Ecology/Écologie

Spatio-temporal variability of faunal and floral assemblages in Mediterranean temporary wetlands

Variabilité spatio-temporelle des assemblages faunistiques et floristiques des zones humides temporaires méditerranéennes

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A R T I C L E   I N F O

A B S T R A C T

Six temporary wetlands in the region of Sejenane (Mogods, NW Tunisia) were studied in order to characterize the aquatic flora and fauna and to quantify their spatio-temporal variability. Samplings of aquatic fauna, phytosociological relevés, and measurements of the physicochemical parameters of water were taken during four different field visits carried out during the four seasons of the year (November 2009–July 2010). Despite the strong anthropic pressures on them, these temporary wetlands are home to rich and diversified biodiversity, including rare and endangered species. Spatial and temporal variations affect fauna and flora differently, as temporal variability influences the fauna rather more than the plants, which are relatively more dependent on spatial factors. These results demonstrate the interest of small water bodies for maintaining biodiversity at the regional level, and thus underscore the conservation issues of Mediterranean temporary wetlands that are declining on an ongoing basis currently.

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R É S U M É

Six zones humides temporaires de la région de Sejenane (Mogods, Tunisie du Nord-Ouest) ont été étudiées afin de caractériser leur faune et leur flore aquatiques, et de quantifier leur variabilité spatio-temporelle. Des échantillonnages de la faune aquatique, des relevés phytosociologiques, et des mesures de paramètres physicochimiques de l'eau ont été réalisés au cours des quatre saisons (novembre 2009–juillet 2010). Malgré la forte pression anthropique qui les affecte, ces milieux humides temporaires hébergent une biodiversité riche et diversifiée, avec des espèces rares et menacées. Les variations spatio-temporelles peuvent affecter différemment la faune et la flore, la faune étant relativement plus influencée par la variabilité saisonnière, alors que les plantes sont davantage dépendantes des facteurs spatiaux. Ces résultats révèlent l'intérêt des petits plans d'eau pour le maintien de la biodiversité à l'échelle régionale, et soulignent ainsi les enjeux de conservation des zones humides temporaires méditerranéennes, aujourd'hui en déclin continu.

1. Introduction

Mediterranean temporary wetlands are characterized by alternating phases of flooding and drying and by a very self-contained hydrology [1]. Their roles are important with respect to the landscape in terms of flood control, renewal of groundwater, retention of toxic products, and the recycling of nutrients [2,3]. They also provide various resources to the human population, including water availability, storage for grazing and agriculture, or harvesting of medicinal plants [4,5]. Last but not least, they host many rare and endangered taxa, even supporting species and communities that are not found in other water bodies [6]. These habitats there benefit from conservation policies in most European Mediterranean countries [7,8]. At the same time, the ecological relevance of these wetlands contrasts with the decline of Mediterranean temporary wetlands during the last decades, particularly in North Africa where the decline has been severe [9–13]. The temporary hydrology and reduced size of these ecosystems make them highly vulnerable to anthropogenic impacts and pressures from both agricultural practices and urban growth [1,3,4,14–16]. It is thus extremely timely to identify those factors controlling biodiversity in Mediterranean temporary wetlands and also the ultimate cross-taxon congruence patterns that could help determine priorities for their preservation.

The tremendous biodiversity found in wetlands has been attributed to their high spatio-temporal variability [17–19]. Changes in such environmental conditions as the duration of flooding, water depth [6,13,20–22] and surface area [8,23,24] are known to affect both faunal and floral assemblages [25–29]. These environmental characteristics may all vary in any given wetland during the hydroperiod and across wetlands, making it difficult to distinguish between the effects of spatial and of temporal variability. Moreover, none of the studies referred to have considered both flora and fauna at the same time. Only recently have some studies on Mediterranean temporary wetlands begun to consider both faunal and floral assemblages by means of cross-taxon congruence approaches (e.g., [27–31]). The scarcity of available information to date suggests that flora is relatively more determined by spatial variables, whereas faunal groups are probably more closely linked to temporal variability [19–30]. Nevertheless, there are overriding factors that determine biodiversity in local assemblages in some cases such as the size of the ecosystem: it is hypothesized that larger wetlands support more species than smaller ones regardless of the taxonomic group. Yet when tested in temporary habitats (e.g., [23,32,33]), this idea (see Theory of Island Biogeography [31]) has yielded contradictory outputs. The climate in which a wetland is located can be another overarching factor, since this large-scale environmental filter can disrupt the cross-taxon congruence relationships in small areas within a regional scale [34,35]. Overall, to improve the management and conservation strategies for these habitats, it is crucial to further identify the variability (spatial *vs.* temporal) affecting faunal and floral assemblages of Mediterranean temporary wetlands, and to identify the species-area and/or cross-taxon congruence relationships that may hold across larger scales.

Many temporary wetlands are located in Tunisia, essentially in the northern part of the country [36]. Scientific studies have focused to date on the great wetland complexes such as the Ichkeul National Park (e.g., [37–41]) and have more or less ignored the northern temporary Tunisian wetlands, with the exception of some late 19th century studies [42] and others carried out between 1930 and 1960 [43–46]. Since that time, no further research on Tunisian temporary wetlands has been undertaken until the appearance of several studies, which have focused primarily on vegetation (e.g., [36,47–54]), Crustaceans (e.g., [55,56]) and on amphibians (e.g., [57–60]). The present paper presents the first study integrating both aquatic faunal (amphibians and macroinvertebrates) and floral assemblages in North African temporary wetlands.

Our overarching aim was to characterize flora and fauna of six temporary wetlands in the Sejenane region of northern Tunisia and to quantify their spatio-temporal variability. As found in previous cross-taxon congruence studies in other Mediterranean climate areas, we predicted that:

- temporal variability would be more relevant for faunal than for floral assemblages;
- the converse would be true for spatial variability.

2. Material and methods

2.1. Study sites

The study was carried out on six temporary wetlands near Sejenane (Mogods region, north-western Tunisia; Fig. 1). This region experiences a Mediterranean wet bioclimate of mild winters, and annual rainfalls ranging from 800 to 1000 mm. The Mogods Hills, composed of Oligocene sandstone, are covered by degraded thermo-Mediterranean cork oak forests and scrub. The six temporary wetlands differ mainly in their mesological parameters (Fig. 1; Table 1).

MCH is a semi-permanent freshwater acidic lake located atop Jbel Choucha (445 m), surrounded by an overgrazed cork oak forest. The area is used to pasture cattle, sheep and goats, and is also a bountiful source of leeches used by the local population for traditional health treatments. The five other sites (GUE, GS1, GS2, GGT AND EEZ) are located in and around Garâa Sejenane, a vast endorheic plain formed by a mosaic of cultivated-pastured lands and shallow temporary pools formed on hydro-morphic soils [49]. GS1 and GS2 are situated at the northeastern border of Garâa Sejenane, and are respectively a large temporary pond and an extended temporary marsh. The two sites were completely mowed in the summer. GGT is also a large temporary marsh, located in Garâa Guetma, 6 km east of Garâa Sejenane. GUE and EZZ are two small temporary ponds located on the roadside. EZZ is an artificial pond with irregular topography that is cultivated in the summer (e.g., peppers, melon). GUE is neither cultivated nor grazed, but is located close to residential developments. MCH and Gue are clearly delineated by three vegetation belts (marginal, intermediate and central), EZZ has only two zones (marginal and central), and GS1, GS2 and GGT show no zonation.

2.2. Data collection

Water, plant cover and aquatic fauna were sampled simultaneously over a period of 10 months (from November 2009 to July 2010) during four field visits
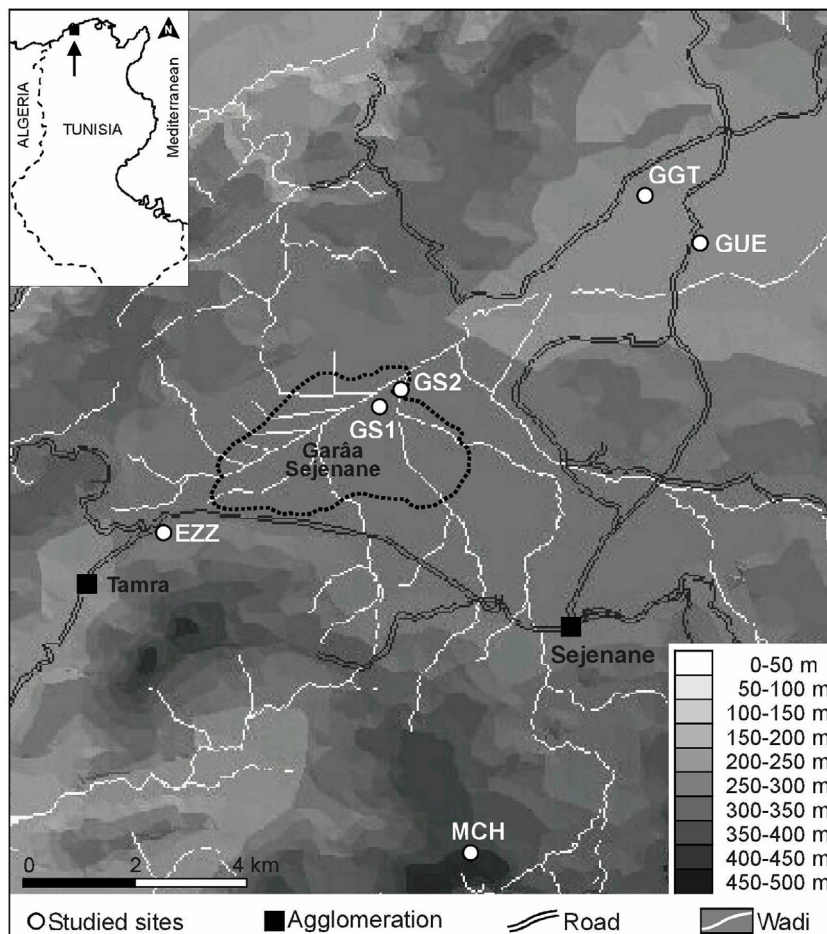

Fig. 1. Location of the six temporary wetlands studied (in Mogods region, Northern Tunisia). EZZ: Ezzoubia; GGT: Garâa Guetma; GS1: Garâa Sejenane1; GS2: Garâa Sejenane2; Gue: Guetma; MCh, Majen Choucha.

Table 1

Mesological parameters for the six temporary wetlands studied. COD, chemical oxygen demand; A, autumn; W, winter; P, spring; S, summer. See Fig. 1 for site codes.

Site	GUE	GS1	EZZ	GS2	GGT	MCH
Type	Temporary pond	Temporary pond	Temporary pond	Temporary marsh	Temporary marsh	Semi-permanent lake
Altitude (m)	98	101	117	102	96	445
Latitude N	37°07'37"	37°05'56"	37°04'40"	37°06'12"	37°08'02"	37°00'38"
Longitude E	09°15'59"	09°11'39"	09°08'36"	09°12'06"	09°15'06"	09°12'42"
Area (m^2)	400	15 000	1000	30 000	65 000	4500
Flooding duration (seasons)	2	2	3	3	3	4
Maximal water depth (cm)	20	20	50	45	65	120
Organic matter (%)	9.1	2.7	2.2	2.2	2.7	14.2
Carbonates (%)	8.2	18.7	5.7	16.7	14.8	3.9
Particles > 63 μm (%)	47.89	86.67	20.80	40.53	97.92	20.27
Particles < 63 μm (%)	37.10	46.00	79.93	19.99	16.00	79.74
Human activities	Close to homes	Mowed	Cultivated	Mowed	–	Pastured

	GUE		GS1		EZZ				GS2			GGT		MCH			
Season	A	W	A	W	A	W	P	A	W	P	A	W	P	A	W	P	S
Water level (cm)	20	10	20	20	50	50	30	45	30	15	65	20	20	100	120	110	45
Temperature (°C)	9.8	13.4	10.2	17.0	10.5	18.0	23.6	14.4	13.0	18.0	13.0	18.0	19.3	7.4	12.5	16.5	31.0
pH	7.2	7.5	8.2	7.5	7.6	7.0	6.5	7.4	6.7	7.7	7.4	6.7	7.7	7.1	7.0	8.3	7.8
Conductivity (μs)	277	440	119	92	23	38	693	157	177	238	270	257	293	73	77	87	–
Nitrite (mg/l)	0.000	0.170	0.001	0.001	0.001	0.006	0.001	0.007	0.050	0.050	0.003	0.002	0.004	0.010	0.010	0.030	0.030
Nitrate (mg/l)	1.2	3.0	1.0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	1.2	0.5	0.6	0.5	0.5	0.7	0.7
Ammonium (mg/l)	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Azote total (mg/l)	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	35
Total phosphorus (mg/l)	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
COD (mg/l d'O_2)	10	10	130	10	30	30	26	75	10	37	46	40	12	172	10	24	234

carried out during all four seasons. Water variables (temperature, depth, conductivity and pH) were measured *in situ*. Substrate texture (particle size, carbonates and organic matter) and nutrients (nitrate, nitrite, total nitrogen, total phosphate and chemical oxygen demand) were analyzed in a laboratory (Table 1). Aquatic fauna was sampled using a 250 μm mesh dip-net (20 cm diameter), and the sampling procedure was based on 20 rapid-succession dip-net sweeps covering all different microhabitats visually detected in the littoral zone of the wetlands. Samples were preserved in 4% formalin. Aquatic fauna was identified mainly to family level as per the extant literature (e.g., [61–63]). The abundance of fauna is expressed in the number of specimens per sample. Phytosociological relevés were carried out in all sites in the area of sampling fauna using the Braun-Blanquet [64] method with an abundance/ dominance scale from + to 5. Plant nomenclature follows Le Floc'h et al. [65]. Moreover, the ecological requirements of plants were established using Bagella and Caria [66].

2.3. Data analysis

2.3.1. Relationships between assemblage parameters and wetland sites and season

Three assemblage parameters were estimated: taxonomic richness, Shannon–Wiener diversity [67] and Jassby–Goldman succession index [68]. The latter was calculated as per the equation:

$$S_j = \left[\sum_i \left(\frac{C_{ia} - C_{ib}}{a - b} \right)^2 \right]^{1/2}$$

$$C_{ia} = \frac{b_{ia}}{\left[\sum_i (b_{ia})^2 \right]^{1/2}}$$

where S_j is the daily rate of the community change, $(a\text{-}b)$ is the time interval in days, C_{ia} and C_{ib} are the contributions of the species i in the abundance of the community on days a and b respectively, b_{ia} is the abundance of the species i on day a.

An analysis of variance (ANOVA, one-way) was performed using the function 'aov' of the R program [69] on the three assemblage parameters to check the significance effect of the site or the season on each dataset (flora and fauna). For the flora, two datasets, one at species level and the other at family level, were used to check whether, in our study, ANOVA results were related to taxonomic resolution.

2.3.2. Variability in faunal and floral composition

We used an analysis of similarities (ANOSIM; [70]) to test for changes in assemblage composition among sites and seasons (ANOSIM, 999 iterations, significance level = 0.05). Two ANOSIM analyses were performed for each dataset (i.e. fauna and flora), using *site* and *season* respectively as factors. In the case of flora, ANOSIM tests were performed using matrices at species and family levels, to determine whether the results depended on taxonomic resolution. For cases with significant differences, similarity percentages (SIMPER analysis; [71]) made it possible to identify the particular species that typified each site relatively to seasons, and each season relatively to sites (*site* and *season* as factors). Such 'typifying' taxa of one particular site (season) explain the highest proportions of the between-seasons (sites) similarity in this site (season). Finally, we used non-parametric multidimensional scaling (NMDS) to visualize how aquatic faunal or floral assemblages differed among the sites and during the various seasons. Statistical tests (NMDS, ANOSIM, SIMPER) and some assemblage parameters were calculated using PRIMER v6 [72].

3. Results

3.1. Faunal and floral assemblages' overview

A total of 106,627 faunal specimens (vertebrates and macroinvertebrates) belonging to 68 taxa were identified during the study (see Supplementary Material, Appendix S1). The macroinvertebrates were qualitatively dominated by insects (52 taxa), of which 23 were Coleoptera, 15 Diptera, 8 Hemiptera, 4 Odonata, and 1 Trichoptera. Gastropods (4 taxa), macrocrustaceans (3 taxa), Hydracarina (2 taxa) and Oligochaeta (1 taxon) were also found. Amphibians were represented by one species of newt and two anurans: *Bufotes boulengeri* (Lataste, 1879) was found only in EZZ, while *Discoglossus pictus* (Otth, 1837) and the Algero-Tunisian endemic *Pleurodeles nebulosus* (Guichenot, 1850) were found in all sites except GGT (see Supplementary Material, Appendix S1). Taxa richness was roughly the same in all sites (24 - 36 taxa; Table 2) and seasons (16 - 21 taxa; Table 3). In terms of abundance, gastropods (mainly Planorbidae) dominated in all sites except in EZZ and MCH, where Chironomidae and Baetidae were the dominant groups respectively (Fig. 2). Moreover, fauna showed seasonal variations in relative abundance (Fig. 2): whereas in autumn and winter, Gastropoda was the most abundant group and Ephemeroptera dominated in summer. Lower dominances were observed in spring when Ephemeroptera, Chironomidae, Gastropoda and Notonectidae were the most abundant (Fig. 2).

A total of 79 plant species belonging to 27 families were recorded in the six temporary wetlands (see Supplementary Material, Appendix S2). Therophytes (annual species) dominated species richness, with 50 species (63%). Thirty-nine species (49%) were hydrophytic or characteristic of temporary wetlands. Eighteen species were rare or infrequent, of which 7 were endangered in North Africa according to the IUCN categories ("critically endangered" or "near threatened" [73]). The remaining species (38% of the total species richness) were opportunists. When comparing wetlands by size, small pond species richness (GUE and EZZ) was higher or similar (34 and 41 species, respectively) than that of the larger habitats such as marshes (GGT and GS2; 38 and 26 species, respectively), the large pond of GS1 (29 species) and the semi-permanent lake of MCH (25 species) (Table 2). Overall, the most abundant families in the wetlands were Poaceae and

Table 2

Number of samples, total taxonomic richness (cumulative richness), taxonomic richness, ecological diversity (Shannon–Wiener index) and succession rate (Jassby–Goldman index) for each temporary wetland. For the latter three variables, average (AVE) and standard deviation (STD) are given. The last column (P-value) shows the one-way ANOVA results. See Fig. 1 for site codes.

Site		GUE	GS1	EZZ	GS2	GGT	MCH	P-value
FAUNA (at family level)								
Number of samples		2	2	3	3	3	4	
Total taxonomic richness		25	24	29	29	36	32	
Taxonomic richness	AVE	20.0	17.5	20.0	18.7	19.7	15.8	> 0.05
	STD	2.8	0.7	1.0	2.9	3.2	3.9	
Ecological diversity	AVE	1.40	1.93	2.50	1.06	2.02	2.00	> 0.05
	STD	1.04	0.81	0.99	0.58	0.93	0.43	
Succession rate (month^{-1})	AVE	0.15	0.43	0.42	0.34	0.46	0.46	> 0.05
	STD	–	–	0.07	0.45	0.20	0.10	
FLORA (at species level)								
Number of samples		4	3	4	4	4	4	
Total taxonomic richness		34	29	41	26	38	25	
Taxonomic richness	AVE	15.3	17.7	26.0	13.0	19.0	12.8	> 0.05
	STD	7.1	6.7	7.2	7.5	9.0	4.9	
Ecological diversity	AVE	3.47	3.78	4.49	3.20	3.82	3.37	> 0.05
	STD	0.62	0.47	0.36	1.27	0.63	0.57	
Succession rate (month^{-1})	AVE	0.31	0.29	0.23	0.39	0.27	0.21	> 0.05
	STD	0.12	0.28	0.10	0.14	0.08	0.13	

Table 3

Number of samples, taxonomic richness, ecological diversity (Shannon–Wiener index) and succession rate (Jassby–Goldman index) for each season. For the latter three variables, average (AVE) and standard deviation (STD) are shown. The last column (P-value) shows the one-way ANOVA results. Similar letters noted in superscript indicate significant correlations.

Season		Autumn	Winter	Spring	Summer	P-value
FAUNA (at Family level)						
Number of samples		6	6	4	1	
Taxonomic richness	AVE	16.3	19.0	20.7	18.0	> 0.05
	STD	3.3	2.3	1.9	–	
Ecological diversity	AVE	2.05[a,b]	1.24[b]	2.57[a]	1.38[a,b]	0.04
	STD	0.74	0.55	0.68	–	
Succession rate (month^{-1})	AVE	–	0.36	0.47	0.35	> 0.05
	STD	–	0.22	0.15	–	
FLORA (at Species level)						
Number of samples		6	6	6	5	
Taxonomic richness	AVE	13.3[b]	16.2[a,b]	26.0[a]	12.8[b]	0.03
	STD	3.6	5.3	7.0	8.1	
Ecological diversity	AVE	3.44[a,b]	3.66[a,b]	4.41[a]	3.14[b]	< 0.01
	STD	0.42	0.50	0.38	1.15	
Succession rate (month^{-1})	AVE	–	0.15[b]	0.35[a]	0.35[a]	< 0.01
	STD	–	0.06	0.13	0.06	

Cyperaceae, except in MCH where Haloragaceae, with a single species (*Myriophyllum alterniflorum*) was most abundant (Fig. 3). This could be due to the fact that this has the longest hydroperiod, as this species was present here only. *Isoetes velata* had also a high abundance at MCH (the third most abundant species after *M. alterniflorum* and *Glyceria spicata*), contrasting with its abundance in the other wetlands where it was present (GS1 and EZZ). Relative abundances among families did not differ seasonally, although the abundance of Ranunculaceae decreased from autumn to spring and was quasi absent in summer (Fig. 3).

3.2. Spatio-temporal variability

When assessing the potential effects of taxonomic resolution (ANOVA, ANOSIM and NMDS in species-*vs.* family-level matrices), we observed coincident outputs.

For this reason, we only show the results obtained using species level.

None of the three assemblage parameters (taxonomic richness, ecological diversity, and succession rate) used to measure fauna and flora differed significantly from site to site (ANOVA, Table 2). By contrast, ecological diversity differed from season to season, peaking for both flora and fauna in the spring, at a minimal level in the winter for animals and in the summer for plants (Table 3). The succession rate was significantly low for plants in the winter.

With regard to the spatial component, different results were obtained for fauna and flora: fauna presented homogeneous compositions (ANOSIM, $R = 0.034$, $P = 0.347$) while the flora differed significantly among wetlands (ANOSIM, $R = 0.466$, $P = 0.001$). In contrast, both fauna and flora showed significant differences for composition across seasons (fauna: $R = 0.373$, $P = 0.006$; flora: $R = 0.118$, $P = 0.034$). These results were in accordance with
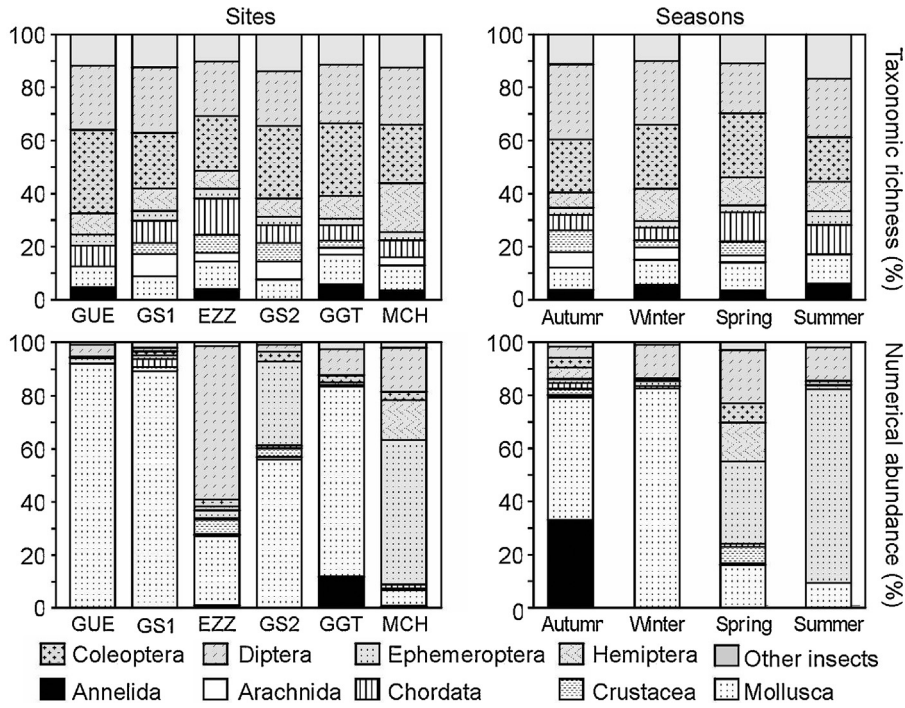
Fig. 2. Percentages of taxonomic richness (upper panels) and abundance (lower panels of the faunal groups. Site faunal composition (left panels) and seasonal faunal composition (right panels) are shown. See Fig. 1 for site codes.
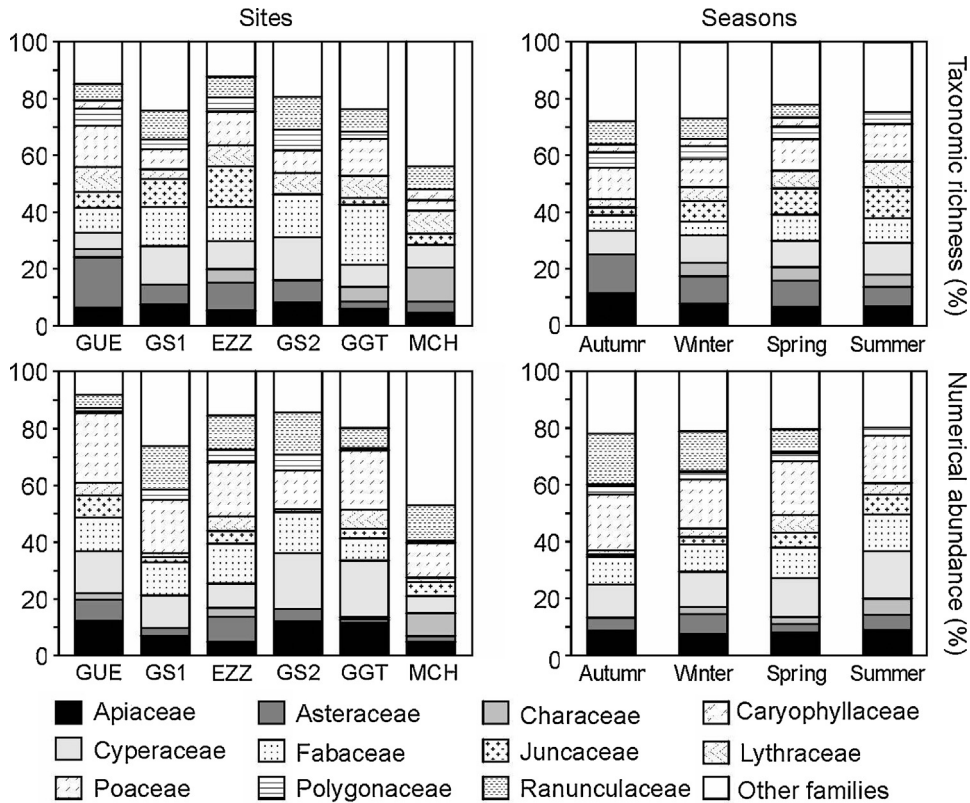

Fig. 3. Percentages of taxonomic richness (upper panels) and abundance (lower panels of the flora groups. Site floral composition (left panels) and seasonal floral composition (right panels) are shown. See Fig. 1 for site codes.
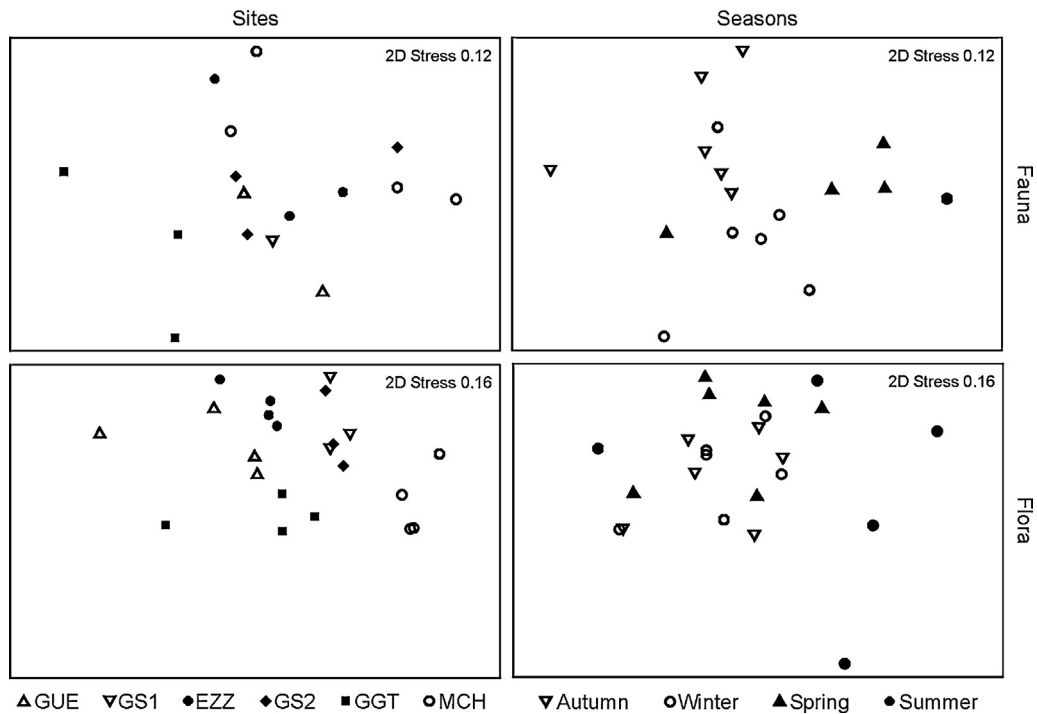
Fig. 4. Nonmetric multidimensional scaling (NMDS) plots of faunal (upper panels) and floral (lower panels) assemblages among sites (left panels) and seasons (right panels). See Fig. 1 for site codes.

the NMDS ordination analysis (Fig. 4), with samples grouped by sites for flora only. Moreover, NMDS plots showed seasonal clustering for both faunal and floral assemblages (Fig. 4).

SIMPER analyses identified taxa that contributed highly to the similarity among samples for each season, i.e. 'typifying' taxa (Table 4). Some of these typified the three seasons that were analyzed, such as Chironomidae and Planorbidae, while others were characteristic of two seasons (i.e. Lymnaeidae in autumn and winter, or Baetidae in winter and spring), or only one (i.e. Corixidae in autumn, Salamandridae in winter, and Dixidae in spring). Note that from autumn to spring, some taxa showed an increase in their contribution to similarity (i.e. Baetidae), while others showed a decrease (i.e. Planorbidae). When SIMPER tests were run for plant species (Table 5), we identified only one of the five species contributing highly to seasonal similarity that consistently

typified the assemblage across all seasons (*Eleocharis palustris*), whereas some other species characterized just one season (*Ranunculus sardous* in autumn, *Myosotis sicula* in winter, *Alopecurus bulbosus* in spring, and *Mentha pulegium* in summer). The set of characteristic species in summer was clearly different from the rest, with four of the five taxa characterizing summer alone, and two characteristic species of the other seasons absent from the 'summer set' (*Glyceria spicata* and *Alisma lanceolatum*). Finally, SIMPER analyses identified the five plant species that

Table 5
Floral species typifying each season (SIMPER analysis). The five species contributing that contribute most to between-sites similarity were selected.

Autumn		Winter	
(69.4% average similarity)		(61.2% average similarity)	
Taxa	%	Taxa	%
Glyceria spicata	27.5	*Glyceria spicata*	22.0
Ranunculus baudotii	11.9	*Ranunculus baudotii*	13.2
Eleocharis palustris	10.2	*Eleocharis palustris*	12.2
Alisma lanceolatum	10.1	*Alisma lanceolatum*	8.4
Ranunculus sardous	9.7	*Myosotis sicula*	5.4
Spring		Summer	
(40.9% average similarity)		(81.5% average similarity)	
Taxa	%	Taxa	%
Glyceria spicata	9.9	*Mentha pulegium*	33.8
Alisma lanceolatum	9.2	*Bolboschoenus glaucus*	15.4
Eleocharis palustris	8.7	*Lotus hispidus*	13.7
Alopecurus bulbosus	7.9	*Cynodon dactylon*	10.2
Ranunculus ophioglossifolius	5.2	*Eleocharis palustris*	8.4

Table 4
Faunal species typifying each season (SIMPER analysis). The five species that contribute most to between-sites similarity were selected.

Autumn		Winter		Spring	
(64.5% average similarity)		(76.2% average similarity)		(58.1% average similarity)	
Taxa	%	Taxa	%	Taxa	%
Planorbidae	32.2	Planorbidae	52.2	Baetidae	22.5
Chironomidae	10.1	Chironomidae	7.0	Chironomidae	14.0
Notonectidae	8.7	Lymnaeidae	6.0	Planorbidae	7.5
Corixidae	6.9	Baetidae	6.0	Dixidae	7.4
Lymnaeidae	6.6	Salamandridae	5.0	Dytiscidae	6.7

Table 6

Floral species typifying each site (SIMPER analysis). See Fig. 1 for site codes. The five species that contribute most to between-seasons similarity were selected.

GUE		GS1		EZZ	
(72% average similarity)		(51.8% average similarity)		(36.3% average similarity)	
Species	%	Species	%	Species	%
Lotus hispidus	18.5	*Myosotis sicula*	12.9	*Paspalum distichum*	8.1
Eryngium pusillum	16.1	*Glyceria spicata*	10.8	*Lotus hispidus*	8.0
Juncus fontanesii	15.5	*Alisma lanceolatum*	10.5	*Alisma lanceolatum*	6.9
Eleocharis palustris	11.3	*Ranunculus sardous*	9.0	*Eleocharis palustris*	6.8
Glyceria spicata	10.6	*Eleocharis palustris*	8.6	*Cynodon dactylon*	6.5
GS2		GGT		MCH	
(58.6% average similarity)		(61.3% average similarity)		(68.4% average similarity)	
Species	%	Species	%	Species	%
Bolboschoenus glaucus	28.3	*Bolboschoenus glaucus*	18.8	*M. alterniflorum*	18.6
Glyceria spicata	8.2	*Eryngium pusillum*	14.6	*Isoetes velata*	15.4
Rumex tunetanus	8.0	*Panicum repens*	11.4	*Glyceria spicata*	14.9
Myosotis sicula	7.6	*Schoenoplectus lacustris*	8.4	*Ranunculus baudotii*	9.9
R. ophioglossifolius	6.5	*Glyceria spicata*	8.1	*Eleocharis palustris*	9.6

contributed highly to the similarity among samples of each site (Table 6). Two sites with a high similarity in percentage (GUE, 72.0%; MCH, 68.4%), a site with a low percentage (i.e., EZZ, 36.3%), and the four remaining sites with intermediate percentages (51.8%–61.3%) (Table 6). Moreover, MCH had the highest number of typifying species that were uncharacteristic of the other wetlands (three of the five species). GUE and GS1, by contrast, each harbored only a single species of this kind (*Juncus fontanesii* and *Ranunculus sardous*, respectively).

4. Discussion

4.1. Fauna communities

The temporary wetlands that we studied were rich in fauna, most of the taxa were known from the temporary wetlands of Morocco [74–77], Italy [78–80] and Spain [17,81,82]. While certain taxa such as *Lepidurus apus* subsp. *lubbocki* are known exclusively in temporary wetlands [83], others are widespread in all types of aquatic habitats. This is true for *Pleurodeles nebulosus*, *Discoglossus pictus* [57], some Coleoptera (Dytiscidae, Gyrrinidae, Haliplidae, Hydrochidae, Noteridae) [84,85], Ephemeroptera (Baetidae [86]), Hemiptera (Coriidae, Naucoridae including *Naucaurus masculatus*, Notonectidae, Gerridae, Pleidae [87]) and Oligochaeta (Enchytraeidae [88]). Within this context, the temporary wetlands that we examined contained two different types of aquatic macroinvertebrates [76]:

- on the one hand, resident taxa that have developed adaptive strategies against desiccation (e.g., production of resistant forms), such as Branchiopoda [89,90], gastropods (Physidae, Planorbidae, Lymnaeidae [76]), some coleopterans (Hydrophilidae: *Berosus* [91]; *Helophorus* and *Laccobius* [76]), and some dipterans (Chironomidae: *Chironomini* [92]);
- on the other hand, migrant taxa originating from permanent aquatic habitats, temporarily colonizing the

body of water and leaving it before desiccation, such as heteropterans (Corixidae, Notonectidae), some coleopterans (Dytiscidae, Hydrophilidae [76]) and some dipterans (Chironomidae, Culicidae, Ceratopogonidae).

In accordance with previous studies [81,93,94], we observed that insects were the most diverse macroinvertebrate group, dominated by the order of dipterans and family of Chironomidae [81,95]. Our results also confirmed the presence of the three amphibian species that were supposed to occur in the region: the *Bufotes boulengeri* toad, the Mediterranean Painted Frog *Discoglossus pictus*, and the Algero-Tunisian Ribbed Newt *Pleurodeles nebulosus* [57,58,96,82]. However, in contrast with previous studies (e.g., [97–99]) and while the total taxonomic faunal richness is lower in sites with the lowest hydroperiod duration (2 months), no significant changes in faunal assemblages can be attributed to hydroperiod duration (temporary vs. semi-permanent). Such an apparent homogeneity between sites with different hydroperiods could be explained, at least partially, by the low taxonomic resolution achieved in this study.

4.2. Plant communities

The wealth of plants recorded in this study (79 species in six temporary wetlands) fall into a similar range (Pearson correlation: $R = 0.970$; $P < 0.001$) to those observed in the Mogods-Kroumirie region: (244 species in 36 wetlands [54]), and from different Mediterranean areas such as Sardinia (113 species in 9 pools [19]), Minorca (360 species in 63 pools [100]), Portugal (168 species in 29 pools [101]), Morocco (253 species in 48 pools [102]), and Algeria (136 species in 26 pools [103]). Annual species predominated, accounting for 66% of the total number of species, including hydrophytes and opportunistic species, a finding that is consistent with previous studies in a variety of Mediterranean-climate regions, namely North Africa [11,13,54,73,104–106], Southwest Europe [1,100,107,108] and California [105]. This

dominance reflects a strong adaptation to the fluctuating environmental conditions of temporarily wet habitats [3]. Constraints such as these favor short-cycled species that invest more in sexual reproduction than in vegetative development [13,107,109]. The presence of 11 rare species, including 7 that are endangered in North Africa [73], confirms the importance of Mediterranean temporary wetlands as a key habitat for the conservation of rare and endemic flora [1,107,110,111]. In this sense, it is important to note that we also found *Rumex tunetanus*, a strict endemic of Garâa Sejenane found only in the two sites of this garâa (GS1 and GS2), and *Nitella opaca* and *Pilularia minuta*, two species recently discovered in Tunisia [36,49,54].

4.3. Seasonal dynamics

The temporary wetlands that we studied are affected by the Mediterranean climate, which during a year typically alternates between at least one flooded phase from September to April, and one dry summer phase. It was not surprising, therefore, that seasons have a significant effect on both floral and faunal compositions. In the case of flora, the alternation between wet and dry phases probably favors the establishment of two distinct groups of plants: an assemblage of aquatic and amphibious species during the flooded period, and an assemblage of terrestrial species during the dry period (as described by [1,112,113]). In the case of fauna, compositions appear to depend primarily the length of the hydroperiod and secondarily, on seasonality [3,114,115]. This observation is consistent with other studies that have shown the unique importance of the length of the hydroperiod for both faunal composition [34,116,117] and richness [118,119]. Indeed, in temporary habitats, community structure is well known to change as the hydroperiod advances [28]: In autumn, when temporary wetlands are usually filled, macroinvertebrates begin to recolonize the habitats [1,3,120,121]. Taxa that are resistant to dry phases, such as pioneer crustaceans (Anostraca, Notostraca), oligochaetes, gastropods, water mites and some insects (e.g., the hydrophilid *Berosus* or the chironomid *Chironomus*), appear early after inundation [98,122–124]. Additionally, other insects (e.g., dytiscids, baetids, notonectids, libellulids) take advantage of their mobility and great capacity to discover and colonize "new" water bodies [125]. Later, a second wave of insects may cause further increases in species richness during winter [95], although it is not before spring that the richness of some particular insect groups (mostly coleopterans and heteropterans) typically peaks. During this period, tadpoles accelerate their development (as observed in the longer-hydroperiod sites; EZZ, GS2, GGT and MCH). Subsequently, aquatic insects generally migrate to permanent waters until the next filling phase (if their adult stage is aquatic) or alternatively, survive as terrestrial adults [114].

4.4. Spatial patterns

Although the wetlands we studied were situated relatively close to one another (except MCH, higher than

the rest), the sites differed greatly in their plant assemblages. This finding confirms the importance of habitat type (pond, marsh, lake) for floral composition, as already described from the same region by Ferchichi-Ben Jamaa et al. [54]. In accordance with their observations, both Garâa Sejenane sites (GS1 and GS2) harbor similar hydrophytic (amphibious and helophytic) communities.

To date, several studies have described significant species richness-area relationships for both fauna and flora in temporary wetlands [8,19,23,24,30,76,126,127]. The Theory of Island Biogeography [128] applied to isolated wetland metacommunities would predict that relatively larger bodies of water bodies allow for more ecological niches and thereby accommodating more taxonomic groups [23]. While some authors have found positive relationships between plant richness and wetland size [19,23,30], our study did not show this relationship. Rather, we observed that small bodies of water were richer than larger ones. This result could be triggered by higher microhabitat heterogeneity in small wetlands when compared to larger ones [54]. It could be also related to the biological type of the present species, as clonal perennial species have a tendency to create more homogeneous communities than do annual species. However, our data do not support this last hypothesis (not significant Pearson correlations). Nevertheless, for fauna, our study shows comparable taxa richness among sites. The lack of richness-area relationship for fauna could be explained by the fact that our study:

- was carried at the level of major taxonomic groups that include species with diverse ecological requirements;
- has not taken into account overriding filters, such as hydroperiod length [34,118], biotic interactions [129], water chemistry (e.g., [130,131]), or human activities, particularly cultivation [132,133].

Although it is not possible to disentangle the effects of these potential drivers from our study, we think that agriculture practices may have had a significant impact on the observed spatial patterns, as has been described by studies that explicitly address the influence of agriculture in wetland communities [132].

4.5. Congruence between faunistic and floristic patterns, and implications for biodiversity conservation

Many authors have showed positive correlations between plant and fauna diversities [8,23,134–137]. Hydrophytic plants generally play a major role in freshwater ecosystems by structuring the habitat [138], providing refuges [139] and egg-laying sites, and constituting a food source for macroinvertebrates and amphibians. In our study, the effects of the varying lengths of the hydroperiod and agricultural practices seem to obscure the relationship between fauna and flora richness as they seem to affect respectively the faunistic and floristic assemblages. Nevertheless, congruence relationships between faunal and floral assemblages can be useful for helping to define and prioritize areas of conservation interest.

Therefore, while our results exemplify that such relationships can be "broken" by overriding factors such as those discussed (or even larger scale factors such as climate [32]), we consider that congruence should continue to be explored.

Overall, the present study demonstrates that temporary wetlands harbor rich and diversified floral and faunal assemblages (including rare and endangered species), even when submitted to strong anthropogenic pressures. This study also supports the idea that spatial and temporal variations affect fauna and flora differently, with fauna being relatively more influenced by seasonal dynamics [19–30], and plants more dependent on spatial factors. Although predicting global patterns based solely on fauna or flora remains difficult, our results show how small bodies of water can help maintain regional biodiversity, which is relevant for the purposes of conservation in light of the ongoing decline of Mediterranean temporary freshwater habitats.

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Appendices 1 and 2. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.crvi.2014.09.006.

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