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Author(s): Blanca Martínez-García, Oier Suarez-Hernando, Jone Mendicoa and Xabier Murelaga

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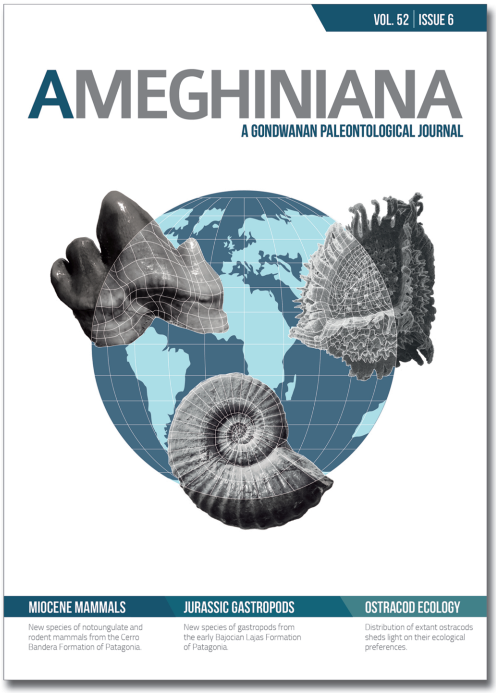

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BLANCA MARTÍNEZ-GARCÍA
OIER SUAREZ-HERNANDO
JONE MENDICOA
XABIER MURELAGA

Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco (UPV/EHU), B. Sarriena s/n, Apartado 644, Bilbao, E-48080, Spain.

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LIVING OSTRACOD SPECIES FROM PERMANENT AND SEMI-PERMANENT PONDS OF BARDENAS REALES DE NAVARRA (NORTHERN SPAIN) WITH REMARKS ON THEIR ECOLOGICAL REQUIREMENTS

BLANCA MARTÍNEZ-GARCÍA, OIER SUAREZ-HERNANDO, JONE MENDICOA AND XABIER MURELAGA

Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco (UPV/EHU), B. Sarriena s/n, Apartado 644, Bilbao, E-48080, Spain. *blancamaria.martinez@ehu.es*; *oier.suarez@ehu.es*; *jone.mendicoa@ehu.es*; *xabier.murelaga@ehu.es*

Abstract. Ostracod species living in 13 ponds (25 sample points) in Bardenas Reales de Navarra Natural Park and World Biosphere Reserve are studied for the first time. Nineteen species were identified, nine of them being the most abundant. According to statistical analyses (cluster and Correspondence Analysis), the distribution of ostracod species in this semi-arid area is mainly controlled by water conductivity and pH. The hydroperiod, sediment type, dissolved oxygen, altitude and vegetation cover play a secondary role. Thus, in semi-permanent waters with conductivity between 4.5 and 5.4 mS/cm and pH from 7.95 to 8.73 the most abundant species is *Sarscypridopsis aculeata* (Costa). In ponds with water conductivity from 0.3 to 2 mS/cm, pH between 7.1 and 7.78 and dissolved oxygen from 0.1 to 7.95 mg/l, *Cypridopsis vidua* (Müller) is the most abundant species. When the vegetation cover increases in this type of ponds, *Limnocythere inopinata* (Baird) and *Potamocypris villosa* (Jurine) appear as more abundant. Finally, in ponds with conductivity between 0.34 and 2.8 mS/cm and sporadic input of running waters *Ilyocypris bradyi* Sars, is the most important species. When the internal water current increases in these ponds, *Pseudocandona albicans* (Brady) appears as most abundant. However, the accumulation of dead organic matter within the bottom sediment of these ponds favours the decrease of dissolved oxygen and the development of *Eucypris virens* (Jurine). With this work, we contribute to the knowledge of the ostracod biodiversity of this semi-arid environment and the ecological preferences of this group.

Key words. Freshwater. Ostracods. Ecology. Ponds. Bardenas Reales de Navarra.

Resumen. ESTUDIO DE LAS ESPECIES DE OSTRÁCODOS VIVOS EN BALSAS PERMANENTES Y SEMI-PERMANENTES DE BARDENAS REALES DE NAVARRA (NORTE DE ESPAÑA) CON COMENTARIOS SOBRE SUS REQUISITOS ECOLÓGICOS. Se estudian por vez primera las especies de ostrácodos que habitan en 13 balsas (25 puntos de muestreo) del Parque Natural y Reserva Mundial de la Biósfera de Bardenas Reales de Navarra. Se han identificado 19 especies siendo nueve de ellas las más abundantes. Según los análisis estadísticos (cluster y Análisis de Correspondencias), la distribución de las especies en esta área semi-árida está controlada principalmente por la conductividad y el pH, siendo secundarios el hidroperiodo, tipo de sedimento, oxígeno disuelto, altitud y cobertura vegetal. Así, en balsas semi-permanentes con valores de conductividad entre 4,5 y 5,4 mS/cm y pH de 7,95 a 8,73 la especie más abundante es *Sarscypridopsis aculeata* (Costa). En balsas con conductividades de 0,3 a 2 mS/cm, pH entre 7,1 y 7,78 y oxígeno disuelto de 0,1 a 7,95 mg/l, *Cypridopsis vidua* (Müller) es la más abundante. Cuando la cobertura vegetal aumenta en estas balsas, *Limnocythere inopinata* (Baird) y *Potamocypris villosa* (Jurine) aparecen como más abundantes. Finalmente, en balsas con conductividades entre 0,34 y 2,8 mS/cm y entrada esporádica de agua corriente, *Ilyocypris bradyi* Sars, es la más importante. Cuando aumenta la corriente interna en estas balsas, *Pseudocandona albicans* (Brady) aparece como más abundante. Sin embargo, la acumulación de materia orgánica en descomposición en el sedimento del fondo de esas balsas favorece la disminución del oxígeno disuelto y el desarrollo de *Eucypris virens* (Jurine). Con este trabajo contribuimos al conocimiento de la biodiversidad de ostrácodos de este ambiente semi-árido y de sus requisitos ecológicos.

Palabras clave. Agua dulce. Ostrácodos. Ecología. Balsas. Bardenas Reales de Navarra.

OSTRACODS are a group of bivalved microcrustaceans inhabiting all aquatic environments, from continental to abyssal oceanic areas and from fresh to hipersaline water (Rodríguez-Lázaro and Ruiz-Muñoz, 2012). In freshwater ecosystems, their distribution is related to several physicochemical parameters of water such as temperature, salinity, pH or dissolved oxygen, and several characteristics of the sediment, such as average grain-size or sedimentation rates (Ruiz *et al*., 2013). Their rapid response to changes of these ecological variables, in addition to the fact that ostracods occur in all aquatic environments, favours the use of this group as a bioindicator in those ecosystems in which

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other groups cannot be used, such as stagnant or temporary waters. The application of this recent ecological knowledge is very useful both in paleoenvironmental reconstruction of aquatic environments and in monitoring the anthropogenic impact in these ecosystems (Rodríguez-Lázaro and Ruiz-Muñoz, 2012; Ruiz *et al.*, 2013).

In northern Spain, the semi-arid area of Bardenas Reales de Navarra presents a unique and fragile landscape and biological community, which is protected by the legislation about Natural Parks and World Biosphere Reserves. Several studies are being conducted in Bardenas Reales de Navarra using macrofaunistic groups such as birds, amphibian or reptiles in order to evaluate the natural evolution of the ecosystems in relation to climate change (Madoz *et al.*, 2013). However, no previous extensive work on the microfauna (*i.e.*, ostracods) and/or physico-chemical parameters of water has been carried out in this area.

This work is an initial study of the distribution of freshwater ostracod species living in several ponds of Bardenas Reales de Navarra (northern Spain), and the influence of environmental parameters on this distribution. In addition to contributing to the knowledge of the biodiversity of this Natural Park and World Biosphere Reserve, we corroborate the use of ostracods as proxies to carry out future ecological studies of the aquatic ecosystems and paleoenvironmental interpretations of the Quaternary sequences preserved in the study area.

STUDY AREA

Bardenas Reales de Navarra is a National Park and a World Biosphere Reserve located in northern Spain, next to Pamplona/Iruñea and Zaragoza localities (Fig. 1). It covers an area of 420 km^2 at an altitude ranging between 280 and 659 m above sea level (**masl**) (Murelaga, 2000).

Geologically, the study area belongs to the western sector of the Ebro Basin, a triangular-shaped middle Eocene–late Miocene basin lying at the foreland of the Pyrenees, the Iberian Range and the Catalan-Coastal Ranges (Alonso-Zarza *et al.*, 2002). According to the geomorphological remarks, age and lithology of the outcrops (Fig. 1), Bardenas Reales de Navarra can be divided into three areas: the northern part, called La Plana (ponds 10 to 12), where the relief is composed of an alluvial Quaternary terrace overlying Miocene rocks (Sancho *et al.*, 2008); the most depressed area located in the central part, La Blanca (ponds 0 and 4 to 8), which is an extensive semi-enclosed depression excavated in Miocene materials and partially overlain by alluvial Quaternary deposits (Sancho *et al.*, 2008); and the southern part, La Negra (ponds 1 to 3), where the landscape is formed by Miocene limestones (Larrasoaña *et al.*, 2006).

The climate in this area is of semi-arid continental Mediterranean type, with equinoctial, scarce, irregular and torrential precipitations, particularly high during spring and autumn (Comunidad de Bardenas Reales de Navarra, 1998). The mean annual precipitation ranges between 400 and 500 mm and is irregularly distributed along Bardenas Reales de Navarra, being lowest in the central part (La Blanca) and highest in the southern one (La Negra). The average annual temperature is between 13 and 14 °C, with average values of 4–6 °C in January and 22–24 °C in July. Heat waves are common during summer, with temperatures as high as 44 °C (Comunidad de Bardenas Reales de Navarra, 1998).

The hydrological network lacks continuous water currents, being composed by a complex system of drainage canyons in which water flows only during rainfall periods (Comunidad de Bardenas Reales de Navarra, 1998). The semi-arid climate and the absence of aquifers retaining rain water are held responsible for this drainage network. The only water storage points are artificial ponds, supplied by surface runoff. Along the Bardenas Reales de Navarra area there are more than 150 of these artificial, permanent or semi-permanent ponds (diameter from 1 to 40 m and less than 3 m water depth), whose main function is to supply water to farming and animal husbandry. However, in the first decade of the twenty-first century many of them have been abandoned and have undergone a natural evolution without human intervention (Comunidad de Bardenas Reales de Navarra, 1998). Thirteen of these abandoned ponds are studied in this work (Fig. 1).

MATERIALS AND METHODS

The ostracod species living in 13 different abandoned ponds of Bardenas Reales de Navarra were studied (Fig. 1; Supplementary Online Information). The study was carried out along altitudinal precipitation transects and covered different substrate types. On average, two sampling points were selected in each pond (total sample points n= 25). Samples were obtained in July (summer) of 2013 using a

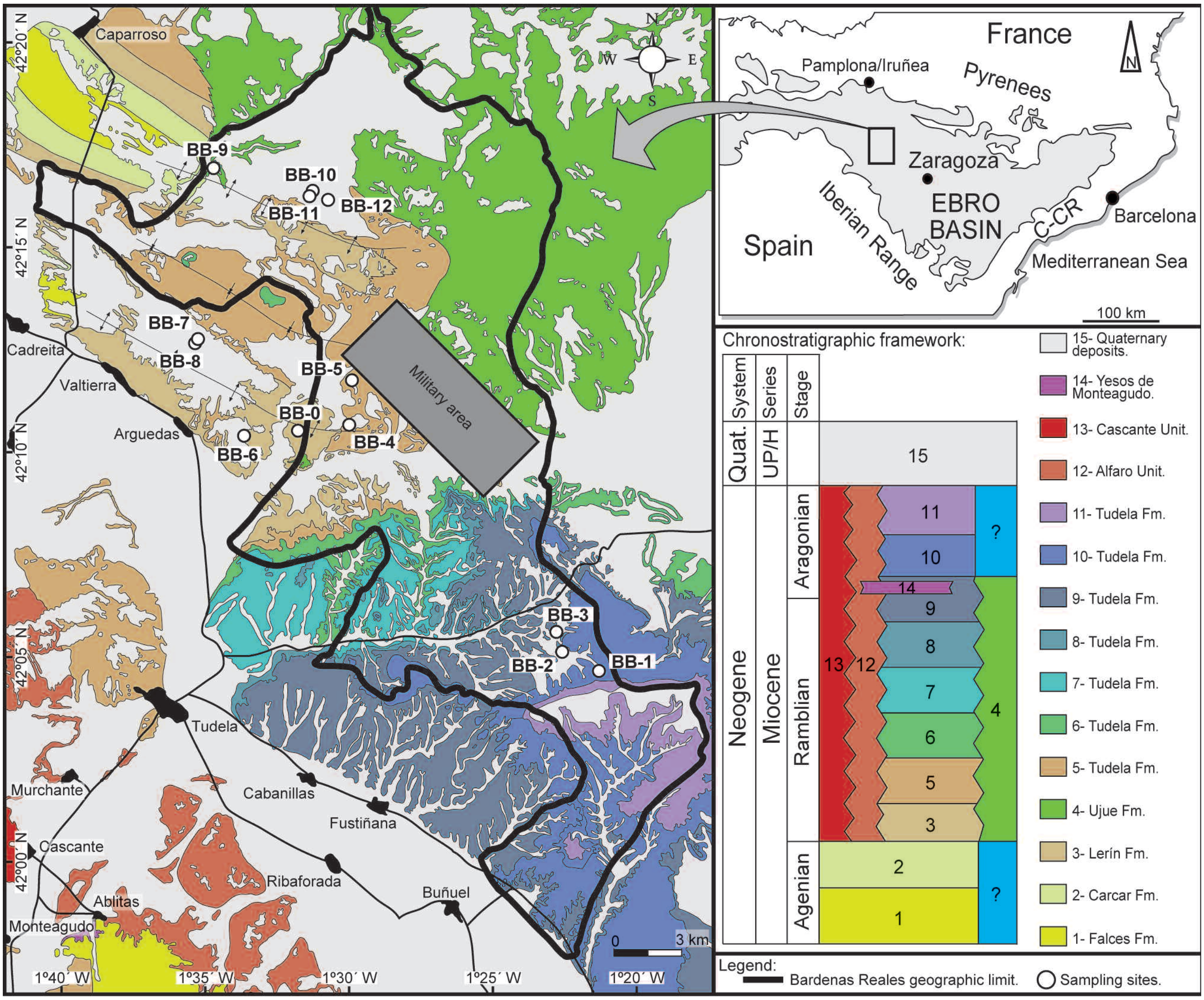

Figure 1. Geographical and geological location of the studied ponds (geological framework modified from Murelaga, 2000). **C-CR,** Coastal-Catalan Ranges; **UP/H,** Late Pleistocene/ Holocene. Chronostratigraphic framework: **1,** Claystone and gypsum; **2,** Gypsum, claystone, sandstone and scarce limestone; **3,** Gypsum and claystone; **4,** Claystone, siltstone and sandstone; **5,** Red claystone with sandstone, limestone and gypsum nodules; **6,** Brown claystone and marl with sandstone and limestone; **7,** Grey limestone and marl; **8,** Red claystone with gypsum nodules and limestone; **9,** Brown claystone and marl with limestone; **10,** Red and grey claystone with sandstone-paleochannels and limestone; **11,** Limestone, grey-brown marl, and red claystone with sandstone and gypsum; **12,** Claystone and red siltstone with interbedded scarcely cemented sandstone; **13,** Conglomeratic channels alternating with sandstone, siltstone, claystone and gypsum; **14,** Gypsum with silex, claystone and red siltstone.

150 µm mesh hand net. In order to avoid the reduction of oxygen production and pH values during the night hours due to the absence of photosynthesis, the studied samples were taken only during day hours (from 10:00 to 17:00, GTM+1:00 hour) in two consecutive days. Because we used the living individuals during sampling period to analyse the recent environmental conditions, only the topmost sediment (< 3 cm) was collected. The sampling area includes approximately the 10 m^2 around the sampling point, and a total volume of 500 ml of wet sediment was collected in each sample. The ostracod assemblage was thus representative of each sample point or the entire small ponds studied in this paper. These wet sediments were kept in plastic vials with 70% ethanol. Several physico-chemical parameters of the water were measured during the sampling period (temperature, conductivity, dissolved oxygen and pH; Supplementary Online Information) using an Orion 810 Meter (water dissolved oxygen and temperature), a Hanna

HI 9033 Meter (conductivity), and a Hanna HI 9025 pH-Meter. Each sample was washed and sieved (150 μm mesh size) and the residual sediment was dried at room temperature. The description of the substrate type was based on the measurements of particle size using a Laser Diffraction Particle Size Analyzer LS 13 320 (**UPV/ EHU**); the coordinates, time of permanence of the water layer, altitude, vegetation cover (numerical value that ranged between 1= very scarce or less than 10% of the sample point area covered by vegetation, and 6= very abundant or more than 50% of the sample point area covered by vegetation) and type (taking into account only the abundance of *Magnopotamion*, reed grass of the genus *Typho-Schoenoplectetum*, rush grass of the genera *Molinion-Holoschoenion* and *Juncetea*, green algae and *Scirpetum*), and area of each pond, included in the Supplementary Online Information, are taken from Comunidad de Bardenas Reales de Navarra (1998) and Alejandro Urmeneta (director of the staff of Comunidad de Bardenas Reales de Navarra, *pers. comm.*, 2013).

At least 100 living specimens per sample were picked, as a lower number involves a loss of statistical power. However, when less than 100 specimens were available in the sample, the total number was considered. Only adults and last stage of juvenile individuals (A-1 instars) were considered in this work. The biocoenosis was identified following the criteria of Carbonel (1980), and we considered live individuals during sampling period those whose soft parts were observed inside the closed carapaces. The taxonomic analysis of the ostracod species was based mainly on Meisch (2000), completed with Meisch (1984, 1985) for the genus *Potamocypris* Brady, 1870 and Karanovic and Lee (2013) for the genus *Ilyocypris* Brady and Norman, 1889.

According to their percentage with respect to total specimens per sample, we considered as more abundant those species that appear with > 10% in at least one sample (Tab. 1). Several richness and diversity indices were calculated for each sample using the statistics software PAST (PAleontological STatistics; Hammer *et al.*, 2001) version 3.06 (2015): number of species (**S**), Dominance (**D**), Shannon (**H**) and number of ostracods per gram of dry sediment (**nO**).

Species assemblages, using Hellinger-transformed abundances (Legendre and Legendre, 2012), and their distribution in the studied samples were analysed using the PAST software cluster analysis. In Q-mode cluster analysis to obtain sample groups we used the Ward method, while in R-mode cluster analysis to obtain species groups we used the **UPGMA** (Unweighted Pair-Group Method using arithmetic Averages) method and the correlation index. Both dendrograms were validated to assess their best statistical significance by consistency, congruency and robustness tests using the PAST software. In the consistency test the results of each cluster analysis must have sense in relation to some external data (*e.g.*, ecological variables). In the congruence test we obtained similar results with different measuring methods (*e.g.*, presence/ absence of species). Finally, in the robustness test the grouping pattern was maintained slightly modifying the data (*e.g.*, eliminating a species or a sample). A Detrended Correspondence Analysis (**DCA**) was carried out to study the correlation among species and samples. The first two axes explain most of the variance percentage and can be interpreted as complex ecological variables of which variation gradients can be determined along the diagram. The relationship between species and ecological parameters was studied using a Canonical Correspondence Analysis (**CCA**) by running the PAST software and using the scale type 1 of Legendre and Legendre (2012). All ecological variables were transformed $[\ln(x + 1)]$ before the statistical analyses, and the Monte Carlo test (100 permutations) was used to provide significance levels for each variable using CANOCO program (Ter Braak, 1988). One-way ANOVA with unequal-variance (Welch) was used to check for normality of samples and species using the PAST software. To highlight correlations among ecological variables and species we used the Pearson linear correlation analysis. Water temperature was excluded of this statistical analysis because its variability in the sample points during sampling period is due to the daily solar exposure of the water. The area of each pond was also removed from the statistical analysis because it had a high non-significant influence in the distribution of ostracod species ($p \approx 1$).

RESULTS

Of the 25 studied samples, one of them (BB-9) did not contain living ostracods during the sampling period, while in other three samples (BB-2a, BB-2b and BB-2c) less than 100 individuals were found (Tab. 1). A total of 2,355 living ostracod specimens were obtained in the studied samples,

Table 1. Distribution of ostracod species determined in samples of Bardenas Reales de Navarra. Values are absolute number of live individuals. * areas depict most abundant species (> 10 %). In the lower part, richness and diversity indices are indicated.

species/ sample	*BB-0*	*BB-1a*	*BB-1b*	*BB-2a*	*BB-2b*	*BB-2c*	*BB-3a*	*BB-3b*	*BB-4a*	*BB-4b*	*BB-5a*	*BB-5b*	*BB-5c*	*BB-5d*	*BB-5e*	*BB-5f*	*BB-6a*	*BB-6b*	*BB-7a*	*BB-7b*	*BB-8*	*BB-10*	*BB-11*	*BB-12*	*TOTAL*
Candona candida *(Müller, 1968)*																			*1*	*1*					*2*
Candona neglecta *Sars, 1887*								*1*																	*1*
Cyclocypris ovum *(Jurine, 1820)*	*1*	*6*	*5*																						*12*
Cypridopsis vidua *(Müller, 1776)*	***25****										***51****	***83****	***18****	***53****	*9*	***31****	***77****	***96****	***20****	*5*	***17****				***485***
Cypris bispinosa *Lucas, 1849*																					*1*	*1*			*2*
Darwinula stevensoni *(Brady and Robertson, 1870)*		*3*	*2*								*2*									*2*	*1*				*10*
Eucypris pigra *(Fischer, 1851)*											*1*	*2*	*2*										*3*	*1*	*9*
Eucypris virens *(Jurine, 1820)*		*8*	*4*				*3*	***38****		*4*					***20****								*2*		***79***
Fabaeformiscandona breuili *(Paris, 1920)*																			*4*	*9*	*3*				*16*
Fabaeformiscandona spelaea *(Klie, 1941)*																					*1*				*1*
Herpetocypris brevicaudata *Kaufmann, 1900*	*1*										*2*	*7*													*10*
Heterocypris incongruens *(Ramdohr, 1808)*																	*2*								*2*
Ilyocypris bradyi *Sars, 1890*	*3*	***62****	***52****	***8****	***34****	***7****	***61****	***32****	***56****	***86****	***19****	*1*	***58****	*10*	***79****	***71****	***15****	*9*	***42****	***39****	***59****	***22****	*2*	*3*	***830***
Ilyocypris gibba *(Ramdohr, 1808)*		***11****	*7*	***2****	*3*			*1*	***21****	*6*	*2*		*4*		*2*				*7*	*6*	*6*				***78***
Limnocythere inopinata *(Baird, 1843)*	***40****			***6****	***7****	***5****	***24****	*2*	***11****	*10*	*11*		***25****	***46****											***187***
Potamocypris pallida *Alm, 1914*		*7*	***19****								***18****						*9*	*3*	***31****	*1*	*5*	*2*	***15****	***14****	***124***
Potamocypris villosa *(Jurine, 1820)*	***32****	*1*	*7*								*2*						*4*	*1*							***47***
Pseudocandona albicans *(Brady, 1864)*	*1*						*2*	*2*				***11****				*1*				***49****	***13****				***79***
Sarscypridopsis aculeata *(Costa, 1847)*	*8*	*9*	***12****	*1*	*1*		***14****	***30****	***20****	*5*	*6*	*1*		***14****		*3*						***82****	***87****	***88****	***381***
TOTAL	*111*	*107*	*108*	*17*	*45*	*12*	*104*	*106*	*108*	*111*	*114*	*105*	*107*	*123*	*110*	*106*	*107*	*109*	*105*	*112*	*106*	*107*	*109*	*106*	*2355*
Number of species S	*8*	*8*	*8*	*4*	*4*	*2*	*5*	*7*	*4*	*5*	*10*	*6*	*5*	*4*	*4*	*4*	*5*	*4*	*6*	*8*	*9*	*4*	*5*	*4*	
Dominance D	*0.3*	*0.4*	*0.3*	*0.4*	*0.6*	*0.5*	*0.4*	*0.3*	*0.4*	*0.6*	*0.3*	*0.6*	*0.4*	*0.4*	*0.6*	*0.5*	*0.6*	*0.8*	*0.3*	*0.3*	*0.4*	*0.6*	*0.7*	*0.7*	
Shannon H	*1.5*	*1.4*	*1.6*	*1.1*	*0.8*	*0.7*	*1.1*	*1.3*	*1.2*	*0.8*	*1.7*	*0.8*	*1.2*	*1.2*	*0.8*	*0.8*	*0.9*	*0.5*	*1.4*	*1.4*	*1.4*	*0.7*	*0.7*	*0.6*	
ostracods/ gramme nO	*300*	*126*	*103*	*6*	*22*	*3*	*452*	*379*	*1964*	*3759*	*579*	*113*	*15714*	*1025*	*3235*	*131*	*206*	*908*	*500*	*908*	*589*	*635*	*450*	*713*	

belonging to 19 species (14 genera). Nine of these species appear as more abundant (> 10% in at least one sample; Tab. 1): *Cypridopsis vidua* (Müller, 1776), *Eucypris virens* (Jurine, 1820), *Ilyocypris bradyi* Sars, 1890, *Ilyocypris gibba* (Ramdohr, 1808), *Limnocythere inopinata* (Baird, 1843), *Potamocypris pallida* Alm, 1914, *Potamocypris villosa* (Jurine, 1820), *Pseudocandona albicans* (Brady, 1864), and *Sarscypridopsis aculeata* (Costa, 1847).

Cluster analysis

The R-mode cluster differentiates two main species groups with seven ostracod subgroups in total (Fig. 2). The group 1 (with three subgroups) is formed by eight ostracod species and includes the abundant species *C. vidua*, *L. inopinata*, *P. villosa*, *S. aculeata* and *P. pallida*. The group 2 (with four subgroups) contains eleven species, with the abundant species *I. gibba*, *I. bradyi*, *P. albicans* and *E. virens*.

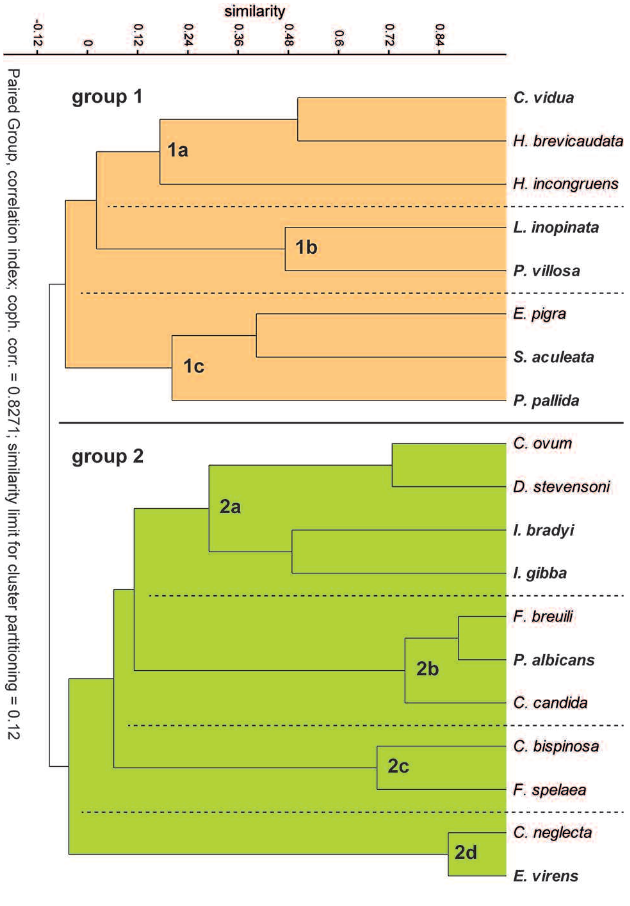

Figure 2. Multivariate analysis of ostracod species (R-mode cluster) identified in the studied ponds of Bardenas Reales de Navarra. **In bold,** more abundant ostracod species. Online version: **in orange,** species group 1; **in green,** species group 2.

The Q-mode cluster gathers the studied samples into three main groups, the last one subdivided in two subgroups (Fig. 3). Group I is composed by six samples located in the central part of the study area, in altitudes ranging between 292 masl and 310 masl. Ostracod richness is low, although the diversity is relatively high, compared with other groups. Group II includes the three samples obtained from the northern part of the study area, at altitudes from 418 to 423 masl. Ostracod richness is higher than in Group I, but the diversity is lower. The average values of the physico-chemical parameters of the water are the highest of the sample groups and subgroups identified in the cluster analysis. Group III includes the remaining studied samples obtained from the central and southern parts of the studied area, and it can be divided into two subgroups (Fig. 3). Subgroup IIIa includes ten samples, with altitudes ranging between 292 and 539 masl. Subgroup IIIb includes five samples, the three samples with less than 100 living individuals (BB-2a, BB-2b and BB-2c) located in the southern part of the study area and samples BB-3b and BB-7b from the central one (Fig. 1). The mean values of richness and diversity are lower than in Subgroup IIIa, being the average values of the physico-chemical parameters of the water similar in the two subgroups (Fig. 3).

Distribution of ostracod species

The distribution of ostracod species in the study area, *i.e.*, the relationship between studied samples and more abundant ostracod species, is shown in Figure 4. The samples that form Group I are characterized by the dominance of *C. vidua* (23–88%). In sample BB-5d *L. inopinata* is also abundant (37%). Sample BB-0 is slightly different, because *L. inopinata* (36%) and *P. villosa* (29%) are the most abundant species. In the samples of Group II the species *S. aculeata* is the most abundant (77–83%). The samples included in Group III are mainly influenced by *I. bradyi* (30–77%), but Subgroup IIIb shows some particularities: in BB-7b *P. albicans* (44%) is the most abundant species; in BB-3b the most common species is *E. virens* (36%).

Correspondence Analysis

The factorial plane of axes 1 and 2 of DCA analysis accounts for 47.2% of the total variance. In the graphical representation of these first two axes (Fig. 5.1), the sample groups and species are separated along axis 1 based on an increase in the values of conductivity, pH, dissolved oxygen and altitude from the left part of the diagram (lower values of axis 1) to the right part (higher values of axis 1). Axis 2 represents a combination of a decrease in vegetation cover and an increase in average grain size from the lower part of the diagram (lower values of axis 2) to the upper part (higher values of axis 2).

In CCA, the factorial plane of axes 1 and 2 accounts for 44.3% of the total variance. Taking into account the environmental variables selected for this analysis, the Monte Carlo test (permutations n= 100) renders an average value with $p < 0.05$ for conductivity and pH and, thus, they have a significant influence on the distribution of ostracod species and samples. The other variables, in particular altitude gradient ($p < 0.1$), dissolved oxygen, substrate type, time of permanence of the water layer, and vegetation cover ($p > 0.1$), had a non-significant influence. In the graphical representation of the two first axes of CCA (Fig. 5.2), axis 1 is positively related with conductivity, oxygen, pH and alti-

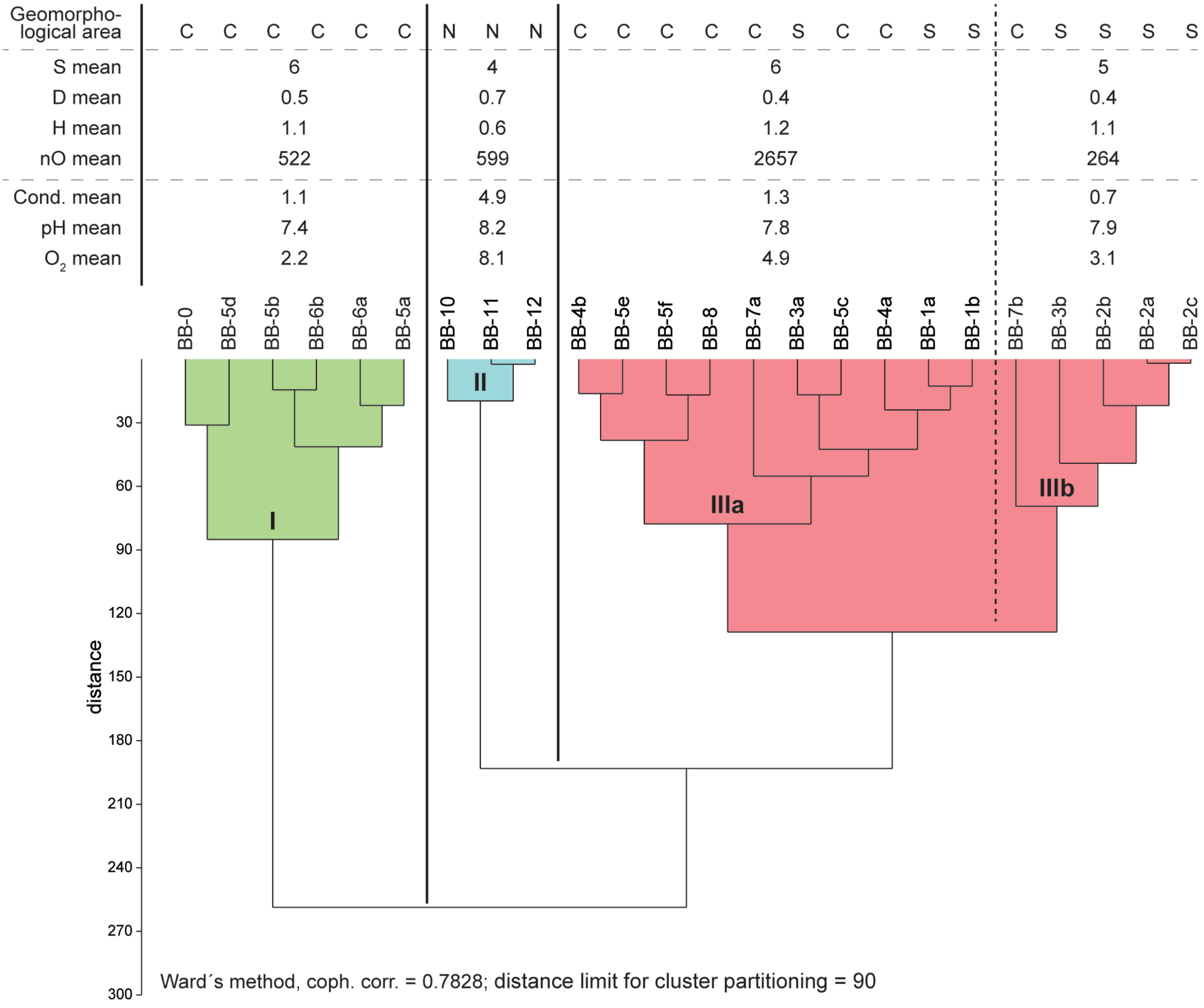

Figure 3. Multivariate analysis of samples (Q-mode cluster) based on main ostracod species identified in the studied ponds of Bardenas Reales de Navarra. In the upper part, average values for richness and diversity indices and for physico-chemical parameters of each Group and Subgroup. **S,** number of species; **D,** Dominance; **H,** Shannon index; **nO,** ostracods/gramme; **Cond.,** conductivity (mS/cm); in the geomorphological area: **C,** central part; **N,** northern part; **S,** southern part. Online version: **in green,** samples of Group I; **in blue,** samples of Group II; **in red,** samples of Group III.

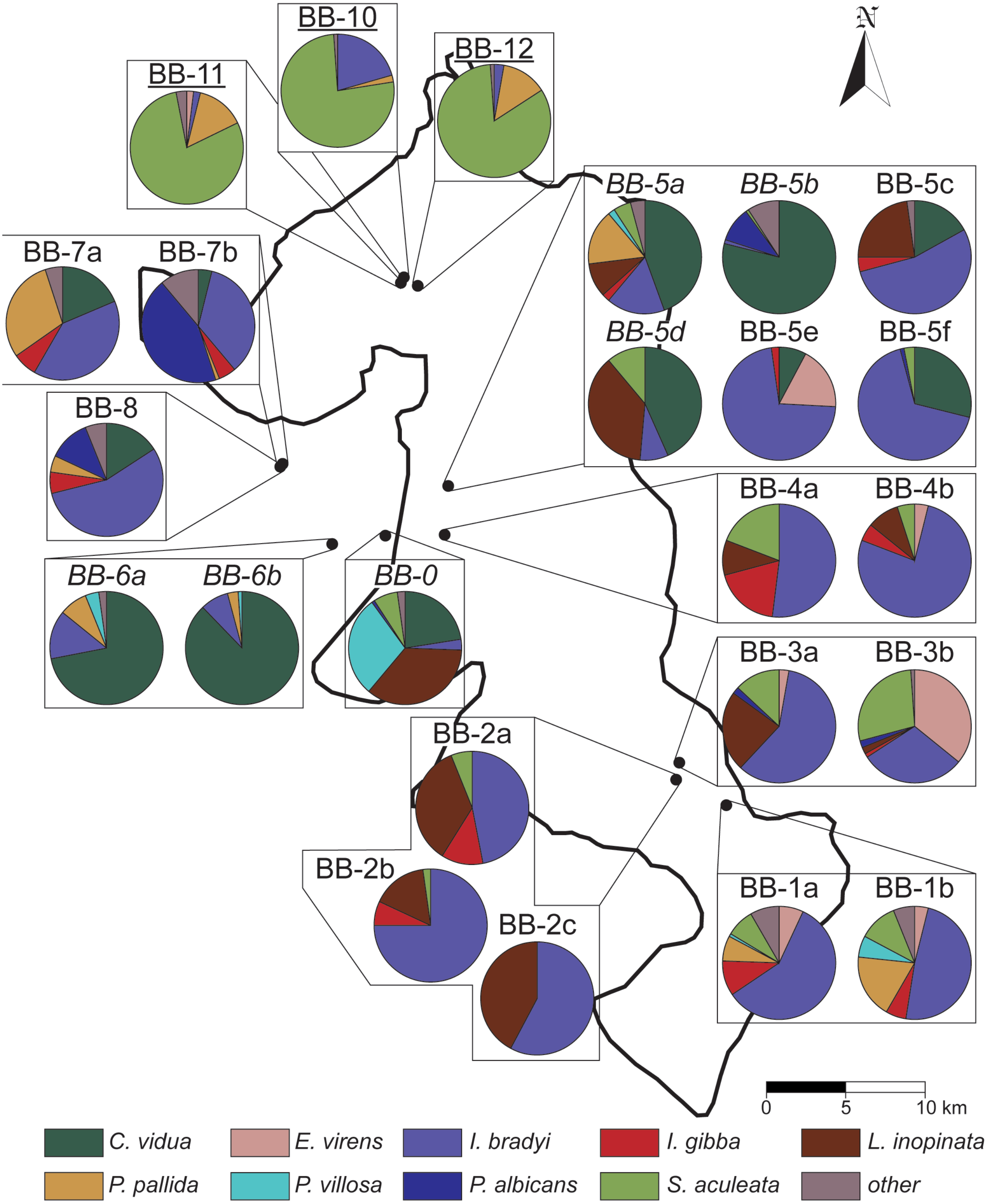

Figure 4. Distribution of more abundant ostracod species identified in the studied sample points. **In italics,** samples of Q-mode cluster Group I; **underlined,** samples of Q-mode cluster Group II; **in regular,** samples of Q-mode cluster Group III.

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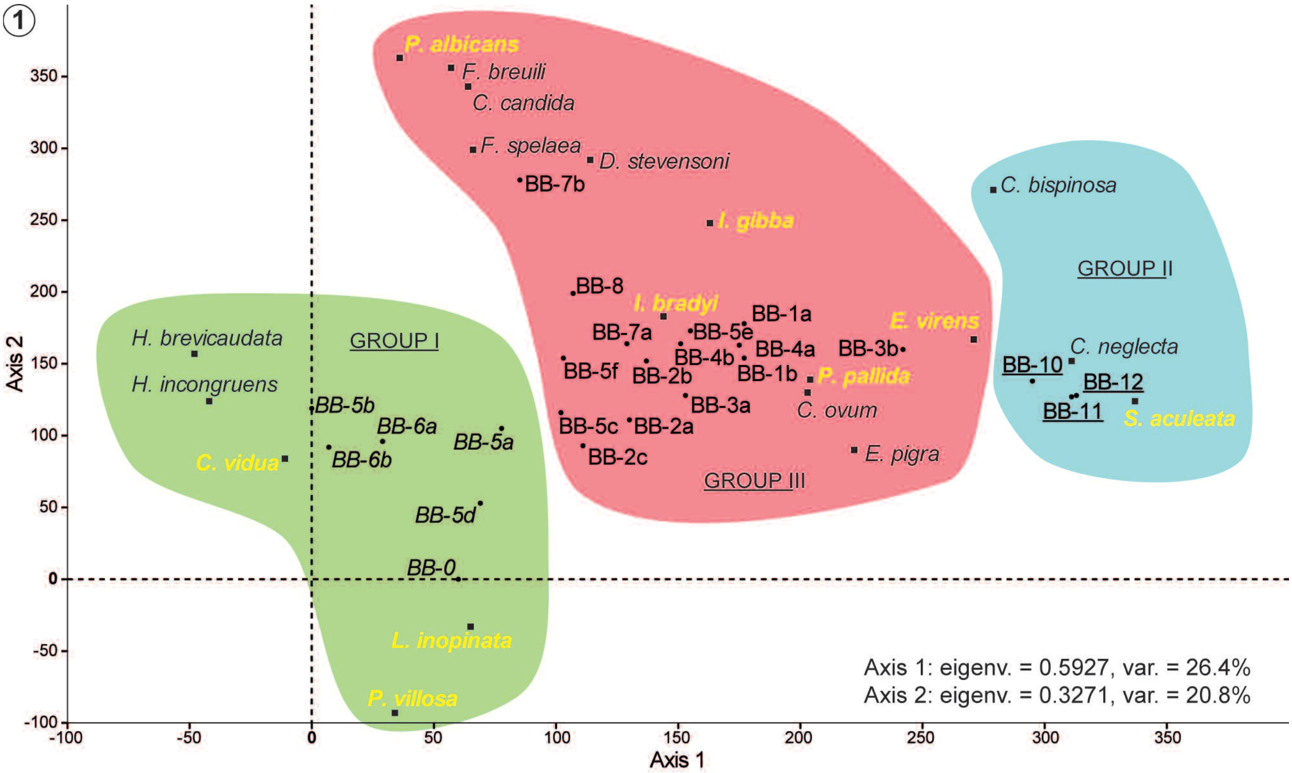

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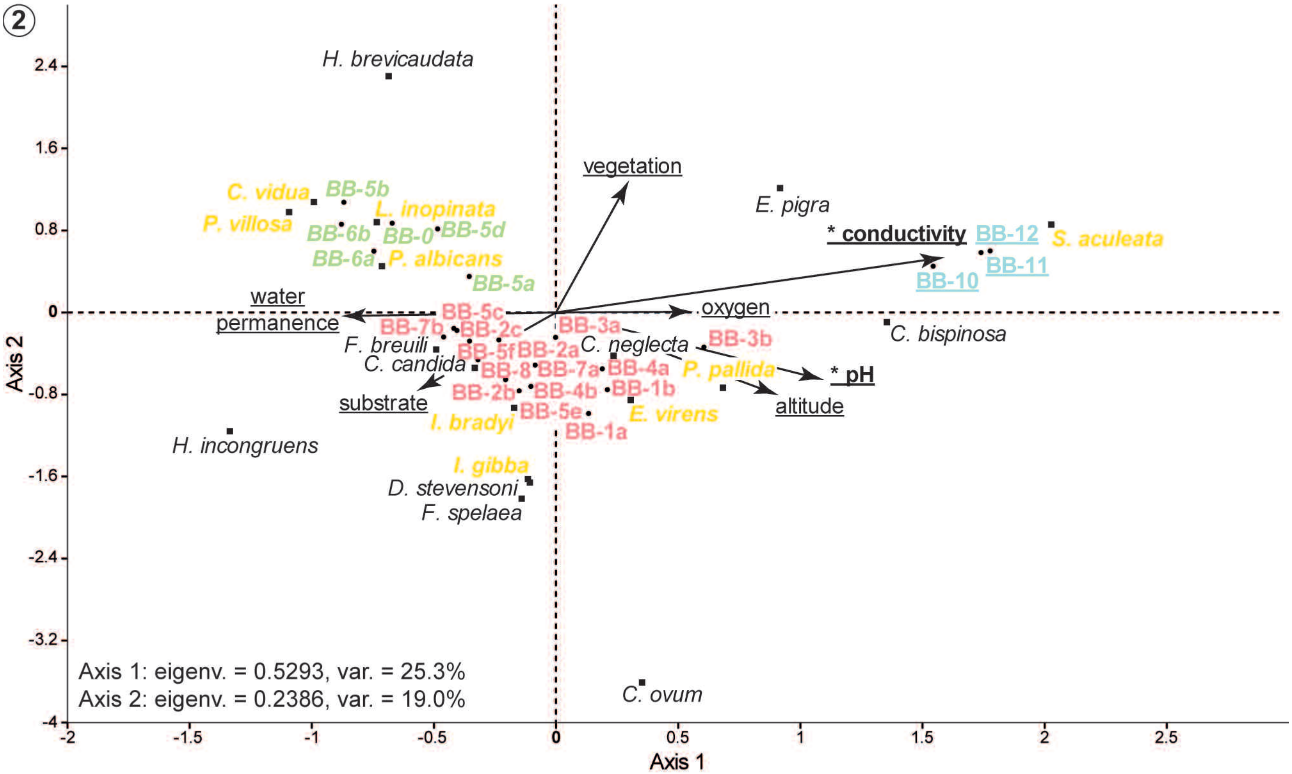

Figure 5.1. Ordination analysis (indirect gradient analysis) by Detrended Correspondence Analysis (DCA) of samples and species of ostracods. Q-mode cluster groups of samples are separated. **5.2.** Ordination analysis (direct gradient analysis) by Canonical Correspondence Analysis (CCA) of samples and species of ostracods; *, significant variables in the distribution of ostracod species. For species: **in italics and bold,** more abundant ostracod species. For samples: **in italics,** samples of Q-mode cluster Group I; **underlined,** samples of Q-mode cluster Group II; **in regular,** samples of Q-mode cluster Group III. Online version: **in green,** samples of Q-mode cluster Group I; **in blue,** samples of Q-mode cluster Group II; **in red,** samples of Q-mode cluster Group III; **in gold,** more abundant ostracod species.

tude gradient and negatively related with time of permanence of the water layer, while axis 2 is positively correlated with vegetation and negatively with substrate type.

Pearson linear correlation analysis

The correlation between ecological variables and ostracod species has been established based on the Pearson linear correlation analysis (Tab. 2). Taking into account only the most abundant ostracod species, *C. vidua* shows a strong negative correlation with pH and the altitude gradient. *Eucypris virens* is less influenced by the ecological parameters measured in this work, with a slightly negative correlation with dissolved oxygen and the substrate type, and positive with the altitude gradient. *Ilyocypris bradyi* and *I. gibba* species are both negatively influenced by the vegetation cover. *Limnocythere inopinata* has a clear positive correlation with the vegetation cover and a negative relation with the altitude gradient. Both dissolved oxygen and altitude gradient show scarce positive correlation with *P. pallida*, while time of permanence of the water layer has a negative correlation with this species. *Potamocypris villosa* has a slightly positive correlation with the vegetation cover and negative with the substrate type. Similarly, *P. albicans* does not show a great correlation with the studied ecological parameters, being slightly negatively correlated with water conductivity. However, *S. aculeata* presents strong positive correlation with water conductivity and pH and negative with time of permanence of the water layer.

DISCUSSION

In several springs of the eastern Iberian Peninsula, Mezquita *et al.* (1999a) showed that R-mode cluster groups

Table 2. Pearson linear correlation index (r) for ostracod species and measured physico-chemical parameters of the water.

	Cond.	*pH*	*Oxyg.*	*Alt.*	*Subs.*	*Veg.*	*Type*
C. candida	-0.24	-0.32	0.22	0.02	-0.04	0.01	-0.08
C. neglecta	-0.10	0.01	-0.19	0.17	-0.27	0.01	0.16
C. ovum	-0.20	0.49	-0.20	0.61	0.16	-0.48	0.25
C. vidua	-0.24	-0.67	-0.27	-0.59	-0.05	0.26	0.12
C. bispinosa	0.18	0.10	0.31	0.10	-0.15	0.15	-0.39
D. stevensoni	-0.25	0.27	-0.30	0.43	0.07	-0.33	0.27
E. pigra	0.43	0.13	0.33	-0.13	-0.41	0.44	-0.28
E. virens	-0.02	0.06	-0.26	0.17	-0.18	-0.12	0.08
F. breuili	-0.27	-0.23	0.10	0.03	-0.02	0.01	-0.04
F. spelaea	-0.17	0.06	0.18	0.02	-0.11	0.01	-0.27
H. brevicaudata	0.04	-0.21	-0.20	-0.29	-0.37	0.30	0.22
H. incongruens	-0.18	-0.22	-0.18	-0.18	0.33	-0.18	-0.27
I. bradyi	-0.15	0.02	-0.06	-0.03	0.11	-0.40	-0.08
I. gibba	-0.15	0.21	0.07	0.08	0.07	-0.32	-0.19
L. inopinata	-0.16	-0.15	0.21	-0.31	-0.29	0.40	0.23
P. pallida	0.09	0.04	0.26	0.25	-0.16	-0.03	-0.31
P. villosa	-0.22	0.03	0.09	-0.10	-0.26	0.28	0.18
P. albicans	-0.20	-0.16	-0.16	-0.02	-0.5	0.06	0.14
S. aculeata	0.86	0.41	0.25	0.28	-0.39	0.36	-0.42

Abbreviations: Cond., *conductivity;* ***Oxyg.,*** *oxygen;* ***Alt.,*** *altitude;* ***Subs.,*** *substrate;* ***Veg.,*** *vegetation;* ***Type,*** *time of permanence of the water layer.*

the ostracod species according to (micro-) habitat similarities rather than environmental features of the springs. These authors explain this conclusion because ostracod species, mainly cosmopolitan or pioneer species with a short life span, can coexist in spring habitats with different physico-chemical characteristics (Mezquita *et al.*, 1999a).

However, Q-mode cluster analysis groups the samples based on the ostracod species. The consistency, congruency and robustness tests confirm their best statistical significance and validate the relationship between the groups and the physico-chemical parameters measured on the water. On the other hand, CCA relates directly the species distribution to the ecological characteristics of the studied ponds. The previously performed DCA confirms the distribution of ostracod species and samples along complex ecological gradients, providing a consistent pattern that can be interpreted in ecological and biological terms.

According to CCA (Fig. 5.2), the ostracod species identified in several ponds of Bardenas Reales de Navarra are mainly influenced by water conductivity and pH. The sediment type, time of permanence of water layer, dissolved oxygen, altitude and vegetation cover play a secondary role in this distribution. The influence of conductivity as the main factor to determine ostracod distribution had been previous identified in other lacustrine environments, such as the Tibetan Plateau (Mischke, 2012) or the Yucatán Peninsula (Pérez *et al.*, 2010). However, the influence of other bio-ecological factors on ostracod distribution in the studied ponds can not be rejected, such as species competition (both between different ostracod species and with other taxa), food availability or predator pressure, which were not taken into account in the statistical analysis. Based on Q-mode cluster and CCA, three main groups of ponds were distinguished in the study area, characterized by an ostracod species and related with some ecological parameters.

Semi-permanent ponds with higher values of water conductivity

The first group includes the semi-permanent ponds located in the northern part of the study area (BB-10, BB-11 and BB-12; Fig. 1), at a relatively high altitude (418–423 masl), with higher values of water conductivity (4.5–5.4 mS/cm), pH (7.95–8.73) and dissolved oxygen (2.75–12.01 mg/l) (Q-mode cluster Group II; Fig. 3). The most abundant species in these ponds is *S. aculeata* (Fig. 4), which presents a positive correlation with conductivity and pH of the water and negative with time of permanence of the water layer, according to CCA (Fig. 5.2; Tab. 2).

Sarscypridopsis aculeata is a cosmopolitan species commonly occurring in temporary and shallow water bodies such as pools and marshes, being highly abundant in oligohaline to mesohaline waters (Petkovski, 1964; Ganning 1971; Meisch and Broodbakker, 1993; Martens *et al.*, 1996). Thus, salinity is the principal factor controlling the dominance of *S. aculeata* in the ponds located in the northern part of the studied area. Due to their high-altitude location without great input of runoff waters, their semi-permanent character and their small area (see Supplementary Online Information), the increase in water conductivity in these ponds probably responds to a combination of the percolation of water that dissolves the gypsum (with scarce levels of glauberite and halite) forming the substrate (Falces, Calcar, Lerín and Tudela formations; Fig. 1), and the partial evaporation of the stagnant water accumulated in the ponds, which increase the concentration of salts in the remaining water.

The high vegetation cover of these ponds (see Supplementary Online Information), consisting mainly of *Magnopotamion* species (Comunidad de Bardenas Reales de Navarra, 1998), triggers an increase of the internal eutrophication process that enhances the decomposition of organic matter. This high productivity of vegetation cover could be responsible for the high values of dissolved oxygen and pH of the water. These physico-chemical and ecological parameters (pH, dissolved oxygen and, with less importance, the vegetation cover) show a positive correlation with the abundance of *S. aculeata* in CCA (Fig. 5.2; Tab. 2).

The low diversity measured in these ponds (Fig. 3; Tab. 1) reflects the establishment of an unstable environment for the development of ostracods, probably related to high water conductivity and eutrophication processes, which favours the dominance of tolerant species such as *S. aculeata*.

Ponds with low values of pH and water conductivity

Ponds placed in the central part of the study area (ponds BB-0 and BB-6, and sample points BB-5a, BB-5b and BB-5d; Fig. 1) at low altitude (292–310 masl), with the lowest values of water conductivity (0.3–2 mS/cm), pH (7.1–7.8) and dissolved oxygen (0.1–7.95 mg/l) (Q-mode cluster Group I; Fig. 3) are included in this second group. The higher values of diversity indices of Group I in relation to Group II indicate the development of a more favourable environment for ostracod species. This group is characterized by the dominance of *C. vidua* (Fig. 4), which shows a strong negative correlation with pH and altitude gradient, and with minor importance, negative relation with dissolved oxygen and positive correlation with the vegetation cover in our CCA (Fig. 5.2; Tab. 2). This might be related to the lower pH of less saline waters.

Cypridopsis vidua is considered cosmopolitan and inhabits a wide variety of ecosystems with a relatively large tolerance to variation of water physico-chemical parameters (Külköylüoğlu, 2004; Külköylüoğlu and Yilmaz, 2006; Laprida, 2006; Dügel *et al.*, 2008). It is very common in aquatic macrophyte-rich waters, dominated by *Chara* species (Mbahinzireki *et al.*, 1991), being capable of living in oligotrophic to eutrophic water environments (Roca *et al.*, 1993). This phytophilic character can be identified in our CCA thanks to the positive correlation of this species with the vegetation cover (Tab. 2). However, the vegetation cover developed in the ponds that form this group (see Supplementary Online Information) is not enough to provide high concentrations of dissolved oxygen in the water. Therefore, the decomposition of organic matter, which in turn consumes the oxygen of the water, is more important. In addition, this anaerobic process could favour the decrease of the pH of bottom waters, which is the principal ecological factor that controls the distribution of *C. vidua* in the studied samples, according to CCA (Fig. 5.2; Tab. 2).

Nevertheless, in sample point BB-5d and pond BB-0, *L. inopinata* appears as abundant species, together with *P. villosa* in the latter (Fig. 4; Tab. 1). Both species are considered cosmopolitan and live in a wide range of environmental conditions (Baltanás, 1992; Mezquita *et al.*, 1999b; Meisch, 2000), commonly in mesotrophic to eutrophic environments with waters rich in macrophyte debris (Meisch, 2000; Mezquita *et al.*, 2000, 2001). This last characteristic is confirmed in this work by the positive correlation of both species with the vegetation cover observed in CCA (Fig. 5.2; Tab. 2). The higher vegetation content of BB-5d and BB-0, composed by filamentous and mucilaginous green algae, respectively, in relation to the other sample points from this Group I (see Supplementary Online Information) causes an increase in dissolved oxygen in the water.

Ponds with low values of water conductivity and sporadic inputs of running water

This last group is formed by ponds located in the central and southern part of the studied area (ponds BB-1, BB-2, BB-3, BB-4, BB-7 and BB-8, and sample points BB-5c, BB-5e and BB-5f; Fig. 1) in a wide range of altitude (292–539 masl) with low water conductivity (0.34–2.8 mS/cm) and intermediate dissolved oxygen content (0.09–14.41 mg/l) and pH (7.18–8.5) values compared to the other two sample groups (Q-mode cluster Group III; Fig. 3). These ecological features of the water favour the development of a stable environment for ostracod species, according to the relatively high diversity measured in the ponds that form Group III.

Despite the two subgroups identified in the statistical analysis (Fig. 3), the most abundant species in these ponds is *I. bradyi* (Fig. 4). This species is indicative of running water environments such as permanent streams, small rivers and rheocrene and helocrene springs (Henderson, 1990; Roca and Baltanás, 1993; Külköylüoğlu, 1999; Wu *et al.*, 2001). However, this species also occurs in temporary ponds and lacustrine environments with stagnant waters (Henderson, 1990), probably due to the occasional inflow of water from adjacent streams (Curry, 1999). According to that, the high percentage of *I. bradyi* observed in the studied area responds to the sporadic input of running water into the ponds that form Group III from nearby streams.

Ilyocypris bradyi prefers cooler water (Henderson, 1990), but it is present in a wide temperature range (3.7–27 °C) (Delorme, 1991; Roca and Baltanás, 1993; Meisch, 2000; Mezquita *et al.*, 2001; Bunbury and Gajewski, 2005), being an ostracod species with relatively high tolerance to variations on water conductivity, pH and dissolved oxygen (Mezquita *et al.*, 1999a, 2001; Meisch, 2000; Külköylüoğlu *et al.*, 2007). It has been reported as dominant species on vegetation-rich waters (Petkovski, 1958; Staplin, 1963) and eutrophic streams (Mezquita *et al.*, 2001). Nevertheless, in our CCA *I. bradyi* presents a negative correlation with the vegetation cover (Fig. 5.2; Tab. 2), indicating the preference of this species for relatively poorly vegetated ponds.

Taking into account the two subgroups of samples observed in Q-mode cluster (Fig. 3), the statistical separation of samples obtained in pond BB-2 (Subgroup IIIb) from the other ponds included in the Subgroup IIIa is probably due to the scarce living ostracods found in these samples (< 100 individuals; Tab. 1). The sediment type is invoked to explain this scarcity of living ostracods. In particular, the abundance of sandy sediment at the bottom of pond BB-2 (see Supplementary Online Information) seems to be unfavourable for ostracods. Probably, this is the same reason for the absence of living ostracods in pond BB-9, where the bottom sediment consists of coarse sand with pebbles.

However, the statistical differentiation of sample points BB-7b and BB-3b (Fig. 3) seems to correspond with some ecological particularities of these samples. In sample point BB-7b *P. albicans* appears as more abundant (Fig. 4; Tab. 1). This species inhabits muddy sediments with abundant vegetation in shallow margins of lakes (Diebel and Pietrzeniuk, 1990), being considered as mesotermophilic, titanoeuriplastic, mesoreophilic and reoeuriplastic species (Meisch, 2000). In Bardenas Reales de Navarra this species is not highly influenced by the measured physico-chemical parameters (Tab. 2) and shows a scarce negative correlation with water conductivity, pH and dissolved oxygen. According to the mesoreophilic character of this species, the high abundance of *P. albicans* in sample point BB-7b probably responds to the location of this sample next to an inflow point from a nearby stream into the studied pond that helps increase its internal current and favours the dominance of this species.

On the other hand, in sample BB-3b *E. virens* appears as more abundant (Fig. 4; Tab. 1). This is a cosmopolitan species with wide tolerance ranges to several physico-chemical parameters of the water (De Deckker, 1981; Neale, 1988; Mezquita *et al*., 1999a, c; Külköylüoğlu, 2000). *Eucypris virens* lives in temporary ponds that suffer extreme environmental stress (Williams, 2006) and is very abundant in ephemeral environments where the temporal and/or spatial variation in ecological parameters promotes local specialization to different habitats (Ayre, 1995). This complex ostracod species (Meisch, 2000) probably reflects strong eutrophic characteristics of the habitats (Roca *et al*., 2000), because it feeds on periphyton and dead organic material (Schmit *et al*., 2007). Since the abundance of these nutrients varies seasonally or stochastically, it probably limits the survival of *E. virens* in aquatic environments (Martins *et al*., 2010). In our statistical analysis, a low negative correlation has been obtained between dissolved oxygen and *E. virens* (Tab. 2). The scarce vegetation cover in sample point BB-3b (see Supplementary Online Information), composed by rush and reed grass, seem to be the responsible of relatively low index of dissolved oxygen. The consequent dead organic matter accumulated into the bottom sediments probably favours the development of *E. virens* in this sample point.

CONCLUSIONS

The most important physico-chemical parameters controlling the distribution of ostracod species in ponds of Bardenas Reales de Navarra (northern Spain) are water conductivity and pH, while the hydroperiod, sediment type, dissolved oxygen, altitude and vegetation cover play a secondary role. Thus, in ponds from high altitude and higher values of water conductivity, pH and dissolved oxygen, the most abundant species is *S. aculeata*. This species shows a positive correlation with water conductivity, being this parameter the main ecological factor controlling its dominance. In ponds from low altitude and the lowest values of water conductivity, pH and dissolved oxygen, *C. vidua* is the most abundant species, which shows a strong negative correlation with pH. Organic matter decomposition due to anaerobic processes could contribute to the decrease of the pH of bottom waters, favouring the abundance of this species. When the vegetation cover in these ponds increases, *L. inopinata* and *P. villosa* appear as more abundant. Both species show a positive correlation with this ecological factor. Finally, in ponds located in the central and southern part of the study area, within a wide range of altitude, low water conductivity and intermediate dissolved oxygen content and pH values, *I. bradyi* is the most important species. The dominance of this species is controlled by the input of running water into the studied ponds. In addition, when the internal water current increases, *P. albicans* appears as more abundant. Similarly, the accumulation of dead organic matter within the bottom sediment of these ponds favours the development of *E. virens*. In conclusion, this study highlights the use of ostracod species as proxies to conduct ecological interpretations in permanent and semi-permanent ponds developed in semi-arid environments.

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