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Conservation issues of temporary wetland Branchiopoda (Anostraca, Notostraca: Crustacea) in a semiarid agricultural landscape: What spatial scales are relevant?

David G. Angeler^{a,*}, Olga Viedma^a, Salvador Sánchez-Carrillo^b, Miguel Alvarez-Cobelas^b

^aInstituto de Ciencias Ambientales, Universidad de Castilla – La Mancha, Avda. Carlos III s/n, E-45071 Toledo, Spain

^bInstituto de Recursos Naturales (CSIC), Serrano 115 dpdo, E-28007 Madrid, Spain

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ABSTRACT

Ecologists increasingly recognise the importance of spatial scale for conservation. This study focuses on threatened temporary wetland crustaceans, the fairy shrimp *Branchinecta orientalis* Sars (Anostraca) and the tadpole shrimp *Triops cancriformis* Bosc (Notostraca). Using redundancy analyses with a canonical variance partitioning approach, we studied how local habitat conditions and landscape features influence their densities at 4 spatial scales (100 m buffer strip around ponds, 1 km, 5 km and 10 km catchment scales). *Branchinecta* densities were negatively related with local conditions (trophic status) at all scales. Landscape effects (catchment:wetland size ratio) were only significant at the 10 km scale. However, trophic state conditions were influenced by local contamination rather than landscape conditions. Local degradation tended to be more pronounced in wetlands situated in catchments with a higher cover of natural vegetation compared to those in agricultural catchments. *Triops* was less influenced by local effects at all scales. The importance of landscape effects increased with landscape scale but effects were only significant at the 10 km scale, and were negatively explained by irrigated croplands. The importance of broad landscape scales and the difficulty to restore locally degraded sites challenges management. Because rationalisation of large-scale agricultural practises can conflict with socio-economic demands, a first step to the conservation of actual Branchiopoda populations in this remnant wetland complex could benefit from the creation of vegetated buffer strips around the wetlands and/or hedgerows around agricultural fields to counteract atmosphere-mediated flux of particles and solutes from croplands to wetlands at broad landscape scales.

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1. Introduction

It is becoming increasingly clear that lakes and wetlands must be viewed as integral landscape units that depend on, and interact with, landscape processes across spatiotemporal hierarchies, rather than comprising isolated and independent

microcosms (Forbes, 1887). Although studies investigating the impacts of land use/land cover (LULC) change on aquatic ecosystems have shown varied results, an increasing number of studies highlight the negative impacts of LULC change on the ecological integrity of aquatic ecosystems. Changes in community structure and a loss of species diversity of plants

* Corresponding author. Tel.: +34 925 26 8800; fax: +34 925 26 8840.

E-mail addresses: David.angeler@uclm.es (D.G. Angeler), Olga.viedma@uclm.es (O. Viedma), Sanchez.carrillo@ccma.csic.es (S. Sánchez-Carrillo), malvarez@ccma.csic.es (M. Alvarez-Cobelas).
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(Lougheed et al., 2001; Houlahan et al., 2006), plankton (Pinel-Alloul et al., 2002; Dodson et al., 2005), macroinvertebrates (Hall et al., 2004), amphibians (Houlahan and Findlay, 2003; Gamble et al., 2006), reptiles (Rizkalla and Swihart, 2006; Roe et al., 2006), fish (Evans et al., 1996; Rusuwa et al., 2006) and birds (Liu et al., 2004; Pasinelli and Schiegg, 2006) have been reported as a result of habitat fragmentation, deforestation, agricultural expansion and other landscape changes. Concurrently, alterations of biogeochemical fluxes, i.e., increased inputs of sediments, nutrients and pollutants through runoff (Detenbeck et al., 1996; Luo et al., 1997; Crosbie and Chow-Fraser, 1999; Lougheed et al., 2001; Houlahan and Findlay, 2004) cause changes in the abiotic environment and affect indirectly aquatic biota.

Recent research suggests that life history traits mediate in the strength of influence of local or landscape characteristics on aquatic biota. In their study of playa wetlands of the Southern High Plains of Texas (USA), Hall et al. (2004) have shown that invertebrate taxa with low active dispersal capacities were more adversely affected by agricultural activities in their catchments compared with active dispersers (e.g., winged adult insects), because they cannot avoid anthropogenic stress by migrating between wetlands. Studies on temporary wetlands in the North-American prairie pothole region (Euliss and Mushet, 1999) and on shallow lakes in Wisconsin (USA) (Dodson et al., 2005) support these findings. Based on this preliminary evidence, and because the dormant stages of many resident species form integral parts of wetland resting egg banks (Brendonck and De Meester, 2003; Williams, 2006), it is reasonable to assume that a potential deterioration of egg banks in response to LULC changes can have far reaching impacts on the ecological integrity of temporary waters. Colonisation from egg banks is deemed the single most important colonisation process during early temporary pond succession (Wellborn et al., 1996), and the emerged community may constitute an important food supply for later external colonisers (Jenkins and Boulton, 2007). Colonisation of wetlands from egg banks can be especially important in biogeographically highly isolated wetlands (Angeler and Alvarez-Cobelas, 2005; Angeler and García, 2005), and may contribute to regional diversity (De Meester et al., 2005). Unfortunately, despite recent conservation efforts motivated by the ecological and economic value of wetlands, historical wetland destruction and/or degradation as a result of LULC changes will likely continue with predicted changes in global climate (Ramankutty et al., 2002). Specific combinations of anthropogenic stress and global warming can lead to unexpected results and complicate sound management and mitigation of impact (e.g., Pyke and Marty, 2005).

The large Branchiopoda (Crustacea), comprising fairy shrimps (Anostraca) and tadpole shrimps (Notostraca), are emblematic and phylogenetically old members of the resident community of temporary waters that are sensitive to climate change (Pyke, 2005). Because of reaching large body sizes (on average 1–3 cm; Alonso, 1996) in short time frames after pond rewetting, they are highly susceptible to fish predation, and therefore absent from permanent water bodies (Bohonak and Whiteman, 1999). Their confinement to temporary waters makes them especially vulnerable to habitat loss due to conversion to agricultural land, which, combined with deteriora-

tion of remnant wetland patches, poses a high risk to their persistence. Because of their large size they are likely to mediate in key biogeochemical fluxes and community structuring processes (Dumont et al., 1994; Boix et al., 2006). They can also serve as “nexus species” which may be transient in community development but whose presence or absence has profound long-term effects on the communities (Drake et al., 1996; Lockwood and Samuels, 2004). Some studies suggest that they are readily consumed by waterfowl (e.g., Kazantzidis and Goutner, 2005), highlighting their importance in food webs. Therefore understanding the effects of local and/or landscape factors on their population densities may not only inform us about taking action to conserve this unique but threatened group of organisms, but this may also contribute to our understanding of their functional roles relevant for management of ecosystem integrity of increasingly threatened temporary waters.

Landscape ecologists are increasingly recognising that spatial and temporal patterns are hierarchically structured, non-linear processes that vary in function of domain size and study frequencies (Allen and Starr, 1982; Wiens, 1989; Kotliar and Wiens, 1990). Thus the identification of scales at which landscape processes affect aquatic ecosystems locally should be the first step towards an integrated aquatic resources management. This is especially important in agricultural landscapes where the impact of LULC characteristics on local habitat conditions and communities can vary with spatial scale (e.g., Declerck et al., 2006). In this study we adopt a multiscale design to study how regional LULC characteristics interact with local habitat conditions across 4 regional domains (the 100 m buffer strip surrounding the wetlands, and catchment scales at 1 km, 5 km and 10 km) in the regulation of two species of temporary wetland Branchiopoda (Crustacea), the fairy shrimp *Branchinecta orientalis* Sars (Anostraca) and the tadpole shrimp *Triops cancriformis* Bosc (Notostraca). The study was carried out in the Campo de Calatrava, a landscape of semiarid central Spain that shows regional gradients in agricultural exploitation and local gradients in wetland habitat degradation. Because Mediterranean aquatic ecosystems are characterised by high catchment:wetland size ratios (Alvarez-Cobelas et al., 2005), intensive agricultural activity may have disproportionately adverse effects in small wetlands situated in large catchments. Because of our multiscale designs, we expect that the magnitude of LULC impacts on the densities of both species through effects on local habitat quality shall be higher at broader landscape scales. Based on this research, we expect to inform management and conservation of temporary wetlands and some of their peculiar constituent fauna.

2. Materials and methods

2.1. Study area

The Campo de Calatrava region is situated in central Spain (39°00'N, 4°25'W; 38°30'N, 3°23'W). It formed in the late Pliocene and early Pleistocene from volcanic activity and covers 12,227 ha. It once contained a unique, biologically rich wetland complex consisting of more than 50 temporary ponds of different geomorphic types (depressional, piedmont and

volcanic craters) but agricultural activity in the second half of the 19th century caused massive land degradation and wetland loss. Many of the remnant wetlands are degraded locally as a result of, for instance, cattle grazing, waste water discharge, dumping, and channel construction. Yet a unique wetland fauna and flora can still be found in this area (Velazquez et al., 1989; Alonso, 1996; García-Canseco, 2000, Angeler, unpublished data) highlighting the value of the remaining wetlands for regional biodiversity. For this study, twelve wetlands were chosen that represented abiotic variability, landscape characteristics and anthropogenic stress conditions among the few wetlands that remain in the region (García-Canseco, 2000) (Table 1).

2.2. Sampling and experimental design

As most wetlands were dry during our project because of a prolonged supraseasonal drought period, we used an outdoor microcosm design to study the resting egg and plant seed (propagule) bank potential of dry wetland soils of these wetlands and zooplankton community compositions that develop from them. Such microcosm experiments have the advantage to extract species that may not be detected when sampling field communities (Vandekerckhove et al., 2005). Although the use of microcosms is debated in the literature (Huston, 1999), the composition, structure and function of such systems approximates the organisation of larger systems, and the resulting interactions observed in these experimental units should reflect at least a subset of biological and physical-chemical processes that occur in the field (Angeler and García, 2005).

Dry sediments were collected in December 2005 when all wetlands were dry for at least 2–3 years. We collected the uppermost 5 cm layer at randomly chosen points. To cover the widest possible range of species in the egg bank, these points were selected to cover different habitat types (vegetated and unvegetated) across the whole wetland area. The amount of collected sediment in each wetland was standardized to wetland area so that sediment volume was proportional to wetland size. All individual collections were taken in a

10 × 10 cm area, composited in 40 L plastic drums and stored in the laboratory in dark at room temperature for 2 months.

Prior to use in the experiment, sediments were hand sieved for homogenisation and coarse organic matter was removed. For each wetland triplicate microcosms (30 L plastic aquaria) were placed in a complete randomised blocks design on outdoor benches at the Campus Tecnológico of UCLM (Toledo). On 6 February 2006, all microcosms received 4 L of sediment and 20 L tap water to induce zooplankton hatching and community dynamics. The water levels were kept constant throughout the study by adding tap water when necessary. Previous studies have shown that tap water had no influence on hatching and community dynamics compared with distilled water (Angeler et al., 2006). All microcosms were covered with transparent plastic foils to avoid aerial contamination with resting eggs. Air exchange with the atmosphere was guaranteed by drilling holes (5 mm diameter) in the microcosms that were covered with 50-µm plankton net.

2.3. Measurement of local variables

Water quality and microinvertebrates were sampled in weekly intervals from 7 February 2006 to 18 April 2006, which reflected a period when Mediterranean wetlands can be wet in nature, and the meteorological conditions at the Campus were not strikingly dissimilar to those occurring in the Campo de Calatrava during the experiment. Macrophyte development was monitored in the same microcosms that were sampled for water quality and invertebrates, and in another set of three microcosms that were only flooded until soil saturation. This allowed us to evaluate the species set of submerged macrophytes and amphibious plants present in the sampled wetland soils. The microcosms were inspected haphazardly during plant succession and macrophyte taxa were recorded when they occurred at an identifiable stage.

Detailed protocols for water quality measurements (pH, electrical conductivity, dissolved oxygen concentration, Secchi transparency, chlorophyll *a*, total phosphorus and total nitrogen) are given in Angeler et al. (2004). Microinvertebrate abundance evaluation and identification from 6 L concentrated

Table 1 – Summary of characteristics and locations of the study wetlands

Wetland	Geographic location (UTM coordinates)	Municipality	Altitude (m)	Wetland size (ha)	Geomorphic type	Trophic status (total P; mg L ⁻¹) ^a	Salinity (g L ⁻¹) ^b
Alberquilla	Z30, E410731, N4272899	Mestanza	833	6.5	Crater	0.14	0.14
Almodovar	Z30, E398387, N4285646	Almodóvar de Calatrava	640	22.6	Crater	10.05	3.10
Cañada	Z30, E409333, N4298926	Cañada de Calatrava	607	60.2	Piedmont	0.17	0.19
Caracuel	Z30, E407498, N4297226	Caracuel de Calatrava	627	61.4	Piedmont	0.18	0.38
Carrizosa	Z30, E392261, N4299942	Cabezarados	654	21.1	Piedmont	0.21	0.20
Cucharas	Z30, E399958, N4289407	Villamayor de Calatrava	609	106.8	Depression	0.22	0.33
Garbanzos	Z30, E389009, N4299957	Cabezarados	638	21.6	Depression	0.16	0.19
Nava Enmedio	Z30 E4214444, N4336323	Malagón	586	36.2	Piedmont	0.17	0.21
Nava Grande	Z30 E418069, N4337275	Malagón	578	110.2	Piedmont	0.12	2.37
Posadilla	Z30, E408938, N4310859	Ciudad Real	633	13.4	Crater	4.87	0.72
Prado	Z30, E427313, N4308263	Pozuelo de Calatrava	542	51.7	Depression	0.23	1.93
Saladilla	Z30, E399913, N4292226	Villamayor de Calatrava	609	39.3	Depression	1.56	0.66

^a Values obtained from averages of three replicate microcosms sampled in this study.

^b Converted from electrical conductivity values (average of three replicate microcosms) measured in this study using a conversion factor of 0.68 (Hart et al., 1991).

subsamples followed the method described in Angeler et al. (2006). After screening of zooplankton, the filtered water was returned to the microcosms and water loss was replaced with tap water. Microinvertebrate species richness was rarefied using EcoSim 7.0 (Gotelli and Entsminger, 2004). Rarefaction generates the expected number of species in a small collection of n individuals drawn randomly from a large sample (N). This procedure allowed for standardisation of microinvertebrate species richness across wetlands and meaningful comparisons in statistical analyses. Sample size to rarefaction (n) was defined as the lowest number of microinvertebrates detected at a site. Plant species richness was not rarefied because we determined incidence of macrophytes in the whole samples (microcosms); we are confident that we did not miss any taxon using this sampling strategy.

2.4. Measurement of landscape variables

Data of topographic features and LULC percentage covers were determined in a hierarchical design across 4 levels of influence: a 100 m buffer strip surrounding the wetlands, and 3 catchment scales at 1 km, 5 km and 10 km. Topographic data (slopes and altitudes) were calculated from a Digital Terrain Model with 25 m interval lines obtained from the Spanish national centre of geographical information (CNIG). Percentage land use cover was extracted from revised CORINE 2000 (EEA, 2000) and divided into three broad classes: natural vegetation (conifers and deciduous woodlands, dehesas, shrublands and grasslands), and dry and irrigated croplands (both categories comprised of cereals, olives and vineyards). We decided to use such broad LULC classes to reduce co-linearity among individual land use classes, and overfitting of multivariate statistical models (Ter Braak and Šmilauer, 1998). Wetland size was also determined from CORINE maps. Delimitation of catchments was carried out using the digital terrain model processed in the geospatial hydrologic modelling extension (HEC-GeoHMS) model of ArcView GIS (ESRI, 1999).

2.5. Statistical analyses

The mechanistic patterns underlying the regulation of branchiopod densities in the ponds were determined using redundancy analysis (RDA). This method allows for determining the relative importance of local and landscape conditions on the spatial variability of our dependent variables (*Triops* and *Branchinecta* density). We used all local and environmental variables (Table 2) as explanatory variables in a forward selection in redundancy analysis (RDA), with the branchiopod densities as the dependent matrix, in order to find a set of parsimonious explanatory variables for partial redundancy analyses. In Local and Local + Regional models, total nitrogen (TN) and electrical conductivity were the local variables with significant conditional contributions at all scales. In the case of landscape variables, slope, irrigated croplands and catchment:wetland size ratio were significant. We used these significant variables (i.e., TN, electrical conductivity, slope, irrigated croplands and catchment:wetland size ratio) as main local-regional explanatory variables for running partial redundancy analyses and will refer to them as reduced models.

The interaction between local and landscape factors across scales was assessed by Partial RDA (Ter Braak and Šmilauer, 1998). RDA is a canonical or constrained principal component analysis (PCA) that allows extracting patterns from the explained variation of environmental variables (i.e., direct gradient analysis). This multivariate analysis is suitable for short linear or monotonic responses and/or compositional gradients (<2 SD) (Ter Braak and Šmilauer, 1998), the latter being the case for our data set. When RDA includes co-variables (i.e., Partial RDA), the effect of these variables on population response is partialled out, and the sum of canonical eigenvalues represents the variance in the populations explained by the environmental variables after accounting for the co-variables (Ter Braak, 1988). This method replaces environmental variables by their residuals after regressing each environmental variable on co-variables and later fits the residuals to the species matrix. In all analyses, scaling was optimized for inter-sample distance, centred by species, and variables were log-transformed [$\hat{Y} = \log(Y + 1)$] to lessen the effect of skewed distributions.

Partial RDA analyses allowed decomposing the inertia (variance) into various components attributed to different sets of explanatory variables (Ter Braak, 1988). In this study, we decomposed variance attributable to explanatory variables described by Cushman and McGarigal (2002) and Cottenie et al. (2003):

- (1) Local variation [L]: variation explained by local conditions without co-variables.
- (2) Regional/landscape variation [R]: variation explained by landscape conditions. RDA models at buffer and catchment scales (1 km, 5 km and 10 km) without co-variables.
- (3) Pure local variation [L|R]: the fraction of species variation that can be explained by local conditions independently of any landscape condition (corresponds in the univariate case to a partial linear regression procedure).
- (4) Pure landscape variation [R|L]: the fraction of species variation that can be explained by landscape conditions independently of any local characteristic.
- (5) The variation explained by combined local and landscape variables [L + R].
- (6) The shared/confounded variation explained simultaneously by local and landscape conditions [$L \cap R$] ($[L \cap R] = [L] - [L|R] = [R] - [R|L]$).
- (7) The total of unexplained variance ($100 - [L + R]$).

A stepwise selection method for entering variables was applied using a Monte Carlo permutation test (999 runs) in CANOCO software (Ter Braak and Šmilauer, 1998) for significance testing. We used permutations under the reduced model (this permutes the raw data in the [L + R], [L], and [R] analyses, and the residuals from the co-variables in the [L|R] and [R|L] analyses) since this better maintains the Type I error in small data sets (Ter Braak and Šmilauer, 1998). The fractions [$L \cap R$] and $100 - [L + R]$ were derived without significance testing.

To test if the distribution of LULC types is scale-dependent, a two-way analysis of variance (ANOVA) was carried out in STATISTICA 5.1 release (StatSoft Inc., Tulsa, Oklahoma,

Table 2 – Summary of data on local and regional characteristics of the studied wetlands (n = 12)

	Mean	SD	Confidence limits	
			−95%	+95%
Local characteristics				
Wetland size (ha)	45.92	34.14	24.22	67.61
Dissolved O ₂ (mg L ^{−1})	8.53	0.58	8.16	8.90
Temperature (°C)	10.24	0.19	10.11	10.36
Ph	8.35	0.49	8.04	8.66
Electrical conductivity (μS cm ^{−1})	1277.30	1489	331.26	2223.33
Secchi transparency (cm)	17.05	5.17	13.77	20.33
Total P (mg L ^{−1})	1.51	3.02	0.00	3.42
Total N (mg L ^{−1})	5.41	1.57	4.42	6.41
Chlorophyll a (μg L ^{−1})	0.96	0.92	0.37	1.54
Invertebrate expected species richness	41.91	9.41	35.94	47.90
Plant species richness	7.42	3.92	4.93	9.91
<i>B. orientalis</i> (ind. L ^{−1})	0.39	0.52	0.06	0.72
<i>T. cancriformis</i> (ind. L ^{−1})	0.16	0.35	0.00	0.39
Regional characteristics – Buffer scale				
Catchment size (ha)	32.11	15.33	22.37	41.85
Ratio catchment:wetland size	0.94	0.47	0.64	1.24
Altitude (m)	675.98	64.31	635.12	716.85
Slopes	2.54	3.56	0.28	4.81
Natural vegetation (% cover)	39.00	41.70	12.50	65.49
Dry croplands (% cover)	49.16	35.09	26.85	71.45
Irrigated croplands (% cover)	11.85	15.97	1.07	21.99
One kilometer scale				
Catchment size (ha)	471.42	286.31	289.51	653.33
Ratio catchment:wetland size	16.65	14.73	7.29	26.01
Altitude (m)	695.82	56.08	660.19	731.46
Slopes	5.13	3.55	2.87	7.39
Natural vegetation (% cover)	36.94	36.39	13.82	60.06
Dry croplands (% cover)	47.07	28.57	28.11	65.22
Irrigated croplands (% cover)	7.42	9.01	1.69	13.15
Five kilometers scale				
Catchment size (ha)	1225.70	653.9	810.25	1641.15
Ratio catchment:wetland size	57.68	65.13	16.30	99.07
Altitude (m)	690.68	42.18	663.88	717.47
Slopes	4.87	2.17	3.49	6.25
Natural vegetation (% cover)	35.28	28.05	17.46	53.10
Dry croplands (% cover)	50.94	21.71	37.14	64.73
Irrigated croplands (% cover)	10.91	17.39	0.14	21.96
Ten kilometers scale				
Catchment size (ha)	3139.42	1213.24	2368.56	3910.27
Ratio catchment:wetland size	130.90	144.80	38.89	222.90
Altitude (m)	680.06	32.09	659.67	700.45
Slopes	4.30	2.06	2.19	5.61
Natural vegetation (% cover)	34.90	21.89	20.99	48.80
Dry croplands (% cover)	49.97	17.48	38.87	61.07
Irrigated croplands (% cover)	11.33	9.07	5.56	17.10

USA). LULC type (natural vegetation, irrigated and dry croplands) and landscape scale (buffer strip, 1 km, 5 km, 10 km) were the independent factors, and the arcsin-transformed percentage cover of LULC types across landscape scales was the dependent variable.

3. Results

3.1. Environmental variability

The wetlands included in this study showed a wide range of variation in the measured limnological variables, as the data

from the microcosms show (Tables 1 and 2). Most notably three of the wetlands (Almodovar, Saladilla, Posadilla) showed extraordinary high total P concentrations (>1.5 mg L^{–1}), with the maximum recorded in the severely degraded Almodovar pond while the Alberquilla pond was the least P enriched (Table 1). Highest electrical conductivity levels were found in La Nava Grande while the minimum was again recorded in La Alberquilla. Carrizosa and Garbanzos ponds showed the highest plant species richness. No plants germinated in microcosms pertaining to Almodovar pond. Rarefied microinvertebrate species richness was highest in Garbanzos pond and lowest in Carrizosa pond. *B. orientalis* occurred in 7 wetlands.

Fig. 1 – Mean densities and standard deviations of *Branchinecta orientalis* and *Triops cancriformis* observed in the wetland microcosms throughout the study.

The highest and lowest density was found in Cañada pond and Prado pond, respectively (Fig. 1). When *T. cancriformis* was found, it showed sympatric occurrence with *Branchinecta* (in 4 wetlands) (Fig. 1). Highest *Triops* densities were recorded in Carrizosa pond and the lowest in Nava de Enmedio pond.

The landscape was dominated by dry croplands which covered on average ca. 50% of the catchments across all scales (Fig. 2). Also natural vegetation cover and irrigated cropland cover were equally distributed across scales, with a mean coverage around 40% and 10%, respectively, in the catchments. The differences in land use types resulted in a highly significant LULC category effect in the two-way ANOVA ($F_{2,132} = 24.99$; $P < 0.0001$). However, the effects of scale and the interaction of LULC category and scale were not significant ($P > 0.05$) suggesting that the proportion of LULC types remains similar at all scales studied here.

3.2. Redundancy analysis

3.2.1. *Branchinecta*

This species was influenced chiefly by local conditions [L] at most scales, which explained >60% of the variance (Table 3, Fig. 3). The reduced RDA model suggests that electrical conductivity and total nitrogen had significant ($P < 0.05$) negative

Fig. 2 – LULC characteristics of the Campo de Caltrava are compared within and between spatial scales. Shown are the means from the 12 studied wetlands and the standard deviations.

effects on the densities of this species at the local scale (Figs. 3 and 4), which resulted in an absence of *Branchinecta* in the most eutrophic ponds. Despite their contribution to factor loading in the RDA ordination plots (Fig. 4), landscape effects [R/L] were only significant at the 10 km scale (Table 3), where the catchment:wetland size ratio correlated negatively with *Branchinecta* densities (Fig. 3). However, the negative values obtained for [L∩R] suggest that there was no shared variance between local and landscape effects at this scale (Table 3). Landscape characteristics therefore did not seem to affect *Branchinecta* through effects on local water quality.

3.2.2. *Triops*

In contrast to *Branchinecta*, the influence of local characteristics on the densities of this species was less strong (ca. 22%; Table 3, Fig. 3), and the proportion of unexplained variance ($100 - [L + R]$) was rather high. Despite local effects explaining significantly *Triops* density, none of our water quality variables showed significant factor loadings in the RDA (Figs. 3 and 4). Landscape effects were also only significant at the 10 km scale. Although landscape effects were not significant at the buffer-, 1 km-, and 5 km scale, the varying degree of covariation ([L∩R]), suggests that there was at least a slight

Table 3 – Results from RDA analyses showing variance partitioning (Variance explained [%]) and associated P levels (* $P < 0.05$, ** $P < 0.01$, ns: not significant) of *Branchinecta* and *Triops* densities in ponds of the Campo de Calatrava area across four spatial scales

	<i>Branchinecta</i>				<i>Triops</i>			
	Buffer	1 km	5 km	10 km	Buffer	1 km	5 km	10 km
[L + R]	90.1*	78.4*	93.3**	84.8**	25.8*	33.1*	42.2*	73.9**
[L]	61.6**	61.6**	61.6**	61.6**	22.1**	22.1**	22.1**	22.1**
[R]	25.3ns	8.2ns	21.5ns	21.5ns	8.1ns	34.0ns	26.5ns	71.0ns
[L/R]	64.8*	78.4**	71.8**	63.3**	17.7*	5.4**	14.6**	2.9**
[R/L]	28.5ns	25.0ns	31.7ns	23.2*	3.7ns	17.3ns	19ns	51.8*
[L∩R]	−3.2	−16.8	−10.2	−1.7	4.4	16.7	7.5	19.2
100 − [L + R]	9.9	21.6	6.7	15.2	74.2	94.6	58.8	26.1

Notes: The components are: [L + R] total variation explained by combined local and regional variables, [L] variation explained by local environmental variables, [R] variation explained by landscape variables, [L/R] pure local variation, [R/L] pure landscape variation, [L∩R] the regional structuring in the species data that is shared by the local data, and 100 − [L + R] unexplained variation. No significance values were calculated for [L∩R] and 100 − [L + R].

Fig. 3 – Variance partitioning (%) of the data matrix of *Branchinecta* and *Triops* across spatial scales. Four different components are given: pure local variation [L|R] (white areas in bars), pure regional (landscape) variation [R|L] (light grey areas), the shared local and regional variation [L|R] (dark grey areas), and the unexplained variation ($100 - [L + R]$) (black areas). Environmental variables (TN, total nitrogen; Cond., electrical conductivity; Irrig. crop., irrigated croplands; Ratio, catchment:wetland size ratio) that contributed significantly to factor loading in the RDA axes and their correlation coefficients and signs of relationship with the densities of the branchiopods are indicated. Those that were not significant are not shown.

coupling of local and landscape effects in the regulation of *Triops* densities. This is also reflected in the amount of variance that was explained by combined local and landscape ([L + R]; Table 3) effects which increased with increasing scale. Irrigated croplands had a significant negative influence on *Triops* densities at the 10 km scale (Figs. 3 and 4).

4. Discussion

4.1. Local vs. landscape effects

Scale was important in mediating in the strength of landscape effects on *Triops* and *Branchinecta* densities. Local characteristics were important for both species across all scales; however, their influence was species specific. In the case of *Branchinecta* the high amount of variation explained by the negative effects of electrical conductivity or total nitrogen suggests that the increased amount of solutes in the water column could reflect local contamination effects to which this

species is sensitive. Many wetlands in the Campo de Calatrava area and elsewhere have traditionally served as natural waste water treatment areas, storage sites for solid wastes, have subsidised live stock breeding or suffered from other local practices that contributed to severe eutrophication (Brinson and Malvarez, 2002; Alvarez-Cobelas et al., 2005). This was especially evident in some of the wetland microcosms where total phosphorus concentrations were extremely elevated (Tables 1 and 2). Because wetlands are coupled biogeochemically with their catchments (Detenbeck et al., 1996; Luo et al., 1997; Crosbie and Chow-Fraser, 1999; Loughheed et al., 2001; Houlihan and Findlay, 2004), we would have expected LULC characteristics to exert at least a notable influence on local trophic conditions across all spatial scales, which should have been manifest in either a covariation ([L|R]) of local and landscape characteristics on branchiopod densities or significant effects of the landscape scale in our RDA analyses. However, no shared variance was revealed for *Branchinecta* in the RDA consistently across all scales studied, neither was the landscape scale significant at scales below 5 km. This is surprising given that the LULC categories studied here are treated with $20\text{--}210\text{ kg ha}^{-1}\text{ a}^{-1}$ of fertilizers (Consejería de Medio Ambiente, 2004) and this could contribute to local eutrophication because of runoff-related processes. We hypothesise that the lack of significant landscape effects at small-scales in the case of *Branchinecta* was due to severe local contamination that has overridden any LULC mediated effects on local trophic conditions. While LULC effects could have been still relevant, local contamination effects are likely strong enough to lead to a false conclusion that landscape characteristics at small spatial scales are not important.

The only significant landscape effect on *Branchinecta* densities was observed at the 10 km scale through the negative correlation with the catchment:wetland size ratio, suggesting that *Branchinecta* densities are susceptible to a small patch-size effect. Alvarez-Cobelas et al. (2005) have shown that Mediterranean aquatic ecosystems are characterised by a higher size ratio compared to those situated in temperate regions, and our study shows that this effect can directly influence biotic wetland characteristics. However, the catchment:wetland size ratio is a quantitative measure, and may therefore serve as a surrogate for qualitative effects at the local (e.g., trophic status) and regional scale (LULC effects). For example, while no inference can be made about potential LULC effects based on a significant size ratio effect, it is nevertheless reasonable to assume that extensive agricultural use in large catchments can have a proportionally stronger negative effect on this species than in catchments dominated by natural vegetation. This assumption is supported by an alternative RDA approach where we excluded wetlands that did not contain branchiopods (not shown). In this model irrigated croplands had a significant positive effect ($r = 0.75$, $P < 0.05$) on *Branchinecta*, which suggests that agricultural practices at broad landscape scales benefit this species. However, we interpret this contradictory relationship as a result of local contamination events that are especially pronounced in wetlands that tend to be surrounded by catchments with a relatively high degree of natural vegetation cover. This suggests that wetlands located in catchments dominated by irrigated croplands at broad spatial scales should be less degraded from

Fig. 4 – RDA ordination plots showing relationships of branchiopod densities with sites and environmental variables at the buffer (A), 1 km (B), 5 km (C) and 10 km (D) catchment scale. The models were constructed from the reduced set of environmental variables in the L + R analyses (see methods for details). Abbreviation: Electr. cond., electrical conductivity; Ratio, catchment:wetland size ratio.

local contamination, thereby sustaining populations of *Branchinecta*.

The relationships of local and landscape characteristics with *Triops* were different from those observed for *Branchinecta*, likely because the occurrence and density patterns in the pond complex differed between both species. In contrast to *Branchinecta*, the results of *Triops* agreed with our expectation that the influence of landscape effects should become stronger with increasing spatial scale. However, we acknowledge that only a low sample number was available for the analyses so that our results must be viewed with caution as trends rather than mechanistic processes. Local characteristics explained less variation consistently across all scales in *Triops* than in *Branchinecta*. We observed a variable degree of covariation of local and landscape characteristics across scales which were not evident for *Branchinecta*. Although landscape characteristics were not significant at scales below 5 km, the increase of explained variability by combined local and landscape effects ([L + R]; Table 3) suggests that landscape influence on *Triops*, reflected also by the increase of the pure landscape effect ([RIL] in Table 3), became more important with increased scale. Except the significant contribution of irrigated croplands to factor loading in the landscape model

at the 10 km scale, none of our measured variables explained *Triops* densities.

4.2. The importance of broad landscape scale

Our analyses suggest that LULC effects are marginal at small spatial scales. This contradicts the patterns observed in previous studies (Declercq et al., 2006) which have shown adverse LULC effects to be more important in the immediate surrounding of ponds rather than at broad scales. In addition to the strong local contamination effect that have overridden landscape effects, several other reasons may have contributed to a potential underestimation of LULC effects at smaller landscape scales. We have used rather recent land use data, but as has been shown by Harding et al. (1998) and discussed by Declercq et al. (2006), LULC history can be important and have long-lasting effects on ecosystems with past land use data being better suitable for predicting present ecosystem states than recent land use data. Our LULC categories were also rather broad, including land use types which may cover widely different practices. Irrigated and non-irrigated vineyards, olive and cereals plantations require different levels of treatment intensity. When these are lumped into a single

category much of the variability may be lost and could lead to an underestimation of true relationships.

The resolution of our land use categories was sufficient enough to result in a significant pure landscape effect at the 10 km scale only. Even though irrigated croplands were the smallest LULC fraction in this study they had a significant effect on both branchiopod species. Current perspectives invoke nutrient, contaminant and sediment runoff from watersheds as sources of agricultural impact on aquatic ecosystems (Detenbeck et al., 1996; Luo et al., 1997; Crosbie and Chow-Fraser, 1999; Loughheed et al., 2001; Houlahan and Findlay, 2004). While such processes may be essential when taking into account microtopographic characteristics at small landscape scales, these small-scale details are blurred when working at broad landscape scales. For example, several ponds in the Campo de Calatrava area are located in volcanic craters and have therefore relatively low surrounding watershed areas from which runoff can take place. Because of steep slopes, natural vegetation is usually the dominant LULC type in these crater settings. Therefore other mechanisms than runoff must be taken into account if land use practices beyond the watershed boundaries are to affect aquatic ecosystems and their constituent biota locally. Wet and dry atmospheric deposition are increasingly recognised as sources of contaminants to aquatic ecosystems, especially in agriculturally exploited areas (Gil and Sinfort, 2005; Goel et al., 2005; Chen and Mulder, 2007). While storm events are quite common in the Campo de Calatrava area, we lack detailed information on spatiotemporal source – sink dynamics of agricultural contaminants mediated by atmospheric phenomena. Future studies should therefore consider spatial scales that extend beyond watershed boundaries, in addition to local contamination events and runoff-mediated processes within watershed to obtain an integral picture of agricultural impact on aquatic ecosystem integrity.

4.3. Management and conservation implications

In this study, the most striking difference between both species is the relevance of local conditions and the proportion of local and landscape effects on their densities across the spatial scales studied here. Our hypothesis put forward above suggests that local degradation can be so severe to lead to a misleading conclusion that landscape effects are not relevant, and more importantly, to the false picture that agricultural practises can be beneficial to some species. Yet, if landscape effects have a negative influence, populations may deteriorate in the long-term, highlighting the need for a regional conservation perspective. In essence our study highlights that broad catchment scales that extend beyond watershed boundaries may affect Branchiopoda densities. This adds a new dimension to the current believe in temporary wetland ecology that runoff-related processes within watershed are main landscape scale contributors to the impairment of wetland ecological integrity. Both species studied here form integral parts of resting egg banks in temporary wetlands. It will be necessary to reveal how community structural aspects and functional properties derived from resting egg banks will respond to such broad scale impact. This has important implications for biodiversity-related aspects of temporary

wetlands and may be relevant for their management and conservation.

The general conclusions arising from this study suggest that management and conservation can adopt two strategies which are not mutually exclusive. *Branchinecta* could benefit from restoration of water quality at the local scale; however a series of ecological and technical limitations challenge efficient management. For example, dredging of sediments would not only reduce the amount of stored nutrients but also destroy propagule banks through elimination of resting eggs from which the branchiopods emerge. Other costly technological interventions commonly used in lakes such as aeration of the water column are not only doubtful from the ecological perspective but also unviable in this socioeconomically less favoured area. Other management options could focus on landscape schemes and target negative LULC effects in the longer term. Both species could benefit from rationalisation of agricultural practises (reduction of pesticide, nutrient and sediment runoff). However, because large-scale changes in LULC conditions are unlikely to occur in this area, the creation of vegetated buffer strips in the immediate surrounding of ponds and/or the creation of hedgerows around agricultural fields to counteract potential nutrient and contaminant fluxes associated with atmospheric processes could comprise a practical first step to the conservation of temporary wetland resting egg banks, and especially large branchiopod populations.

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