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Diversity and distribution of large branchiopods in Kiskunság (Hungary) in relation to local habitat and spatial factors: implications for their conservation

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Abstract. Large branchiopods are threatened worldwide by the loss and degradation of their temporary aquatic habitats owing to drainage and intensive agriculture. Sound ecological knowledge of their diversity and distribution is a prerequisite to formulate effective conservation measures. In the present study, large branchiopods were collected from 82 temporary freshwater pools belonging to five habitat types in Kiskunság (Hungary). Dormant propagule bank analysis complemented the field survey. Eleven species were found, with large branchiopods occurring in more than half of the study systems. The high regional species richness and occurrence frequency of large branchiopods make Kiskunság a true 'hot spot' of large branchiopod diversity. The local environment was more important than spatial factors (isolation) in explaining the presence of the most common species. Dispersal was most likely not limiting for the large branchiopods in the study area and colonisation success of different species was differentially affected by local conditions, possibly invertebrate predation risk and hydroperiod. Meadow pools and wheel tracks contributed most to regional species richness through the presence of rare and exclusive species. To conserve branchiopod diversity, we stress the importance of high habitat diversity in the landscape and the need to conserve neglected habitats such as wheel tracks.

Additional keywords: Anostraca, habitat size, Laevicaudata, Notostraca, Spinicaudata, transparency, vegetation cover.

Introduction

Large branchiopods are a flagship group for temporary pools (Belk 1998). The relatively rapid growth and maturation and the production of dormant stages make them highly adapted to the recurrent filling and drying of temporary pools, producing both aquatic and terrestrial phases (Brendonck 1996). Most large branchiopod species rely on temporary aquatic systems (Dumont and Negrea 2002) because their relatively large body size does not allow them to coexist with fish predators in permanent ponds and lakes (Kerfoot and Lynch 1987).

Temporary aquatic habitats house a wide array of specialised life forms, often with a high level of endemicity, and thus make an important contribution to regional biodiversity (Williams *et al.* 2004; De Meester *et al.* 2005). Regardless of their particular conservation value, they have been progressively lost from the European landscape or have been degraded over the past decades (Williams *et al.* 2001). Besides the deterioration of habitats, the increasing distance among remaining populations in a metapopulation configuration may also ultimately lead to loss of local populations and eventually of the species from a region (Hanski and Gaggiotti 2004). Especially in Western Europe, drainage and intensive cultivation have had a negative impact on these habitats, thereby threatening the persistence of large branchiopod populations (Mura 1993; Williams 1997; Eder and Hödl 2002). In countries such as Belgium (Brendonck 1989), Great Britain (Williams 1997), Germany (Maier 1998) and Austria (Eder and Hödl 2002), large branchiopods have become rare or even close to extinction. In Eastern Europe, on the other hand, agriculture is usually less intensive and large areas of farmland still support a high habitat and species diversity, often including species of conservation concern (European Environment Agency 2004). The Banat province in Serbia, for example, is a true 'hot spot' of large branchiopod diversity, where 10 frequently coexisting species were found in an area of only 0.3 ha (Petrov and Cvetković 1997). Although environmental pressures are expected to decrease in Western Europe, many areas in Eastern Europe will experience increasing pressure from agriculture. Consequently, in countries such as Poland and Hungary, which have recently joined the European Union, the conservation of large branchiopods and their temporary habitats is of high priority (Oertli *et al.* 2005).

Potential factors explaining large branchiopod diversity patterns at a local and regional scale include: (1) local environmental characteristics: physical habitat characteristics (e.g. pond size, hydroperiod) and abiotic and biotic conditions (e.g. water quality, biotic interactions); (2) landscape features and dispersal possibilities (e.g. connections); and (3) historical factors. Local species richness generally increases with habitat size (McArthur and Wilson 1967), possibly owing to its correlation with habitat heterogeneity (Williams 1943; Douglas and Lake 1994; Brose 2001). For example, a positive relationship between pool

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depth and large branchiopod species richness was observed by Gallagher (1996) and Thiéry (1991). Hamer and Appleton (1991) showed that large branchiopods coexisting in one pool occupied spatially distinct habitat patches strongly differing in vegetation structure and predation risk. Co-occurring anostracan species often have different life cycle strategies to avoid competition (Mura 1991; Maeda-Martínez *et al.* 1997; Moscatello *et al.* 2002; Beladjal *et al.* 2003). The coexistence of species that develop at various times throughout the season is consequently advantaged in long-lasting pools, as suggested by Petrov and Cvetković (1997). On the other hand, owing to low predation pressure in small pools that regularly dry out, some species may prefer, or are restricted to, short-lived habitats such as rain pools, puddles and wheel tracks (Hössler *et al.* 1995). Differences in length of wet phase as well as in local conditions such as turbidity, salinity or presence of vegetation may result in distinct temporary habitat types housing different large branchiopod assemblages (Eng *et al.* 1990; Eder and Hödl 1996; Timms and Sanders 2002). As such, the presence of diverse habitat types in the landscape may support a high regional species richness.

Spatial dynamics may also affect species distributions, through colonisation–extinction dynamics or dispersal limitation, for example (Cornell and Lawton 1992; Shurin 2000). The notion that the spatial structure of natural populations has to be taken into account is the basis of modern metapopulation ecology (Hanski and Gaggiotti 2004). On a local scale, freshwater zooplankton and/or their dormant eggs are readily dispersed by wind (Vanschoenwinkel *et al.* 2008), amphibians (Bohonak and Whiteman 1999) and water connections (Michels *et al.* 2001; Hulsmans *et al.* 2007), whereas probably the most effective long-distance dispersal agents are waterbirds (Figuerola and Green 2002). The effective importance of dispersal limitation for large branchiopods probably varies strongly between geographic areas, depending on the proximity of source populations and the availability of dispersal vectors. Demeter (2005) found that large branchiopod habitats in the Ciuc basin (Romania) were located in areas with high habitat density and thus higher chance for dispersal. He attributed the lack of anostracans from apparently suitable habitats in a high mountain area to the absence of suitable dispersal vectors (Demeter 2004). As species may be absent from otherwise suitable habitat patches owing to dispersal limitation, studies that do not take the spatial configuration of populations (isolation, connectivity) into account may miss out on important information.

The increasing literature on the alarming status of large branchiopods and their habitats contrasts with the limited number of management and conservation measures. Ideally, such measures are based on thorough ecological studies investigating the relative importance of local habitat characteristics and spatial metapopulation structures in explaining diversity patterns and species distribution.

In the present paper, we present the species richness and distribution patterns of large branchiopods in different pool types in the Kiskunság area (Hungary), a relatively pristine area where temporary pools are still relatively abundant. We compare the relative importance of local environmental characteristics as well as spatial factors (isolation) in explaining the distribution of the most common large branchiopod species. Based on our results, we suggest some conservation measures for large branchiopods and their habitats.

Materials and methods

Study area

The Kiskunság National Park in Hungary (Fig. 1*a*), covering an area of almost 500 km^2, is located 85 km south-west of Budapest in the Kiskunság area. We sampled 82 temporary freshwater pools in the western part of this area (Fig. 1*b*). Five different pool types were distinguished: wheel tracks ($n = 29$), clay pits ($n = 6$), meadow pools ($n = 38$), pools in arable land ($n = 8$) and one orchard pool. The geographical distribution of pool types reflects the typical environmental gradient characterising the study area. Eastwards, reed marshes and bog meadows constitute the main biotopes and meadow pools on peat soils typically occur. More westwards, the study area is characterised by salt lakes on alkaline soils and the main pool types are clay pits, wheel tracks and meadow pools on clayey soils. Pools in arable land occur throughout the gradient, whereas orchard pools are rarely observed.

All pools are initially inundated after snow melt in early spring (February–March) and gradually dry by summer. Throughout the year, they can be replenished with rain. The duration and frequency of inundation of the pools strongly depends on pool morphology (depth and surface area) and local weather conditions.

Field sampling

Pools were sampled between mid-April and mid-May in 2005 ($n = 45$) and/or 2006 ($n = 44$) (Table 1). The shape of each pool was compared with known geometric figures of which the dimensions were measured to calculate its surface area (m^2). Maximum depth (cm) was assessed using a calibrated stick. The measurement of water transparency using a Snell's tube was practically impossible in the shallowest habitats (10–20 cm) on clayey soil because clay particles were stirred up and influenced our measurements. For further analyses, bottom visibility (0/1) was therefore used as a measure of water transparency. Depth of pools did not interfere with transparency measurements and pools without bottom visibility were on average shallower. In each pool, an integrated water sample of ~9 L was taken from the surface of three randomly chosen locations. From this sample, temperature (°C), conductivity (μS cm^{-1}), pH and dissolved oxygen concentration (% saturation) were measured in the field using a multimeter (340i, WTW, Weilheim, Germany). When the water was too shallow to collect an integrated water sample, measurements were made directly in the pool. Percentage cover with macrophytes (floating, submersed and emerged vegetation) was visually estimated (10% accuracy). Table 2 provides an overview of the measured values for the different local habitat variables per pool type. The spatial configuration of the pools was reconstructed in a geographic information systems (GIS) environment and the distance between each pair of pools was measured using the distance tool in ArcGIS 8.0 (http://campus.esri.com).

Large branchiopods were sampled qualitatively by searching all subhabitats with a sweep net (250-μm mesh). In clay pits and meadow pools sampled in 2005, quantitative sampling was carried out using quadrats. Four open quadrats were placed on

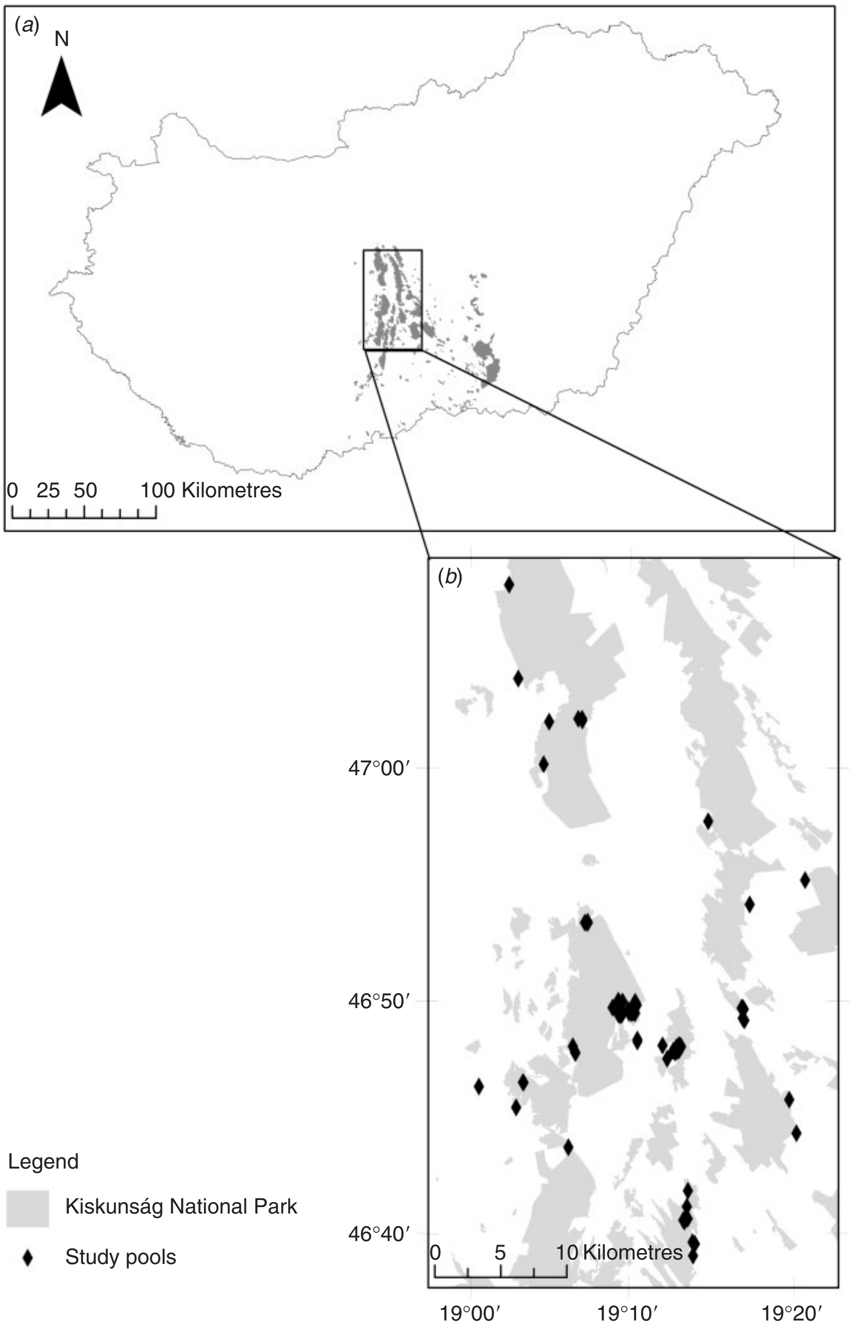

Fig. 1. Location of (*a*) the Kiskunság National Park in Hungary and (*b*) the study pools within the study area.

the bottom of the pool and trapped animals were removed with a sweep net (250-µm mesh). Qualitative samples were simultaneously collected and additionally screened. Collected animals were preserved in 70% ethanol and identified to species level using the identification key in Eder and Hödl (1996). For further analysis, presence/absence data were used.

For a subset of 13 pools (Table 1), the species list was complemented by hatching and identifying viable dormant eggs from the sediment. We selected eight meadow pools and four clay pits because these were generally larger and deeper and the chance that we missed some species in the field was probably higher. The upper 3 cm of sediment was collected in each pool from random locations ($n = 15$–20; $\pm 10 \times 10\,\text{cm}^2$), representative of all existing microhabitats (depth, vegetation type). Sediment with dormant eggs was dried and stored for 3 months in the dark at room temperature. Thereafter, we inundated for each pool (a) dry sediment and (b) dormant eggs isolated from sediment (using the sugar flotation method: Onbé 1978; Marcus 1990). For each pool, ~150 g of sediment was inundated in 2-L aquaria filled with EPA medium (US EPA 1985) at 10 and 20°C. To increase

Table 1. Overview of the number of study pools (n) and the total number of species found (S_{tot}) per pool type during the spring of 2005 and 2006 from dormant egg bank analysis (DEB) and during the whole study

For each pool type, the number of exclusive species (S_{excl}) is also given

	2005		2006		DEB		Whole study		S_{excl}
	n	S_{tot}	n	S_{tot}	n	S_{tot}	n	S_{tot}	
Clay pits	5	0	3	0	4	3	6	3	0
Meadow pools	32	5	10	4	9	7	38	9	4
Pools in arable land	/	/	8	3	/	/	8	3	0
Pool in orchard	/	/	1	1	/	/	1	1	0
Wheel tracks	8	2	22	5	/	/	29	5	2
Total	45	7	44	8	13	7	82	11	

Pools that were not sampled are indicated with an '/'.

Table 2. Overview of local environmental characteristics (mean ± standard error and range) for each of the habitat types

	Clay pits ($n = 6$)	Meadow pools ($n = 38$)	Pools in arable land ($n = 8$)	Pool in orchard ($n = 1$)	Wheel tracks ($n = 29$)
Conductivity (μS cm^{-1})	1775 ± 307	941 ± 52	1110 ± 268	593	1552 ± 247
	563–2510	453–2090	607–2820		415–6370
Temperature (°C)	14.2 ± 0.3	17.8 ± 0.7	19.7 ± 1.3	19.5	20.3 ± 0.9
	13.1–15.1	10.7–27.1	15.1–26.7		11.9–29.3
pH	8.7 ± 0.1	8.4 ± 0.1	7.7 ± 0.1	7.5	8.7 ± 0.1
	8.2–9.0	7.2–9.7	7.3–8.2		7.3–10.0
Oxygen saturation (%)	82 ± 4	100 ± 5	83 ± 7	86	82 ± 5
	71–96	42–185	49–112		18–155
Transparency (Snell's depth in cm)	27.2 ± 2.5	34.0 ± 1.2	16.6 ± 3.9	19.0	*
	20.0–37.5	19.5–50.0	0–29.0		*
Vegetation cover (%)	66 ± 11	90 ± 3	21 ± 8	70	1 ± 0.12
	30–100	40–100	0–50		0–2
Surface area (m^2)	1460 ± 659	11 183 ± 3298	1199 ± 448	1180	9 ± 2
	188–3758	11–77 616	216–3360		0.15–33
Maximum depth (cm)	71.1 ± 13.3	37.5 ± 2.6	24.3 ± 2.4	29.0	14.2 ± 0.7
	43.0–112.5	13.0–90.0	15.0–37.0		10.0–20.0

species detection, dormant eggs were next isolated from ±4 kg of sediment for each pool. They were inundated at 12, 18 and 24°C (EPA medium). Using different temperature treatments, we aimed at optimising hatching conditions for a maximum number of species. During a period of about 1 month, hatchlings were isolated twice a week, grown to adult stage and identified to species level using Eder and Hödl (1996). Finally, isolated dormant eggs that did not hatch were identified to species level using Thiéry and Gasc (1991).

Data analysis

The presence/absence of the most common large branchiopod species (found in more than three pools throughout the study; Table 3) as observed in the field was investigated in relation to local environmental and spatial characteristics using canonical correspondence analysis (CCA). We first applied forward selection on the entire set of measured variables to identify those variables that best explained the branchiopods' distribution. Next, the selected variables were incorporated into variation partitioning models (Borcard *et al.* 1992) to separate the contribution of local and spatial factors in explaining the presence of species. The significance of the models was tested using Monte Carlo permutations ($n = 999$). Analyses were carried out in Canoco for Windows 4.5 (Lepš and Šmilauer 2003).

Local environmental characteristics included morphometry (maximum depth, surface area), water quality (conductivity, dissolved oxygen, pH, temperature and transparency) and percentage vegetation cover. As a spatial factor, we used the average distance of a pool to all other study pools as a general measure of isolation (Isol). This distance measure only included our study pools, but not other pools in the area, and was representative for both years.

The Fager's affinity index was calculated for each pair of species as a relative measure of species co-occurrence, analogous to the approach in Maeda-Martínez *et al.* (1997): $I_F = 2n_{1+2}/(n_1 + n_2)$ where n_{1+2} = number of joint occurrences of species 1 and 2, n_1 = total number of occurrences of species 1 and n_2 = total number of occurrences of species 2. We compared the index calculated from simultaneous co-occurrences in the field and from occurrences in the dormant egg bank and/or during subsequent sampling seasons.

Table 3. Large branchiopod species found in Kiskunság with their number of records, frequency of co-occurrence and European distribution (after Brtek and Thiéry 1995)

The number of records includes records from field collections in 2005 and 2006 (Field) and additional records from dormant egg banks (DEB). The frequency of co-occurrence of a species is expressed as the proportion of its habitats in which it was found together with one or more species simultaneously (Time) or throughout different years and/or in the dormant egg bank (Habitat)

	# Records		% Co-occurrence		Distribution in Europe
	Field	DEB	Time	Habitat	
Anostraca					
Branchipus schaefferi Fischer, 1834	19	6	21	40	Continental Europe and Mediterranean islands
Tanymastix stagnalis (Linnaeus, 1758)	6	7	33	62	Widespread
Chirocephalus carnuntanus (Brauer, 1877)	5	0	40	60	Eastern Europe (Pannonian Lowland)
Chirocephalus shadini (Smirnov, 1928)	2	1	0	66	Eastern Europe and Russia
Branchinecta ferox (Milne Edwards, 1840)	1	0	100	100	Eastern Europe and Spain
Eubranchipus grubii (Dybowski, 1860)	1	0	0	0	Central Europe
Notostraca					
Triops cancriformis (Bosc, 1801)	3	6	100	100	Widespread
Lepidurus apus (Linnaeus, 1758)	8	0	25	25	Continental Europe
Laevicaudata					
Lynceus brachyurus Müller, 1776	6	0	50	50	Eastern Europe, Northern Europe and Russia
Spinicaudata					
Imnadia yeyetta Hertzog, 1935	0	2	/	100	Eastern Europe (Pannonian Lowland) and Camargue
Lepthesteria dahalacensis (Rüppell, 1837)	1	0	100	100	Eastern Europe, Mediterranean Islands and Russia

Results

Species richness and co-occurrence

In more than half of the study systems (48 out of 82), large branchiopods were found in the field and/or in the dormant egg bank. Eleven species were found: six anostracans; two notostracans and three conchostracans (Table 3). *Branchipus schaefferi* and *Tanymastix stagnalis* were the most commonly observed species throughout the study (in 25 and 13 pools respectively).

In the field, usually only one species occurred per pool (82.5% of all species observations). Less frequently, species co-occurred simultaneously with one (five pools, 12.5%) or two (two pools, 5%) other species. Dormant egg bank analysis revealed six additional large branchiopod habitats and increased the number of co-occurrences: two species co-occurred in two more pools and three species occurred in four more habitats. Four and five species were found together each time in the sediment of a single pool.

Except for *Eubranchipus grubii* and *Chirocephalus shadini*, all species were found together simultaneously with one or more species relatively frequent (Table 3). *Triops cancriformis* never occurred alone and was found together with *Lepthesteria dahalacensis* (Fager's index of 0.50) and/or *B. schaefferi* (0.27). *Chirocephalus carnuntanus* was found alone, with *T. stagnalis* (0.33) or with *Lynceus brachyurus* (0.31). *Lepidurus apus* and *L. brachyurus* were also found together in the field (0.28). The subsequent monitoring of pools during two springs, as well as dormant egg bank analysis, revealed a higher frequency of co-occurrence for some species (Table 3). In one pool that was monitored during both years, we found two different species each year (*C. shadini* and *C. carnuntanus* respectively). In two other pools, we did not find any large branchiopods in the field, but we found *B. schaefferi*, *T. stagnalis* and *T. cancriformis* in the dormant egg bank. Species most often found together in the egg bank of the same habitat were: *T. cancriformis* and *T. stagnalis* (0.55; $n = 6$); *T. cancriformis* and *B. schaefferi* (0.53; $n = 9$); and *B. schaefferi* and *T. stagnalis* (0.32; $n = 6$). As for species that were less frequently observed, there was a relatively high affinity between *Imnadia yeyetta* and *C. shadini* (0.40), *T. cancriformis* (0.36) or *T. stagnalis* (0.27) and between *C. carnuntanus* and *C. shadini* (0.25).

Table 4. Results of variance partitioning (percentage of explained variation, *F*- and *P*-value) of canonical correspondence analysis (CCA) model relating the presence of large branchiopod species to local environmental and spatial variables

Local environmental variables ([E]) include maximum depth, oxygen saturation percentage, percentage vegetation cover, pH, surface area and transparency. The average distance to all other study pools was used as spatial variable ([S]). Symbols according to Cottenie *et al.* (2003): [E + S] = total variation explained by environmental and spatial variables; [E] = variation explained by environmental variables; [S] = variation explained by spatial variables; [E|S] = pure environmental variation; [S|E] = pure spatial variation; [E ∩ S] = variation shared by environmental and spatial variables; 1 – [E + S] = unexplained variation

	Variance explained (%)	*F*	*P*
[E + S]	49.8	2.97	0.001
[E]	48.3	3.43	0.001
[S]	9.1	2.71	0.016
[E|S]	44.7	2.83	0.001
[S|E]	2.8	0.61	0.67
[E ∩ S]	2.3		
1 – [E + S]	50.2		

Local environmental and spatial factors

Local environmental factors, including maximum depth, surface area, oxygen saturation percentage, pH, transparency and

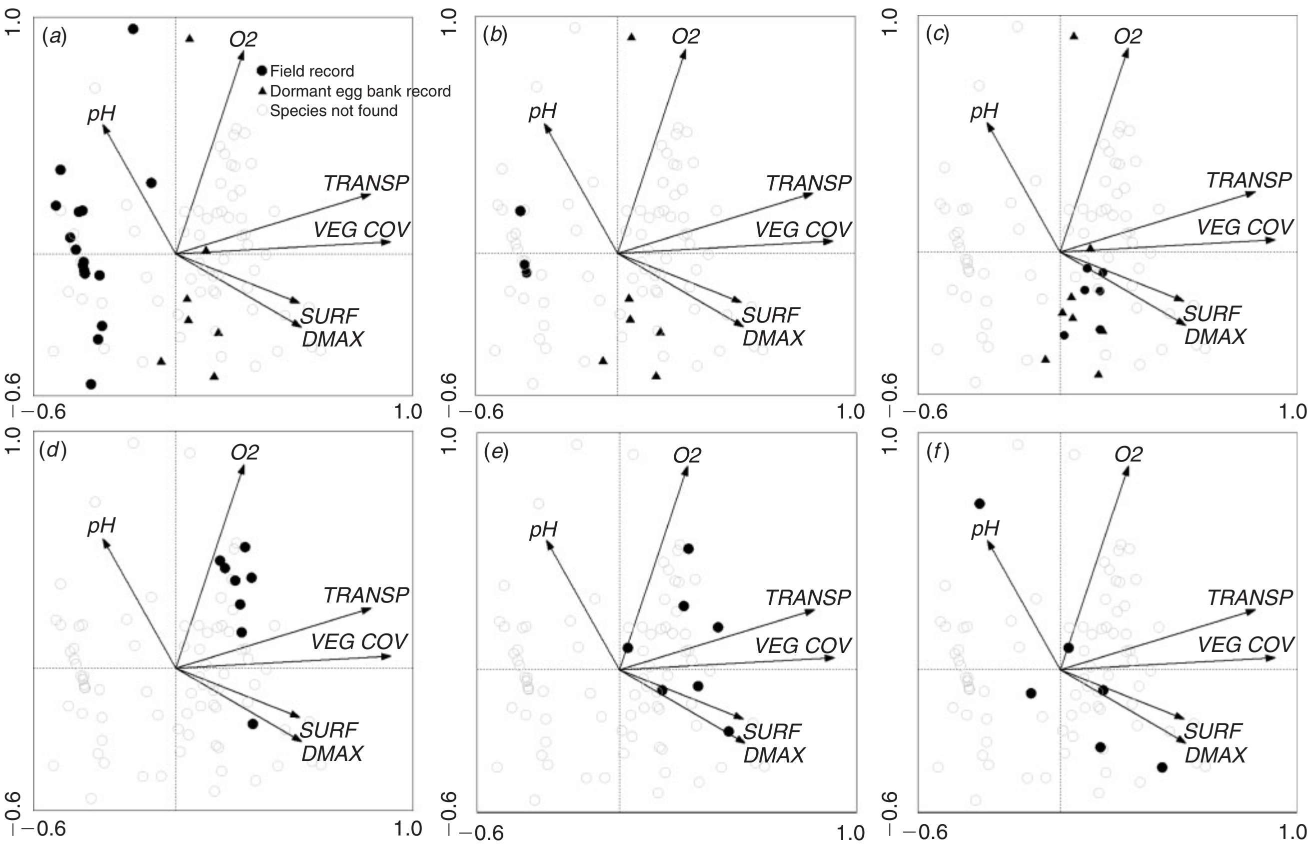

Fig. 2. Ordination plots illustrating the distribution of the most common large branchiopods in Kiskunság in relation to local environmental characteristics (principal components analysis (PCA) of selected local environmental characteristics and samples; first two axes explain 52.1% of total variation in the data): (*a*) *B. schaefferi*; (*b*) *T. cancriformis*; (*c*) *T. stagnalis*; (*d*) *L. apus*; (*e*) *L. brachyurus*; and (*f*) *C. carnuntanus*. Legend to abbreviations: DMAX = maximum depth; O2 = oxygen saturation percentage; pH; SURF = surface area; TRANSP = transparency; VEG COV = percentage vegetation cover.

percentage vegetation cover were more important than isolation effects in explaining the presence of the most common large branchiopod species (Table 4). Local factors significantly explained the presence/absence of species and we never found an independent spatial effect. The shared effect of local and spatial variables was also negligible. About half of the variation in the presence/absence of species (50.2%) remained unexplained by the selected explanatory variables.

Branchipus schaefferi (Fig. 2*a*) and *T. cancriformis* (Fig. 2*b*) were positively associated with turbid, sparsely vegetated pools with a small depth and surface area. In the field, these species were almost exclusively found in wheel tracks. The other species were generally associated with deeper and/or larger pools (Fig. 2). *Tanymastix stagnalis* was found in diverse habitat types in the field and was associated with relatively low pH values (Fig. 2*c*). *Lepidurus apus* (Fig. 2*d*) and *L. brachyurus* (Fig. 2*e*) were associated with transparent pools with a high vegetation cover and *L. apus* was positively associated with high oxygen concentrations. Both species were observed in meadow pools on peat soils. *C. carnuntanus* occurred in different pool types at various local conditions and its presence was not especially associated with any of the selected environmental variables (Fig. 2*f*). *Branchipus schaefferi*, *T. stagnalis* and *T. cancriformis* also hatched from the sediment of clay pits and meadow pools on clay soils (Fig. 2*a*, *b*, *c*). For *L. apus*, *Lynceus brachyurus* and *Chirocephalus carnuntanus*, no new records were added from the dormant egg banks. As for the rare species, the anostracans *Chirocephalus shadini* and *Eubranchipus grubii* were found in transparent, vegetated meadow pools on peat soils, but *C. shadini* also hatched from a meadow pool on clayey substrate. *Branchinecta ferox* and the conchostracan *L. dahalencis* were found in small, turbid wheel tracks. *Imnadia yeyetta* hatched from two meadow pools on clayey substrate.

Habitat type

Meadow pools and wheel tracks were characterised by the highest total species richness (nine and five species respectively) and were the only habitat types with exclusive species (i.e. species not found in any other habitat type) (Table 1). *Chirocephalus shadini*, *E. grubii*, *L. brachyurus* and *L. apus* were only observed in meadow pools, whereas *B. ferox* and *L. dahalacensis* were exclusive species of wheel tracks.

Discussion

Species richness

We encountered eleven large branchiopod species during our study of 82 temporary freshwater pools in and around the

Kiskunság National Park in 2005 and 2006. This is more than half of the described Hungarian large branchiopod fauna consisting of 19 species (Forró 2000). The anostracans *B. schaefferi* and *T. stagnalis* were the most common species in our survey. Both species are also widely distributed in Europe (Brtek and Thiéry 1995), which may be indicative of the eurytopic nature or particular dispersal and colonisation abilities of these species. In our study area, species with a more limited geographical distribution also occurred. *Chirocephalus shadini*, *B. ferox* and the conchostracan species (*L. brachyurus*, *I. yeyetta* and *L. dahalacensis*), for example, more typically occur in Eastern Europe, whereas *C. carnuntanus* is restricted to the Pannonian Lowland (Brtek and Thiéry 1995). Compared with other regions in Europe (Belgium: six species with one observation since 1959 (Brendonck 1989; Loneux 2002); UK: two species from ~20 locations (Williams 1997); Germany: 10 species (Maier 1998); south-west Portugal: five species in 20% of all pools (Machado *et al.* 1999); Eastern Poland: three species in 32% of all pools (Biggs *et al.* 2004); Ciuc Basin Romania: six species in 18% of all pools (Demeter 2005)), many large branchiopod species were found in a relatively high number of pools in the Kiskunság area.

Both Petrov and Cvetković (1997) and Timms and Sanders (2002) defined large branchiopod 'hot spots' (the Banat province in Serbia and the middle Paroo catchment in Australia, respectively) as relatively small areas (0.30 ha and 2000 km^2, respectively), where a high proportion of the regional (national) species pool occurs and species co-occurrence is frequent. In Banat, 53% of the national large branchiopod species pool was represented and more than one species was found in 67% of all habitats (Petrov and Cvetković 1997). In the Paroo, 50% of the known conchostracan fauna and 57% of the national anostracan species pool was observed and species co-occurred in 21% and 55%, respectively, of all collections (Timms and Richter 2002; Timms and Sanders 2002). According to this definition, the Kiskunság area, where 58% of all Hungarian species were found in an area of ~1800 km^2 and species and anostracan co-occurrence was common (31 and 21% of all large branchiopod habitats, respectively), should also be considered as a 'hot spot' of large branchiopod diversity. The presence of such a species-rich area contrasts with the general trend of declining large branchiopod diversity throughout Europe concurrent with an unprecedented rate of habitat destruction or change owing to agricultural and urban development (Brendonck 1989; Maier 1998; Williams *et al.* 2001; Eder and Hödl 2002). Dormant propagule banks may increase the resilience of large branchiopods to anthropogenic stress (Angeler *et al.* 2008). However, for some species, only a few or small populations were found, and as no information on dormant egg banks sizes is available, it is difficult to make unequivocal conclusions on the conservation status of the large branchiopod species in the area.

Spatial factors

The degree of pool isolation did not have a significant independent effect on the presence of the studied species. Our results suggest that in the Kiskunság area, dispersal of large branchiopod species is most likely not limiting. The network of irrigation channels, which establish temporary connections between pools, as well as the abundant amphibian and bird populations possibly constitute important dispersal vectors in the area (cf. Bohonak and Whiteman 1999; Figuerola and Green 2002). Large branchiopod dormant eggs may also be easily dispersed by wind in our study area because pools were separated by distances of a few metres up to 50 km in a flat landscape. Vanschoenwinkel *et al.* (2008) measured considerable wind dispersal of large branchiopod propagules on an isolated rock pool outcrop, though on a very local scale (few hundred metres). Dormant egg transport over longer distances is, however, not unlikely over the long term.

Although we found no strong indications of dispersal limitation in our study area, in the Ciuc basin in Romania, large branchiopods were especially found in areas with high habitat density (Demeter 2005). In a high mountain area, the absence of anostracans was related to the absence of suitable dispersal vectors (Demeter 2004). In areas with physical barriers to dispersal, the creation of new habitats for conservation purposes may not be effective. Because of this, we strongly recommend the integration of spatial factors in any future studies investigating large branchiopod distribution patterns and in the development of conservation schemes.

Local environmental variables

Although species apparently are not dispersal-limited, there was a distinct segregation of species among habitats with contrasting local environments (Fig. 2). Small, turbid and sparsely vegetated wheel tracks were typically inhabited by *B. schaefferi*, *T. cancriformis* and *L. dahalacensis. Branchipus schaefferi* and *T. cancriformis* also occurred in larger clay pits and meadow pools with more abundant vegetation, often together with *T. stagnalis. Lepidurus apus*, *L. brachyurus*, *E. grubii* and *C. shadini* were representative species of meadow pools with very abundant vegetation. In several studies, species were found in similar habitats as in our survey. *Branchipus schaefferi*, *T. cancriformis* and *L. dahalacensis* were found in muddy rain pools in Germany, Austria and Yugoslavia (Hössler *et al.* 1995; Hödl and Eder 1996; Petrov and Petrov 1997). *Eubranchipus grubii* and *C. shadini* occurred in meadow pools in Austria, which were considered as the preferred habitats of the latter species (Hödl and Eder 1996). *Lepidurus apus* and *L. brachyurus* were observed in densely vegetated waters in Spain and Yugoslavia (Alonso 1985; Petrov and Petrov 1997) and in pools on peat marshes in France (Rabet *et al.* 2005). Only our observation of the anostracan *B. ferox* in a wheel track was rather unusual because this species is considered characteristic of alkaline lakes (Löffler 1993; Eder and Hödl 2003).

The significant independent effect of local habitat characteristics on the presence of the most common large branchiopod species indicates that the local environment may have acted as a selective force, resulting in efficient species sorting (Leibold *et al.* 2004; Holyoak *et al.* 2005; Vanschoenwinkel *et al.* 2007) and thereby explaining the observed association of species with contrasting habitats. For example, the presence of abundant vegetation most likely implicates a high abundance of invertebrate predators such as members of the Odonata and beetle larvae (Lombardo 1997; Burks *et al.* 2002; Van de Meutter *et al.* 2004). The low frequency and small size of anostracan populations in the densely vegetated meadow pools may be indicative of such an elevated predation risk. We found anostracans in the field in only 13% of all meadow pools and a maximum of only 15 adult specimens was collected during one 5-min search period (L. Boven, pers. obs.). Anostracans associated with densely vegetated habitats may be locally adapted to high predation pressure by specific hatching or life cycle strategies. *Chirocephalus shadini* and *E. grubii*, for example, are cold-water species typically occurring early in spring (Eder *et al.* 1997; Petrov and Cvetković 1997). By hatching early after snow melt, they probably mature before the predator community is well developed. A similar strategy was observed for anostracans in temporary pools in South Africa that developed before actively dispersing predators colonised their habitats (Hamer and Appleton 1991).

The morphology of pools also affected species distribution, possibly through its association with the duration of inundation. Although hydroperiod is not solely dependent on morphological measurements (Marcus and Weeks 1997; Skidds and Golet 2005), the maximum depth or surface-to-volume ratio of pools is often used as indicators of the length of the aquatic phase (King *et al.* 1996; Marcus and Weeks 1997; Jocqué *et al.* 2007). Small and shallow habitats, in our study typically wheel tracks, are most likely inundated for shorter periods than the other pool types, which had variable dimensions, but were generally larger and deeper (Table 2). *Branchipus schaefferi* and *T. cancriformis* are characterised by very fast growth and maturation, especially at high temperatures (Flössner 1972; Defaye *et al.* 1998; Beladjal *et al.* 2003) and are therefore presumably well adapted to survive in such short-lived habitats. In their larger but relatively shallow habitats, *T. stagnalis* is likewise advantaged by hatching at relatively low temperature and rapidly growing to maturation (Al-Tikirity and Grainger 1990; Grainger 1991; Mura 1991), avoiding extinction through early desiccation. Although not observed in the field, *B. schaefferi*, *T. cancriformis* and *T. stagnalis* also hatched from the sediment of meadow pools and claypits. In these relatively turbid habitats (Fig. 2*a*, *c*), *B. schaefferi* and *T. stagnalis* may be relatively safe from invertebrate predators (Woodward and Kiesecker 1994; Hössler *et al.* 1995), whereas in transparent meadow pools they are possibly more susceptible to visual predation. Another hypothesis that might explain the success of *B. schaefferi* and *T. stagnalis* in these meadow pools and clay pits is that they are possibly restricted to shallow, littoral zones with high desiccation and low predation risk. In temporary pools in South Africa, fast-growing species occupied the peripheral region of a pool, whereas the pelagic area was inhabited by large branchiopods with slower development (Hamer and Appleton 1991). Finally, the slow growth and maturation of *L. brachyurus* (Rabet *et al.* 2005) and *L. apus* (Kuller and Gasith 1996) may limit these species to habitats with a long duration. In temporary pools in France, *L. brachyurus* matured only after 3 months and was found in rather deep systems as well (0.70–2.50 m) (Rabet *et al.* 2005). Although both notostracans were observed together in rain pools in Israel, larval development of *L. apus* was obviously slower than that of *T. cancriformis* (Kuller and Gasith 1996).

Chirocephalus carnuntanus was found in various habitats. Although *C. carnuntanus* possibly is a habitat generalist, the low encounter rate makes it difficult to make any statements on the species' distribution.

Species co-occurrence

Species co-occurred in 31% of all large branchiopod habitats in our study. This percentage was most likely underestimated because field surveys were limited in time and dormant egg banks were only searched for a subset of pools. In temporary ponds in Mexico, Arizona (Maeda-Martínez *et al.* 1997), Serbia (Petrov and Cvetković 1997), the Camargue (France; Waterkeyn *et al.* in press) and Morocco (Thiéry 1991), co-occurrence was more frequently observed (43, 47, 67, 79 and 90% respectively). We found co-occurring anostracans in 21% of all large branchiopod habitats. In north-east Australia, 55% of all collections included more than one anostracan species (Timms and Sanders 2002) and 21% included more than one conchostracan (Timms and Richter 2002), but repeated collections were made for each pool. In Morocco, anostracans co-occurred in 50% of all habitats (Thiéry 1991). As in the mentioned studies, large branchiopod species sometimes co-occurred simultaneously in our study pools (17%), but we only rarely found more than one anostracan at the same time.

The coexistence of branchiopods in temporary wetlands in general is ascribed to a combination of abundant food resources and low intensity of competitive interactions owing to the annual truncation of community development (King *et al.* 1996; Simovich 1998). However, the common co-occurrence of anostracans, notostracans and conchostracans, as also observed during our study, is probably established through resource partitioning as each group uses different food types (Dumont and Negrea 2002). Especially when filter-feeding anostracans co-occur, mechanisms of competition avoidance come into play. Frequently co-occurring anostracans, but also conchostracans in the Paroo catchment, for example, avoided competition through differences in body size and thus in the size of filtered prey or food particles (Timms and Richter 2002; Timms and Sanders 2002). A reduction in temporal overlap of competitive life stages through different life cycle strategies (growth rate, size) also explained the occurrence of two-species assemblages of anostracans (Mura 1991; Hathaway and Simovich 1996; Beladjal *et al.* 2003), as well as the coexistence of six anostracan and up to 10 large branchiopod species in a single pond in Morocco (Thiéry 1991). In our study pools, resource overlap may be too high to allow anostracans to occur simultaneously, even at different life stages. However, other factors such as predation level and food type availability may differ between our study pools and, for example, the Moroccan pools and contribute to the low level of co-occurrence we observed.

Furthermore, species may co-occur in the same habitat but occupy different temporal niches (different times throughout one growing season or different growing seasons). Differences in the seasonal appearance of species explained the co-occurrence of an *Artemia* and a *Branchinella* species in a saline pond in Italy (Moscatello *et al.* 2002), of the notostracans *L. apus* and *T. cancriformis* in Austrian pools (Gottwald and Eder 1999) and enabled the persistence of up to seven large branchiopod species in a single habitat in the Banat province (Serbia; Petrov and Cvetković 1997). In one temporary pond in North America, five anostracans were able to coexist because the species-specific hatching requirements allowed different species to recolonise the habitat from the dormant egg bank from year to year (Donald 1983). Although during subsequent samplings of meadow pools and clay pits during the spring of 2005 (end of March to July) no additional species were found (L. Boven, pers. obs.), dormant egg bank analysis revealed new large branchiopod records for a subset of these pools. Therefore, temporal niche segregation may still be an effective mechanism enabling species co-occurrence in our study pools.

Conclusions and conservation implications

Our observation of a high regional species richness (γ-diversity) and occurrence frequency of large branchiopods in Kiskunság highlights the considerable natural and conservation value of the studied habitats. 'Between habitat diversity' (β-diversity) of large branchiopod communities resulted from the distinct species composition of habitats with contrasting local environments. In the absence of strong dispersal limitation, this probably resulted from efficient species sorting of large branchiopods between different habitat types. The considerable contribution of meadow pools and wheel tracks to the regional species pool owing to the presence of rare and exclusive species furthermore supports the importance of maintaining high habitat diversity (size, transparency, vegetation cover) in the landscape. We also have shown that habitats such as wheel tracks and puddles, which are often overlooked and especially vulnerable to urbanisation (e.g. road hardening), can be of particular conservation interest.

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