).

Monthly variation of macroinvertebrate assemblages within ponds

The variation of the macroinvertebrate composition in the ponds was not only attributable to differences between a wet and a dry year, or to the wet phases. Our study ponds had been chosen within a wide hydroperiod gradient, and while most of them filled in approximately the same month of each year, they clearly differed in the timing of desiccation, with some ponds drying earlier than others. As a consequence of the different desiccation times of the ponds, we observed different monthly variation in macroinvertebrate assemblages: some ponds showing cyclic correlation with similar assemblage composition at the beginning and the end of the hydroperiod, while others differed at these two phases, showing serial correlations instead. These differences may be explained in relation to the capability of many species to move between ponds via dispersal (Bilton et al., 2001; Rundle et al., 2002; Williams, 2006). At the end of hydroperiod, many Dytiscidae and Hydrophilidae suddenly leave the water, dispersing to more permanent waters (Nilsson, 2005a). Some adults and larvae can also leave the water and bury into the mud for pupation or as resistance stages (Hansen, 2005; Nilsson, 2005b, c, d) waiting for the next filling phase. Ponds with serial correlations would correspond to: (a) early drying ponds in which coleopterans and heteropterans were forced to move as desiccation progressed and (b) ponds with very long hydroperiod with a high abundance of heteropterans (mainly corixids) in summer. In contrast, ponds with cyclic correlations would correspond to intermediate hydroperiod ponds which still have water when the other ponds are drying and could act as intermediate

sites during dispersal of organisms towards more permanent aquatic habitats, with similar taxa occurring in drying and filling phases. All the ponds with non-significant or weak correlation values had short hydroperiods, indicating that they were much more fluctuating than the other ponds. It was detected mainly in 15-day sampled pond compositions when compared with monthly samples of the same ponds. Richness and biodiversity have been related to the stability along of time (White, 2004), being invertebrate assemblages more stable in ponds with more permanence of water and highly fluctuating in ephemeral ponds (Shurin, 2007). We recommend increasing the frequency of samples along the time in ephemeral ponds with respect more permanent ponds to record all the variability of their macroinvertebrate assemblages, and maybe of other groups like macrophytes, amphibians and other invertebrates.

General pattern of monthly variation in the macroinvertebrate community

Despite differences in macroinvertebrate composition among ponds and in the same ponds at seasonal and inter-annual scales, a general pattern was detected, with similar variation between both years. This may be associated with the general development of the life cycle of many macroinvertebrates within the hydrological cycle of temporary ponds. From flooding to desiccation, we detected the successive appearance of adults, larvae and nymphs at different phases of the ponds. In long hydroperiod years, this general pattern may be extended from autumn to summer, while in short hydroperiod years it is concentrated. In our two study years, we detected a similar variation in macroinvertebrate composition through both wet phases. We also detected a similar composition between filling months although it occurred in February in the dry year and November in the wet year, as well as between the last month of the drying phases (August). This consistent general pattern revealed a high monthly correlation during both years, which was apparently repeated in the 2 years of the study.

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