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4 **Opposing patterns of zooplankton diversity and functioning along a natural**  
5 **stress gradient: When the going gets tough, the tough get going**

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22 Salinity represents a major structuring factor in aquatic habitats which strongly affects species  
23 richness. We studied the relationships among species richness, density and phylogenetic  
24 diversity of zooplankton communities along a natural salinity gradient in astatic soda pans in  
25 the Carpathian Basin (Hungary, Austria and Serbia). Diversity and density showed opposing  
26 trends along the salinity gradient. The most saline habitats had communities of one or two  
27 species only, with maximum densities well above 1000 ind l<sup>-1</sup>. Similarity of communities  
28 increased with salinity, with most of the highly saline communities being dominated by one  
29 highly tolerant calanoid copepod, *Arctodiaptomus spinosus*, which was at the same time the  
30 only soda-water specialist. Salinity obviously constrained species composition and resulted in  
31 communities of low complexity, where few tolerant species ensure high biomass production  
32 in the absence of antagonistic interactions. The pattern suggests that environmental stress may  
33 result in highly constrained systems which exhibit high rates of functioning due to these key  
34 species, in spite of the very limited species pool.

35

36 Biodiversity–ecosystem functioning (BEF) relationships have recently developed to a  
37 central issue within both community ecology and conservation biology (Loreau et al. 2001;  
38 Balvanera et al. 2006). Initial studies focused on primary production as a function of species  
39 richness (S) especially in terrestrial systems, while recently, more emphasis is put on  
40 functional diversity, complex interactions and food webs (Hillebrand and Matthiessen 2009).  
41 In general, many examples contributed to the increasing evidence that diversity generally  
42 promotes functioning while species loss causes malfunction (Loreau et al. 2002; Hooper et al.  
43 2005; Balvanera et al. 2006; Cardinale et al. 2006). However, most evidence on BEF  
44 relationships resulted from experimental communities (e.g. Naeem et al. 1994; Tilman and  
45 Downing 1994; Tilman 1999; Downing and Leibold 2002; Sherber et al. 2010), together with  
46 a few from degraded systems (e.g. Worm et al. 2006), while examples from natural diversity  
47 gradients are scarce (e.g. MacDougall 2005; Ptacnik et al. 2008). Moreover, the majority of  
48 empirical BEF studies have concentrated on terrestrial ecosystems, while aquatic habitats are  
49 less studied (Covich et al. 2004).

50 Most of our knowledge on BEF relationships comes from short-term and small-scale  
51 experiments. As the effect of biodiversity on ecosystem functioning can vary both in time and  
52 space (Symstad et al. 2003; Covich et al. 2004), the implications of these experiments for  
53 natural (established) communities on longer time or spatial scales may not be obvious.  
54 Therefore, there would also be a great need for long-term and large-scale studies on BEF  
55 relations (Symstad et al. 2003).

56 The current consensus on BEF proposes that functioning generally depends on diverse  
57 assemblages. Therefore, it seems surprising that systems with naturally low levels of diversity  
58 have received little attention within the BEF concept. Compared to other systems, extreme  
59 environments usually harbour limited species pools and are often dominated by highly  
60 specialised species, while common taxa are excluded due to extreme conditions. Apart from

61 extreme environments, even less is known on how diversity and functioning change along  
62 natural stress gradients (such as salinity or acidity in the case of aquatic systems). There are a  
63 number of studies that contributed to our knowledge on such relationships along highly  
64 controlled experimental gradients such as temperature or salinity (Steudel et al. 2012). Far  
65 less have studied habitats along natural stress gradients. Among these few, empirical evidence  
66 showed that stress (flooding or salinity) tolerance could affect the relationship between plant  
67 biodiversity and biomass production in coastal salt marshes (Gough et al. 1994; Grace and  
68 Pugesek 1997).

69 Salinity represents a major structuring gradient in aquatic systems, affecting organisms  
70 directly (through osmotic regulation) and indirectly, as a determinant of other habitat  
71 characteristics, such as biotic interactions (e.g. fish predation) and the presence of biotic  
72 structuring elements (macrophytes). In estuarine systems, a diversity minimum is observed at  
73 intermediate salinities in the transitional zone from freshwater to marine conditions (Remane  
74 1934). In contrast, inland saline lakes rather seem to show monotonous declines in diversity  
75 along salinity gradients (see Table 1). Contrary to estuarine systems, which are populated by  
76 marine taxa at high salinities, inland saline habitats usually harbour no or only a very few  
77 coastal species; in their case, decreasing species diversity is attributable to the gradual  
78 disappearance of freshwater species.

79 Although diversity patterns along natural salinity gradients are known for a long time  
80 (e.g. “Remane’s curve” is already known since 1934), they have received surprisingly little  
81 attention in terms of BEF research. A survey of existing studies on inland saline waters (Table  
82 1) shows that zooplankton diversity generally declines with salinity, while only a few of these  
83 investigations have also looked at density, as a potential proxy for secondary production of  
84 zooplankton. These few suggest that zooplankton secondary production tends to decline with  
85 salinity, parallel with diversity. Such a negative relationship is in agreement with both an

86 overall negative effect of increasing environmental stress, as well as with the negative effect  
87 of species loss.

88 Here, we analyse drivers of biodiversity (diversity of zooplankton) and ecosystem  
89 functioning (secondary production of zooplankton) along a natural stress gradient. The astatic  
90 soda pans in the Carpathian Basin (Central Europe) represent habitats with a natural stress  
91 gradient, provided by a wide range of salinity (from hypo- to sometimes hyper-saline ranges;  
92 Boros 1999). Previous studies revealed that these systems are mostly populated by freshwater  
93 species, while only one specialist is reported from these habitats, *Arctodiaptomus spinosus*  
94 (Copepoda: Calanoida; Megyeri 1999). The absence of fish predators and macrophytes  
95 (which are generally missing from the central part of the pans) makes these systems very  
96 suitable for testing the direct effects of salinity on diversity and functioning. Moreover, in  
97 contrast to e.g. coastal lagoons, which have dynamic boundaries, the representatives of this  
98 habitat type are distinct systems. At the same time, they are also geographically isolated from  
99 other saline environments.

100 In line with other studies (e.g. Tilman and Downing 1994; Tilman 1999; Giller et al.  
101 2004; Hooper et al. 2005), we use biomass, measured as density, as a proxy for ecosystem  
102 functioning for practical reasons. This choice is justified in soda pan zooplankton by the fact  
103 that predation pressure is generally low as the pans are naturally fishless, and invertebrate  
104 predators are numerically scarce in the open water. Soda pans also frequently fall dry in late  
105 summer, hence there is limited time for zooplankton to accumulate over time, and  
106 zooplankton density should be closely linked to the trophic state of a pan. Moreover, as the  
107 density of dominant zooplankters is tightly linked to the number of migrating invertivorous  
108 waterbirds visiting the pans (Horváth et al. 2013b), it represents an important ecosystem  
109 service.

110 Our aims are twofold. By collecting a large number of environmental (biotic and  
111 abiotic) parameters, we first aim at identifying the principal drivers of zooplankton diversity  
112 along the natural stress gradient. In addition to S, we also consider phylogenetic diversity  
113 (PD). If closely related species were similarly sensitive to rising salinity, we would expect a  
114 more sudden drop in PD compared to S. Alternatively, a slower decrease in PD is anticipated  
115 if species from the same taxonomic categories have different salinity tolerance. In addition to  
116 that, PD may better reflect functional diversity than S, as major phylogenetic groups (e.g.  
117 Cladocera, Cyclopoida, Calanoida) show clear differences in their feeding modes and  
118 reproductive strategies (Hutchinson 1967). Second, we analyse drivers of zooplankton density  
119 as a key feature of the functioning aspect of soda pans, trying to separate the potential direct  
120 effect of community diversity on density from environmental parameters along the natural  
121 stress gradient. We hypothesise that with the gradual disappearance of species and increasing  
122 environmental stress represented by salinity will in parallel lead to a decrease in zooplankton  
123 density.

124

## 125 **Methods**

### 126 **Study area**

127 Athalassohaline lakes are inland saline waters which are not of marine origin.  
128 Therefore, their ionic composition can differ substantially from sea water (Hammer 1986).  
129 Astatic soda pans on the Pannonian Plain in the Carpathian Basin (in the lowland territories of  
130 Hungary, Austria and Serbia) are unique and isolated representatives of athalassohaline  
131 waters.

132 Soda pans are shallow intermittent waterbodies, which often dry out in summer and  
133 are naturally fishless. They can cover quite large areas (up to 100–200 ha), although their  
134 water depth is mostly below 1 m (Megyeri 1959) and they are not stratified, which categorises

135 them as ponds rather than lakes (Megyeri 1979). Pans have three main types of origin in the  
136 Carpathian Basin. They can be deflationary, or can be formed by flat, rounded depressions of  
137 loess sediment or former erosional activity of rivers. Their hydrology primarily depends on  
138 the mineral-rich groundwater (Boros 1999). The pH of the pans ranges mainly between  
139 7.5–10 and their ionic composition is dominated by  $\text{Na}^+$ ,  $\text{CO}_3^{2-}$  and  $\text{HCO}_3^-$  (Megyeri 1959).  
140 This differentiates them from all other inland saline waters of Europe, especially from coastal  
141 lakes (Hammer 1986).

142 The hypertrophic state of most soda pans is largely due to guantrophication by  
143 numerous large-bodied waterbirds (Boros et al. 2008). Furthermore, high salinity, pH and  
144 permanent resuspension cause high remineralisation rates of phosphorus (Boros 2007; Moss  
145 1988), with total phosphorus values up to  $34 \text{ mg l}^{-1}$  (Boros 2007).

146 In these soda pans, the vast majority of zooplankters are ubiquist and they frequently  
147 occur in other lowland waters (Megyeri 1959). Recent studies on these systems are scarce and  
148 former investigations on species composition mainly included some restricted parts of the  
149 Basin.

150 According to our knowledge, astatic soda pans of the Carpathian Basin constitute the  
151 only occurrence of this habitat type in Europe (Hammer 1986). The number of these habitats  
152 dramatically declined since the 18th century. This habitat loss is estimated to be  
153 approximately 80% in two investigated regions (Kiskunság in Hungary and Seewinkel in  
154 Austria). Habitat loss is primarily attributable to human disturbance and climatic changes  
155 (Kohler et al. 1994; Boros and Biró 1999). More details on these systems are given by e.g.  
156 Horváth et al. (2013a, b).

157

158 **Sampling**

159           110 astatic soda pans in the Carpathian Basin were involved in our study, in an area of  
160 approx. 125,000 km<sup>2</sup>. 62 pans were located in Hungary (on the lowlands), 38 in East Austria  
161 (Seewinkel, Burgenland) and 10 in Northern Serbia (Province of Vojvodina). In total, they  
162 constitute all representatives of this habitat type in the Basin and also in Europe. We  
163 considered a pan natural if it was of natural origin and was not strongly affected by human  
164 disturbance e.g. artificial inflow of freshwater and related fish stocking and semi-natural, if  
165 strong human disturbance was also absent but the pan was constructed/reconstructed in the  
166 former decades. 21 of the 110 habitats turned out to be in a poor ecological state, having lost  
167 the characteristics of soda pans, e.g. their salinity was low due to artificial freshwater inflow.  
168 These pans were only visited once and were not involved in the analyses. 82 pans were  
169 categorised as natural and 7 as semi-natural (Fig. 1). All of these 89 pans were visited at least  
170 twice: once in early spring (between 4th March and 9th April 2010) and once in early summer  
171 (between 11th May and 20th June 2009 or between 12th May and 2nd June 2010). If water  
172 depth was too low for a representative sample in summer 2009, sampling was repeated in the  
173 same period of 2010.

174           Water depth and Secchi disc transparency were measured at each sampling location,  
175 along with pH, conductivity and dissolved O<sub>2</sub> concentration, which were determined by using  
176 a WTW Multiline P4 universal meter (with TetraCon 325 and SenTix 41 electrodes). The  
177 concentration of total suspended solids (TSS) was measured by filtering water (100–1000 ml)  
178 through pre-dried and pre-weighted cellulose acetate filters (0.45 µm) after oven-drying (at  
179 105 °C). For chlorophyll-*a* concentrations, water (100–1000 ml) was filtered through glass  
180 microfiber filters, and the concentration was determined with a Shimadzu UV 160A  
181 spectrophotometer after hot methanol extraction (Wetzel and Likens 1991). No acidic  
182 correction for phaeopigments was made. Total phosphorus (TP) was determined as molybdate

183 reactive phosphorus following persulphate digestion according to Mackereth et al. (1978). TP  
184 and chlorophyll-*a* were only measured in the summer samples.

185 For zooplankton, 20 litres of water were randomly collected in the open water of each  
186 pan with a one-litre plastic beaker and sieved through a plankton net with a mesh size of 30  
187  $\mu\text{m}$ .

188 A push net (similar to the sledge dredge Jungwirth (1973) used to collect *Branchinecta*  
189 in a soda pan) with a mesh size of 1 mm and an opening of 17 cm was used to collect  
190 Anostraca and other macroinvertebrates. In each pan, a 30 m long transect was pushed along  
191 in the open water (it was reduced to 10 m in summer due to the sometimes very high  
192 abundances of Heteroptera).

193 All samples were preserved in 70% solution of ethanol. Zooplankton abundances were  
194 enumerated by subsampling according to Herzig (1984). Per sample, 300 specimens were  
195 identified to species level. When juvenile individuals could only be identified to genus level  
196 in some samples, or two species showed mixed features in some cases, we used “sp.” in the  
197 analysis (for *Simocephalus* sp., *Cyclops* sp., *Polyarthra* sp., *Encentrum* sp.; in this case,  
198 *Cyclops* sp. was a separate taxon from *Cyclops vicinus*). Bdelloid rotifers were not included in  
199 the analyses based on species, as they could not be identified to species or genus levels in the  
200 preserved samples.

201

## 202 **Data analysis**

203 To ease comparison with other studies, conductivity ( $\text{mS cm}^{-1}$ ) was converted to  
204 salinity ( $\text{g l}^{-1}$ ) by a multiplying factor of 0.774 for soda pan data (Boros and Vörös 2010). We  
205 converted conductivity measurements to salinity from other saline habitats by using the  
206 general multiplying factor of 0.670 for sodium-chloride type of waters, or conversely,  
207 converted salinity to conductivity by dividing by 0.670 (Table 1).

208 We calculated Faith's phylogenetic diversity (PD) with the "picante" package for R  
209 (Faith 1992). We made two separate phylogenetic trees for crustaceans and Rotifera, based on  
210 4 taxonomical categories above species level. For crustaceans, we also included Anostraca  
211 (fairy shrimps), as they belong to the same phylogenetic group (Branchiopoda) as Cladocera.  
212 As phylogenetically more closely related species should be, at the same time, more similar  
213 functionally (Flynn et al. 2011), PD should give a proxy for functional diversity of the  
214 communities.

215 S and PD of all groups dropped exponentially along the non-transformed conductivity  
216 gradient. To obtain a better resolution at low-intermediate conductivity, we ln-transformed  
217 conductivity prior to analysis. The data is therefore plotted on the ln-transformed gradient  
218 (*lnCond*).

219 In order to normalise residuals, we transformed total S by square root and all  
220 organisms densities by double square root (including Heteroptera, the only potential  
221 macroinvertebrate predator of zooplankton that was present in considerable numbers in the  
222 pans), respectively, while we applied ln-transformation to environmental predictors (apart  
223 from Heteroptera density) which had very non-normal distribution (TSS, conductivity, TP,  
224 chlorophyll-*a* concentration, water depth, Secchi disc transparency, dissolved oxygen (DO)  
225 concentration) prior to analyses.

226 To identify the main drivers of S and density, we performed multiple linear regression  
227 analyses with all environmental parameters, with manual backward selection of the variables  
228 applying Akaike's Information Criterion (AIC). We used both spring and summer samples  
229 from all the 89 undisturbed pans. TP and chlorophyll-*a* concentrations were not measured in  
230 spring, but they were strongly correlated with TSS, which was measured in both seasons (see  
231 Fig. A1 in Supplementary material). Therefore, we used ln-transformed TSS (*lnTSS*) as a

232 proxy for trophic state in our analyses. Correlations among environmental predictors that were  
233 measured both in summer and spring are given in Table 2.

234 According to the multiple linear regression models, *lnCond* and *lnTSS* both proved to  
235 be significant predictors for both S and density. Since these two variables were the strongest  
236 predictors of S and density, we continued the analyses by testing their respective effects  
237 separately on S, PD and density for each taxonomic group (Pearson's correlation  
238 coefficients).

239 S generally declined with *lnCond*. In order to test for a conductivity threshold in the  
240 S–conductivity relationship, we compared linear with logistic regression curves. The logistic  
241 curve was fitted using a general additive model (GAM) with logistic link function. Model  
242 selection was done using AIC comparison. The plots illustrating the relationship between PD  
243 and conductivity (*lnCond*) were constructed accordingly.

244 We estimated species-specific conductivity optima for species having at least 5  
245 occurrences by calculating a weighted average from the ln-transformed conductivity (*lnCond*)  
246 and the corresponding densities of a given taxon from all sites where it was found.

247 As an illustration of shifting species composition along the conductivity gradient, we  
248 calculated the cumulative likelihood of occurrence for all taxa. For each species, we first  
249 fitted a smooth curve along the conductivity gradient, representing the likelihood of species  
250 (prevalence) to occur at a given conductivity (GAMs with logistic link functions). For a group  
251 of organisms (Rotifera and crustaceans), these curves were then pooled and normalised to  
252 sum up to 1.

253 Since both microcrustacean S and density were correlated with trophic state (*lnTSS*)  
254 and conductivity (Table 3), we tested for a direct effect of S on density in a multiple linear  
255 regression with *lnTSS* and *lnCond* as additional predictors. We repeated this analysis for the

256 summer subset, where a proxy for the trophic state of pans could be derived from more  
257 variables (including chlorophyll-*a* and TP; see Supplementary material, Table A2).

258 All analyses were made in R (R Development Core Team 2009), with the packages  
259 “vegan” (Oksanen et al. 2012), “picante” (for the calculation of PD; Kembel et al. 2010) and  
260 “mgcv” (for GAMs; Wood 2011).

261

## 262 **Results**

263 S clearly declined with  $\ln Cond$  in all taxonomic groups (Fig. 2, Table 3). For all  
264 groups, species dropped out from the communities with increasing conductivities. However,  
265 this drop in S was most pronounced above 5 mS cm<sup>-1</sup> in the case of Cladocera, while Rotifera  
266 and Copepoda S showed a more continuous decline. Patterns in PD generally resembled those  
267 of S and no clear difference could be observed in either group (Fig. 3).

268 Among microcrustaceans, *Moina brachiata* and *Arctodiaptomus spinosus* were  
269 outstanding at the upper end of the conductivity rank, separated by a gap from the other  
270 crustaceans (Fig. 4). A similar pattern could be observed in the case of Rotifera, with  
271 *Brachionus asplanchnoides* standing out.

272 Likewise, the only two microcrustacean species which had increasing prevalence with  
273 rising conductivity were *A. spinosus* and *M. brachiata*, summing up to 90% prevalence (Fig.  
274 5). These taxa dominated the microcrustacean assemblages at high conductivities. A number  
275 of species were rather equally distributed and therefore, had a more or less constant  
276 prevalence along the conductivity gradient, such as the very frequent *Megacyclops viridis* (the  
277 next species from above) or *Macrothrix hirsuticornis* (in the middle of Fig. 5a). *Daphnia*  
278 *magna* (below *M. viridis* on Fig. 5a) was also very frequent in the pans, but rather stayed  
279 within the conductivity range of 2–10 mS cm<sup>-1</sup>.

280           Although *B. asplanchnoides* was the most frequent rotifer species in the upper part of  
281 the conductivity gradient (Fig. 5b), it contributed on average not more than 30% to Rotifera  
282 communities, and a couple of other species also had slightly increasing prevalence. Rotifera  
283 thus did not become as dominated by few species at high conductivity values as did  
284 microcrustaceans.

285           Densities of total zooplankton, crustaceans and Copepoda were all highly positively  
286 correlated with ln-transformed conductivity ( $\ln Cond$ ) and showed strong positive correlation  
287 with  $\ln TSS$  at the same time (Table 3). Although Cladocera disappeared above 25  $mS\ cm^{-1}$ ,  
288 their densities showed overall a non-significant positive correlation with conductivity.  
289 Rotifera were the only group that decreased in density with increasing conductivity, but this  
290 relationship was non-significant. Densities of all groups showed a significant relationship  
291 with  $\ln TSS$ . This was positive in all cases, except for rotifers.

292           Cladocera and Copepoda reached maximum densities in highly saline pans, while  
293 Rotifera did not show a clear peak with regard to maximum densities. In the most extreme  
294 case, total zooplankton density rose up to 6,229  $ind\ l^{-1}$ . Maximum rotifer density (6,155  $ind\ l^{-1}$ ,  
295  $l^{-1}$ ) was higher than the peak densities of crustaceans (total crustaceans: 5,590, Copepoda:  
296 2,958, Cladocera: 3,790  $ind\ l^{-1}$ ). However, the average densities (total zooplankton:  $423 \pm 58$   
297  $ind\ l^{-1}$ , crustaceans:  $337 \pm 46\ ind\ l^{-1}$ , Copepoda:  $228 \pm 32\ ind\ l^{-1}$ , Cladocera:  $109 \pm 26\ ind\ l^{-1}$ ,  
298 Rotifera:  $86 \pm 39\ ind\ l^{-1}$ ) indicated general dominance of microcrustaceans within the  
299 communities. Since the individual biovolume of an average rotifer is way below that of a  
300 Cladocera or Copepoda, the difference in biovolume or biomass among these groups must  
301 have been even more pronounced (1–3 order of magnitude) than what is evidenced by this  
302 comparison of densities.

303           The pattern seen in microcrustacean S (decrease with conductivity) and density  
304 (increase with conductivity) indicated their inverse relationship (Fig. 6). Therefore, we tested

305 for a direct effect of S on density in a multiple regression including *lnCond* and *lnTSS*.  
306 According to this, density increased with both *lnTSS* and *lnCond*, while there was no partial  
307 effect of S (Table 4). Results were highly analogous in a similar analysis for the summer  
308 subset, with a trophic state proxy derived from more variables (Supplementary material, Table  
309 A2). Both analyses revealed no direct effect of S on density, while they confirmed that density  
310 increased along the gradients of both trophic state and conductivity.

311

## 312 **Discussion**

### 313 **Bottom-up vs. top-down control of zooplankton density**

314 Most invertebrate predators were very scarce in the pans during our study (e.g.  
315 *Chaoborus*, coleopterans, odonates). Only heteropterans (mainly Corixidae) were present in  
316 considerable numbers, but they showed a positive correlation with conductivity (Table 2) as  
317 did zooplankton density (Table 3), and did not exhibit a significant effect on zooplankton  
318 density in the multiple regression analysis (see Methods). Furthermore, Horváth et al. (2013b)  
319 showed that the trophic relationship between zooplankton and planktivorous waterbirds is  
320 bottom-up regulated. Hence, top-down effects on zooplankton density can largely be excluded  
321 as drivers of the density pattern, confirming our initial assumption that density of zooplankton  
322 reflects its secondary production in the pans.

323 This assumption does not necessarily hold for rotifer densities. Copepods, which were  
324 present in very high numbers, may selectively feed on rotifers. *Arctodiaptomus salinus*, a  
325 species similar in size to *A. spinosus*, can predate efficiently on rotifers (Lapesa et al. 2004).  
326 The negative correlation between densities of rotifers and microcrustaceans (Fig. A1 in  
327 Appendix) and the general dominance of microcrustaceans in the communities may therefore  
328 indicate a negative direct impact of microcrustacean zooplankton on rotifers through  
329 predation.

330

331 **Diversity–functioning aspects of soda pans**

332 Positive BEF relationships depend on matching trait diversity and environmental  
333 dimensionality. High trait diversity cannot play out in a low-dimensional environment  
334 (Hillebrand and Matthiessen 2009, Ptacnik et al. 2010a). The inverse relationship between  
335 diversity and functioning seen in the soda pan microcrustaceans suggests that environmental  
336 diversity is overall low, or even decreases with increasing salinity. The absence of fish and  
337 low numbers of macroinvertebrate predators suggests that most interactions which maintain  
338 diversity at low salinity occur within the plankton community. Decreasing diversity thus  
339 possibly represents a gradient of decreasing complexity in terms of biotic interactions, e.g., no  
340 cladocerans or cyclopoids are found in the most saline pans. It has been suggested that  
341 fluctuations arising from biotic interactions within the plankton may be a central driver for the  
342 maintenance of diversity in phyto- and zooplankton, and that such effects increase along  
343 gradients of primary production (Ptacnik et al. 2010b; Fox et al. 2010). Our data show that  
344 environmental stress may prevent a system from exhibiting high environmental complexity in  
345 spite of high nutrient availability. Instead, stress makes the system increasingly constrained,  
346 and a limited set of highly tolerant taxa may ensure high rates of secondary production. This  
347 is confirmed by an analysis of community turnover (Supplementary material, Table A1).  
348 Dissimilarity among communities decreases with increasing salinity, i.e. communities become  
349 more similar with increasing salinity. Hence, environmental stress seems to counteract the  
350 destabilising effect of high nutrient concentrations in these systems (Smith et al. 1999; Smith  
351 and Schindler 2009), which may also explain the absence of direct diversity–functioning  
352 relationship in these systems.

353 Soda pans represent important habitats for waterbirds, and their service as feeding  
354 ground for specialised birds represents an important functioning of these systems. Due to their

355 importance for birds, a large number of pans are listed as internationally protected areas  
356 (Horváth et al. (2013b). In a recent study, Horváth et al. (2013b) have shown that the number  
357 of invertivorous waterbirds using the pans as stopover sites during spring migration is directly  
358 linked to the densities of anostracans (most of all, *Branchinecta orientalis*) and  
359 *Arctodiaptomus* species. As the available amount of *A. spinosus* grows along the salinity  
360 gradient (and the same is true for *B. orientalis* in spring; Horváth et al. 2013a), secondary  
361 consumers like waterbirds, which do not seem to be affected by the high salinity of the pans,  
362 profit from the environmental stress that selectively favours tolerant crustaceans.

363

#### 364 **Richness patterns and thresholds along the salinity gradient**

365 In contrast to density, S clearly decreased with salinity. Declining S with increasing  
366 salinity is a widely observed phenomenon in many other inland saline habitats (see Table 1),  
367 and is also commonly seen along salinity gradients in estuarine habitats from fresh to  
368 mesohaline conditions (“Remane’s curve”, Remane 1934; Pelletier et al. 2010)

369 Comparison of linear vs. non-linear fits of S and PD along the salinity gradient  
370 revealed that both parameters followed the salinity pattern in a similar manner. Overall, PD  
371 decreases with conductivity in the same way as S, refuting our assumption that PD might  
372 exhibit different pattern compared to S.

373 Declining S along salinity can be regarded a common pattern in inland saline waters  
374 (Table 1), but the patterns found in this study seem to differ from other areas. While we found  
375 a pronounced decline especially above  $5 \text{ mS cm}^{-1}$  (corresponding to  $3.9 \text{ g l}^{-1}$ ), Green (1993)  
376 reports a pronounced drop in S at lower values in a study on African lakes, which encompass  
377 a similar range of salinities. Conversely, there are also some examples when S does not  
378 decrease this abruptly e.g. in Australian saline lakes (Williams et al. 1990), presumably due to

379 the presence of halobionts in the regional species set of these lakes, which are missing from  
380 the soda pans.

381

### 382 **Rank and tolerance of species**

383 Dominance patterns were clearly different among the two major groups (crustaceans  
384 and Rotifera). In crustaceans, especially one taxon became highly dominant and in total, only  
385 two taxa (*M. brachiata* and especially *A. spinosus*) showed increasing prevalence along the  
386 salinity gradient. Rotifers did not become dominated by only a few taxa as much as  
387 crustaceans.

388 Especially in microcrustaceans, the salinity range covered by a given species increased  
389 with the salinity rank of a taxon, i.e. those taxa with high rank also exhibited the widest  
390 “niche breadth” with regard to the salinity gradient. This suggests that taxa occurring at higher  
391 salinities are rather more tolerant than specialised to these highly saline waters, as they also  
392 occur at the lower end of the gradient (apart from the only exception of the rotifer *B.*  
393 *asplanchnoides*). *A. spinosus* seems to be both very tolerant to the extremities of low and high  
394 salinity and at the same time, a specialist of soda waters (occurring only in sodic waters;  
395 Einsle 1993). Thus, the most saline habitats are populated by highly tolerant species. Soda  
396 pans seem to differ in this respect from other, more extreme environments like African, North  
397 American and Australian salt lakes, which are often populated by more specialised  
398 halobiontic taxa (e.g. Green 1993; Pinder et al. 2005).

399 Except for *A. spinosus*, all microcrustacean taxa found in the pans are reported from  
400 freshwater habitats across Europe, some of which can also be found in coastal, brackish  
401 habitats (e.g. *Daphnia longispina*, *D. magna*, *M. brachiata*, *Ceriodaphnia reticulata* or  
402 *Metacyclops minutus*; Samraoui 2002; Green et al. 2005). The species pool of rotifers  
403 included less exclusively freshwater and more euryhaline taxa (Fontaneto et al. 2006). *B.*

404 *asplanchnoides*, which had the highest rank, was an interesting exception, as this species was  
405 the only taxon inhabiting the most saline pans which is not known from marine or brackish  
406 habitats. According to Williams (1998), intermittent salt lakes are often dominated by  
407 regionally restricted species, due to their low dispersal capacities. Our study reveals that in  
408 terms of microcrustaceans, the species pool of the soda pans is primarily populated by  
409 continental taxa, occurring in freshwater habitats across Europe and therefore in the vicinity  
410 of the soda pans. We know less about the biogeographic pattern of the rotifer taxa we found in  
411 our pans, except that they generally exhibit a wider tolerance to salinity – many of the taxa we  
412 found are reported both from freshwater and from coastal or marine habitats (e.g. *Lecane*  
413 *lamellata*, *Hexarthra fennica*, *Eosphora ehrenbergi* etc.). Interestingly, we found a rotifer  
414 species (*Keratella eichwaldi*) that has not been reported from inland waters before and has so  
415 far been listed as an entirely marine-brackish taxon (Segers and de Smet 2008).

416         Given its dominant role in highly saline pans, the calanoid copepod *A. spinosus* is a  
417 key species to the soda pans (besides its key role for waterbirds; Horváth et al. 2013b). In  
418 general, calanoid copepods can have wide salinity-tolerance, but only a very few can tolerate  
419 alkaline waters (Hammer 1986). Among them, *A. spinosus* stands out with the ability to  
420 survive under extremely high concentrations of carbonates (Löffler 1961). Along a salinity  
421 gradient, *A. spinosus* exhibits an optimum with regard to egg production and respiration at  
422 approx. 7.7 mg l<sup>-1</sup> salinity (Newrkla 1978). Being freshwater species, most taxa are impaired  
423 by the increasing salinity, while *A. spinosus* actually benefits from moderate-high salinity,  
424 giving it a competitive edge over most other taxa. *A. spinosus* possibly also benefits from the  
425 high amount of suspended solids (up to 29 g l<sup>-1</sup> in the present study) which may represent a  
426 direct food source for *A. spinosus* (Alois Herzig, pers. comm.). This altogether could enable  
427 its success at elevated salinities.

428

429 **Conclusions**

430 Contrary to expectation, we could not detect a positive diversity–functioning  
431 relationship along a steep natural diversity gradient. In context of BEF research, it is  
432 important to note that the diversity gradient in our study is obviously driven by local  
433 environmental conditions (stress), i.e. is not a result of dispersal limitation. This obviously has  
434 consequences with regard to ecological saturation of the communities. As most taxa are  
435 increasingly excluded along the salinity gradient, only few highly tolerant species remain and  
436 find favourable conditions in terms of food supply, but also in terms of lacking antagonistic  
437 interactions (like predation by cyclopoid copepods). It seems that the absence of other species  
438 results in an environment of minimum complexity, which allows for high functioning in terms  
439 of lasting high densities in spite of a very limited number of species.

440

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452

453

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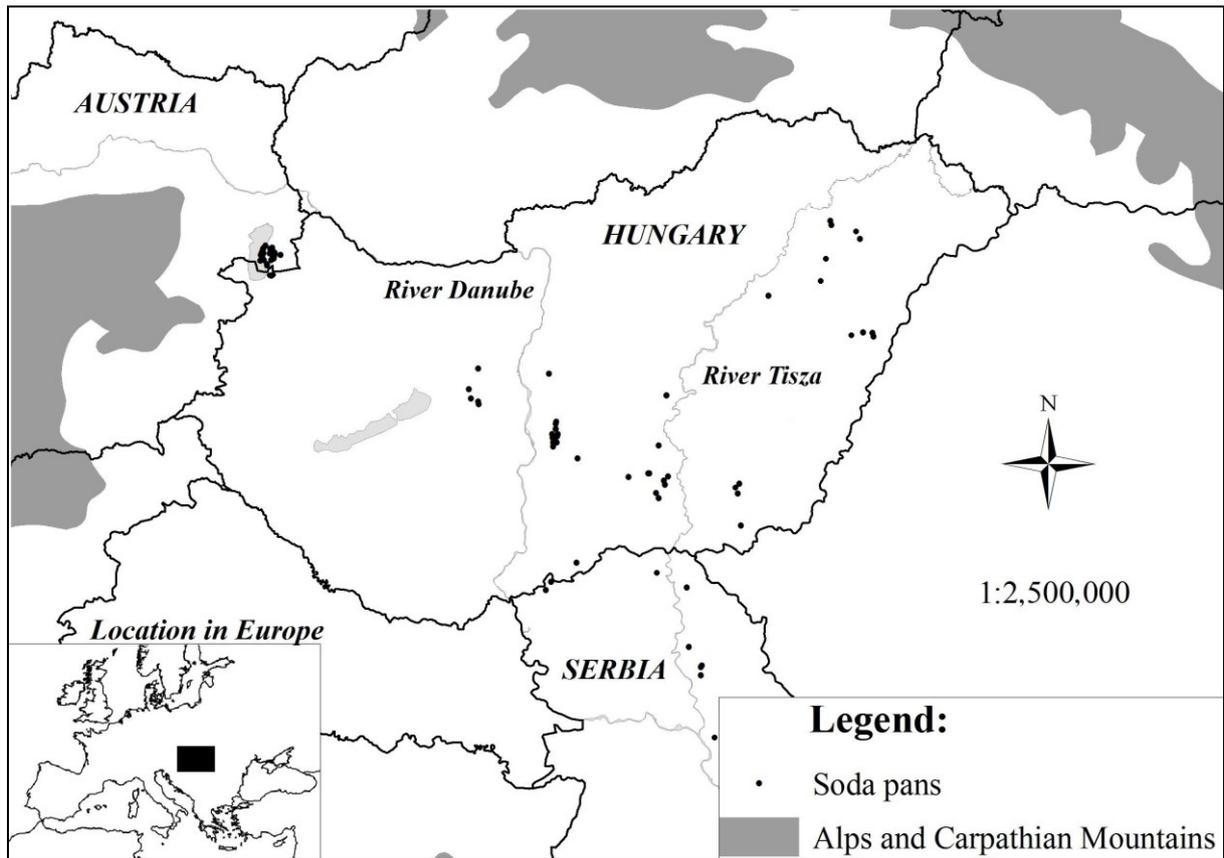
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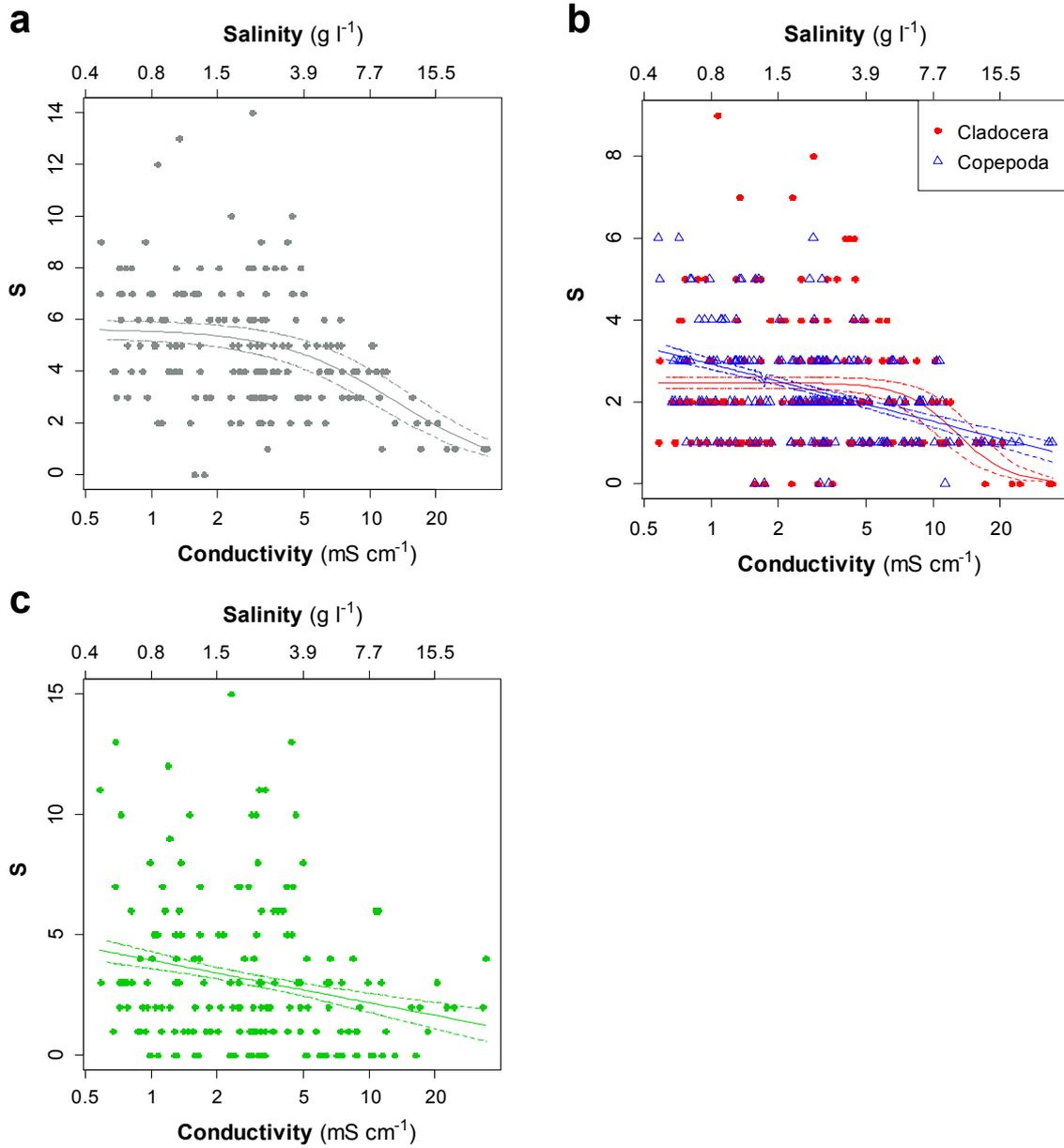


616

617 **Figure 1.** Location of the 89 sampling sites in the three countries

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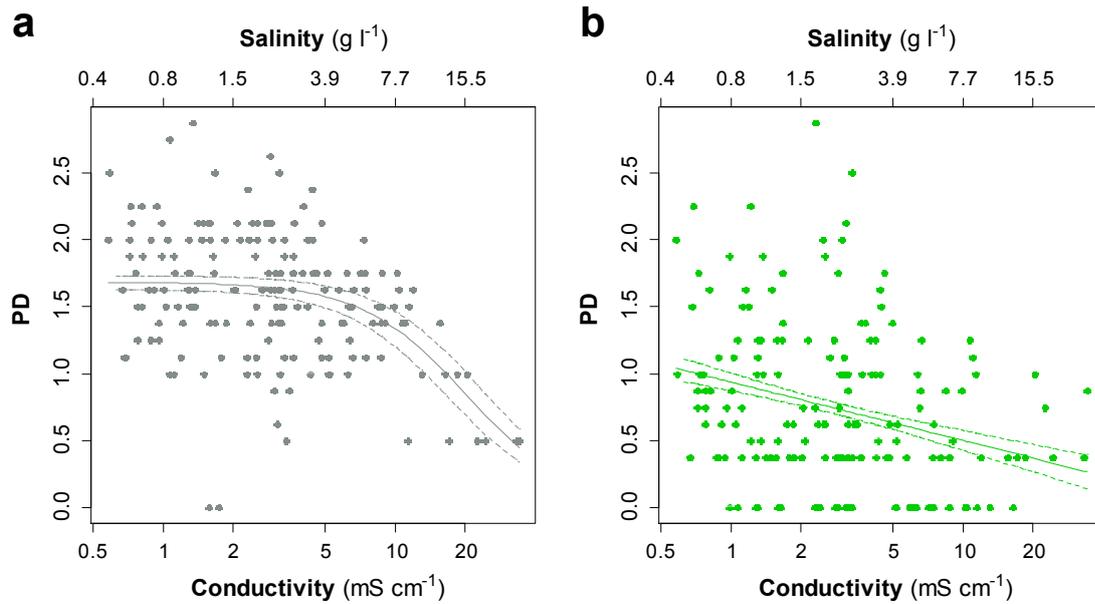


620

621

622 **Figure 2.** Local species richness (S) of crustaceans (Copepoda, Anostraca, Cladocera) (a),  
 623 Copepoda and Cladocera (b) and Rotifera (c) related to the conductivity and salinity of the  
 624 pans (solid lines show the fitted logistic link functions or LMs, while dashed lines indicate ±  
 625 SE)

626

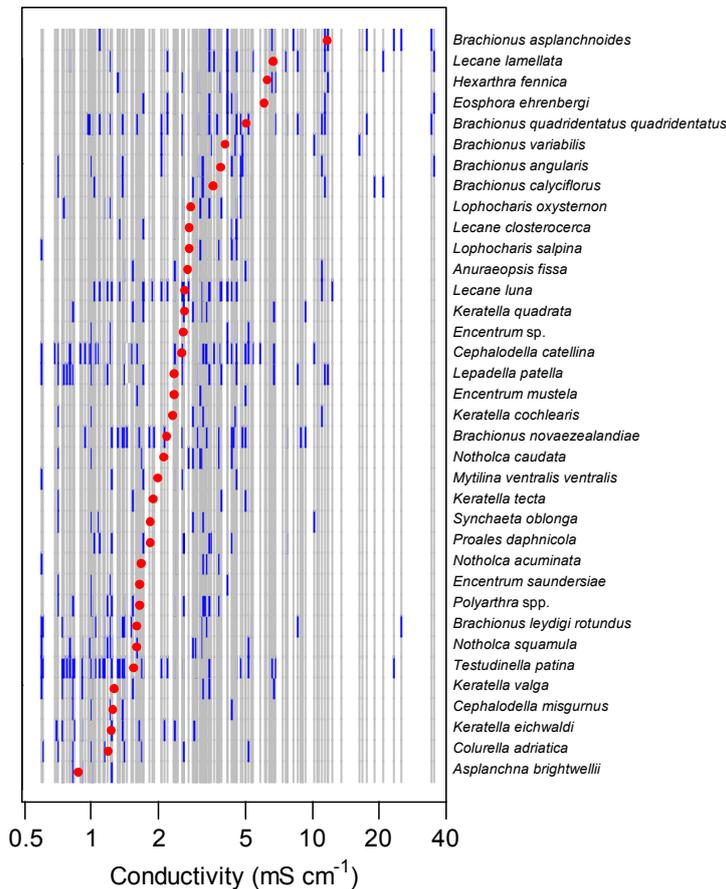
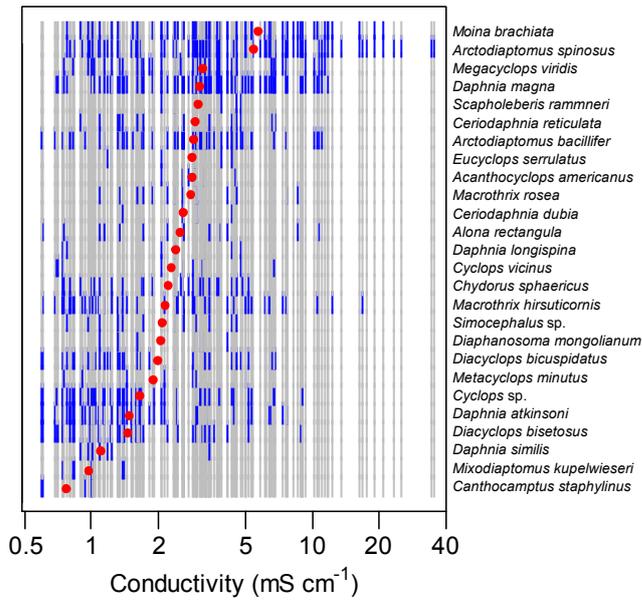


627

628 **Figure 3.** Phylogenetic diversity (PD) of crustaceans (Copepoda, Anostraca, Cladocera; **a**)  
 629 and Rotifera (**b**) related to the conductivity of the pans (solid lines show the fitted logistic link  
 630 function or LM, while dashed lines indicate  $\pm$  SE)

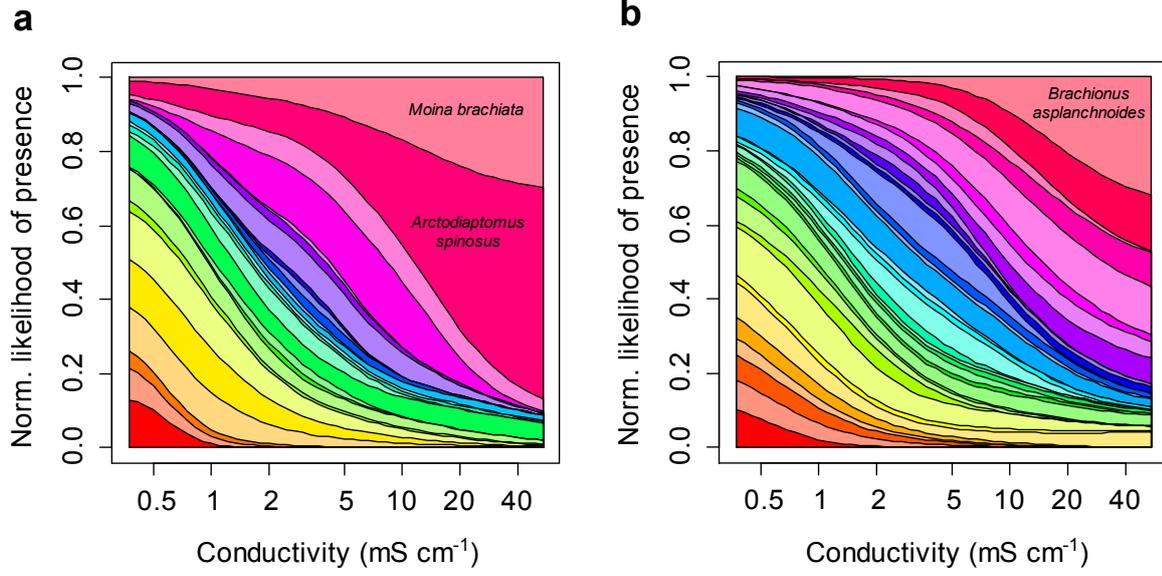
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633

634 **Figure 4.** Rank of microcrustacean (above) and Rotifera species (below) regarding their  
 635 occurrence on the salinity scale, based on spring and summer data together (blue columns: all  
 636 occurrences, grey columns: conductivity of unoccupied pans, dots: mean conductivity for  
 637 each species)

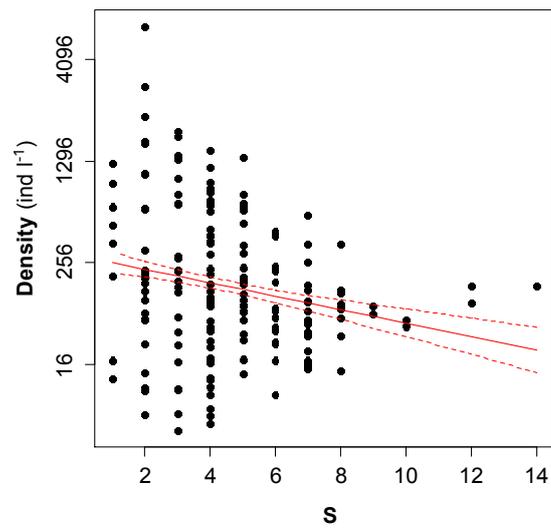


638

639 **Figure 5.** Prevalence of microcrustaceans (a) and Rotifera (b), depending on the conductivity

640 of the pans

641



642  
 643 **Figure 6.** Microcrustacean density (double square root transformed) related to  
 644 microcrustacean species richness (S; untransformed) in the soda pans (N=176). Solid line  
 645 shows the fitted linear model, while dashed lines indicate  $\pm$  SE ( $p < 0.01$ ,  $R^2 = 0.045$ ). Note that  
 646 there was no remaining partial effect of S on density, once conductivity and trophic state  
 647 (TSS) were taken into account (Table 4)

**Table 1.** Patterns and proposed mechanisms underlying zooplankton species richness and density in natural ponds, lakes or wetlands along gradients of salinity. In parentheses, approximation for salinity/conductivity is also shown for comparability, calculated by using the general multiplying/dividing factor of 0.670 for sodium-chloride type of waters. Mechanisms include only effects that were verified by data analysis

| Salinity range                 | Conductivity range                | Species richness |   | Density  |   | Region                      | Reference                |
|--------------------------------|-----------------------------------|------------------|---|----------|---|-----------------------------|--------------------------|
|                                |                                   | pattern          | mechanism   | pattern  | mechanism   |                             |                          |
| (0.03–48.6 g l <sup>-1</sup> ) | 0.05–72.5 mS cm <sup>-1</sup>     | decrease         | -   | -        | -   | East Africa                 | Green 1993               |
| 0.3–343 g l <sup>-1</sup>      | (0.45–511.9 mS cm <sup>-1</sup> ) | decrease         | abiotic stress (salinity)                             | -        | -   | Victoria, Australia         | Williams et al. 1990     |
| (0.21–84.3 g l <sup>-1</sup> ) | 0.32–125.8 mS cm <sup>-1</sup>    | decrease         | abiotic stress (salinity)                             | -        | -   | South Africa                | McCulloch et al. 2008    |
| (0.4–3.4 g l <sup>-1</sup> )   | 0.6–5.0 mS cm <sup>-1</sup>       | decrease         | abiotic stress (salinity and hydroperiod)             | -        | -   | South France                | Waterkeyn et al. 2008    |
| 0.6–43.7 g l <sup>-1</sup>     | (0.9–65.2 mS cm <sup>-1</sup> )   | decrease         | -   | -        | -   | Spain                       | Alonso 1990              |
| 0.03–328 g l <sup>-1</sup>     | (0.04–489.6 mS cm <sup>-1</sup> ) | decrease         | -   | -        | -   | Western Australia           | Pinder et al. 2005       |
| 0.1–85.2 g l <sup>-1</sup>     | (0.15–127.2 mS cm <sup>-1</sup> ) | decrease         | -   | -        | -   | New South Wales, Australia, | Timms 1993               |
| (0.07–69.7 g l <sup>-1</sup> ) | 0.1–104 mS cm <sup>-1</sup>       | decrease         | abiotic stress (salinity)                             | -        | -   | Central Spain               | Boronat et al. 2001      |
| (37.5–90.7 g l <sup>-1</sup> ) | 56–135.4 mS cm <sup>-1</sup>      | decrease         | abiotic stress (salinity, pH), absence of macrophytes | -        | -   | Uganda                      | Rumes et al. 2011        |
| 0–5 g l <sup>-1</sup>          | (0–7.5 mS cm <sup>-1</sup> )      | decrease         | -   | decrease | -   | New Zealand                 | Schallenberg et al. 2003 |
| (4.2–36.5 g l <sup>-1</sup> )  | 6.2–54.4 mS cm <sup>-1</sup>      | decrease         | abiotic stress (salinity)                             | decrease | abiotic stress (salinity) and depth (probably indirect effect through salinity) | Spain                       | Green et al. 2005        |
| 2.8–269 g l <sup>-1</sup>      | (4.2–401.5 mS cm <sup>-1</sup> )  | decrease         | -   | decrease | -   | Canada                      | Hammer 1993              |

**Table 2.** Table of correlations (Pearson's r: lines above; p-value: lines below) between the ln-transformed water depth (*lnZ*), Secchi disc transparency (*lnZs*), conductivity (*lnCond*), TSS (*lnTSS*), dissolved oxygen concentration (*lnDO*), the double square root transformed heteropteran density (*rHet*) and the untransformed pH in the astatic soda pans (N=178). Bold letters indicate significant relationships (p<0.05)

|               | <i>lnZ</i>                      | <i>lnZs</i>                     | <i>lnCond</i>                  | <i>lnTSS</i>                 | <i>lnDO</i>                   | <i>rHet</i>                  |
|---------------|---------------------------------|---------------------------------|--------------------------------|------------------------------|-------------------------------|------------------------------|
| <i>lnZs</i>   | <b>0.579</b><br>< <b>0.001</b>  |                                 |                                |                              |                               |                              |
| <i>lnCond</i> | <b>-0.427</b><br>< <b>0.001</b> | -0.142<br>0.059                 |                                |                              |                               |                              |
| <i>lnTSS</i>  | <b>-0.500</b><br>< <b>0.001</b> | <b>-0.928</b><br>< <b>0.001</b> | 0.111<br>0.146                 |                              |                               |                              |
| <i>lnDO</i>   | 0.095<br>0.211                  | 0.111<br>0.142                  | -0.007<br>0.924                | -0.080<br>0.296              |                               |                              |
| <i>rHet</i>   | <b>-0.436</b><br>< <b>0.001</b> | -0.081<br>0.280                 | <b>0.402</b><br>< <b>0.001</b> | 0.047<br>0.539               | <b>-0.172</b><br><b>0.022</b> |                              |
| pH            | <b>-0.425</b><br>< <b>0.001</b> | <b>-0.174</b><br><b>0.023</b>   | <b>0.306</b><br>< <b>0.001</b> | <b>0.152</b><br><b>0.048</b> | 0.045<br>0.556                | <b>0.226</b><br><b>0.003</b> |

**Table 3.** Correlation table (Pearson's  $r$ ,  $N=178$ ) of  $S$ ,  $PD$  and density of the different groups (total  $S$ : square root transformed, densities: double square root transformed, others: untransformed) with  $\ln$ -transformed conductivity ( $\ln Cond$ ) and TSS ( $\ln TSS$ ). Total zooplankton refers to the sum of Rotifera, Copepoda and Cladocera, while crustaceans means the sum of Copepoda, Cladocera and Anostraca

|                                    |                    | <i>lnCond</i> |     |          | <i>lnTSS</i> |     |          |
|------------------------------------|--------------------|---------------|-----|----------|--------------|-----|----------|
|                                    |                    | <b>p</b>      |     | <b>r</b> | <b>p</b>     |     | <b>r</b> |
| <b>Species richness (S)</b>        | <b>Total</b>       | <0.001        | *** | -0.390   | <0.001       | *** | -0.501   |
|                                    | <b>Crustaceans</b> | <0.001        | *** | -0.387   | 0.093        | .   | -0.128   |
|                                    | <b>Cladocera</b>   | 0.007         | **  | -0.202   | 0.051        | .   | -0.148   |
|                                    | <b>Copepoda</b>    | <0.001        | *** | -0.431   | 0.003        | **  | -0.219   |
|                                    | <b>Rotifera</b>    | 0.003         | **  | -0.222   | <0.001       | *** | -0.534   |
| <b>Phylogenetic diversity (PD)</b> | <b>Crustaceans</b> | <0.001        | *** | -0.368   | 0.420        | .   | -0.062   |
|                                    | <b>Rotifera</b>    | 0.087         | .   | -0.129   | 0.058        | .   | 0.145    |
| <b>Density</b>                     | <b>Total</b>       | <0.001        | *** | 0.571    | <0.001       | *** | 0.249    |
|                                    | <b>Crustaceans</b> | <0.001        | *** | 0.547    | <0.001       | *** | 0.331    |
|                                    | <b>Cladocera</b>   | 0.260         | .   | 0.058    | 0.001        | **  | 0.246    |
|                                    | <b>Copepoda</b>    | <0.001        | *** | 0.532    | 0.008        | **  | 0.202    |
|                                    | <b>Rotifera</b>    | 0.747         | .   | -0.024   | 0.010        | **  | -0.196   |

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**Table 4.** Partial effects of microcrustacean species richness (*S*; untransformed), conductivity (ln-transformed, abbreviated as *lnCond*) and trophic state (ln-transformed TSS, abbreviated as *lnTSS*) on microcrustacean density (double square root transformed) in the soda pans (N=176; zero values of *S* excluded), based on multiple linear regression.

|                                     | <b>Estimate</b> | <b>Std. error</b> | <b>t-value</b> | <b>p</b> |
|-------------------------------------|-----------------|-------------------|----------------|----------|
| <b>Intercept</b>                    | 1.428           | 0.372             | 3.835          | <0.001   |
| <b><i>lnCond</i></b>                | 0.887           | 0.102             | 8.700          | <0.001   |
| <b><i>S</i></b>                     | 0.044           | 0.040             | 1.070          | 0.286    |
| <b>Trophic state (<i>lnTSS</i>)</b> | 0.184           | 0.043             | 4.271          | <0.001   |