3

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^{-1}. 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 Na^+, CO_3^{2-} and 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 guanotrophication 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 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^2. 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_2 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 ^{o}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   μm.

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 (mS cm^{-1}) was converted to

204   salinity (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   (ln*Cond*).

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 (ln*TSS*) 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, ln*Cond* and ln*TSS* 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 ln*Cond*. 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 (ln*Cond*) 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 (ln*Cond*)

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 (ln*TSS*)

254 and conductivity (Table 3), we tested for a direct effect of S on density in a multiple linear

255 regression with ln*TSS* and ln*Cond* 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^{-1} 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^{-1}.

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   ^{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 ± 58

297   ind l^{-1}, crustaceans: 337 ± 46 ind l^{-1}, Copepoda: 228 ± 32 ind l^{-1}, Cladocera: 109 ± 26 ind l^{-1},

298   Rotifera: 86 ± 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 ln*Cond* and ln*TSS*.

306   According to this, density increased with both ln*TSS* and ln*Cond*, 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

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 mS cm^{-1} (corresponding to 3.9 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

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^{-1} 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 competetive edge over most other taxa. *A. spinosus* possibly also benefits from the

425 high amount of suspended solids (up to 29 g l^{-1} 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

Conclusions

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

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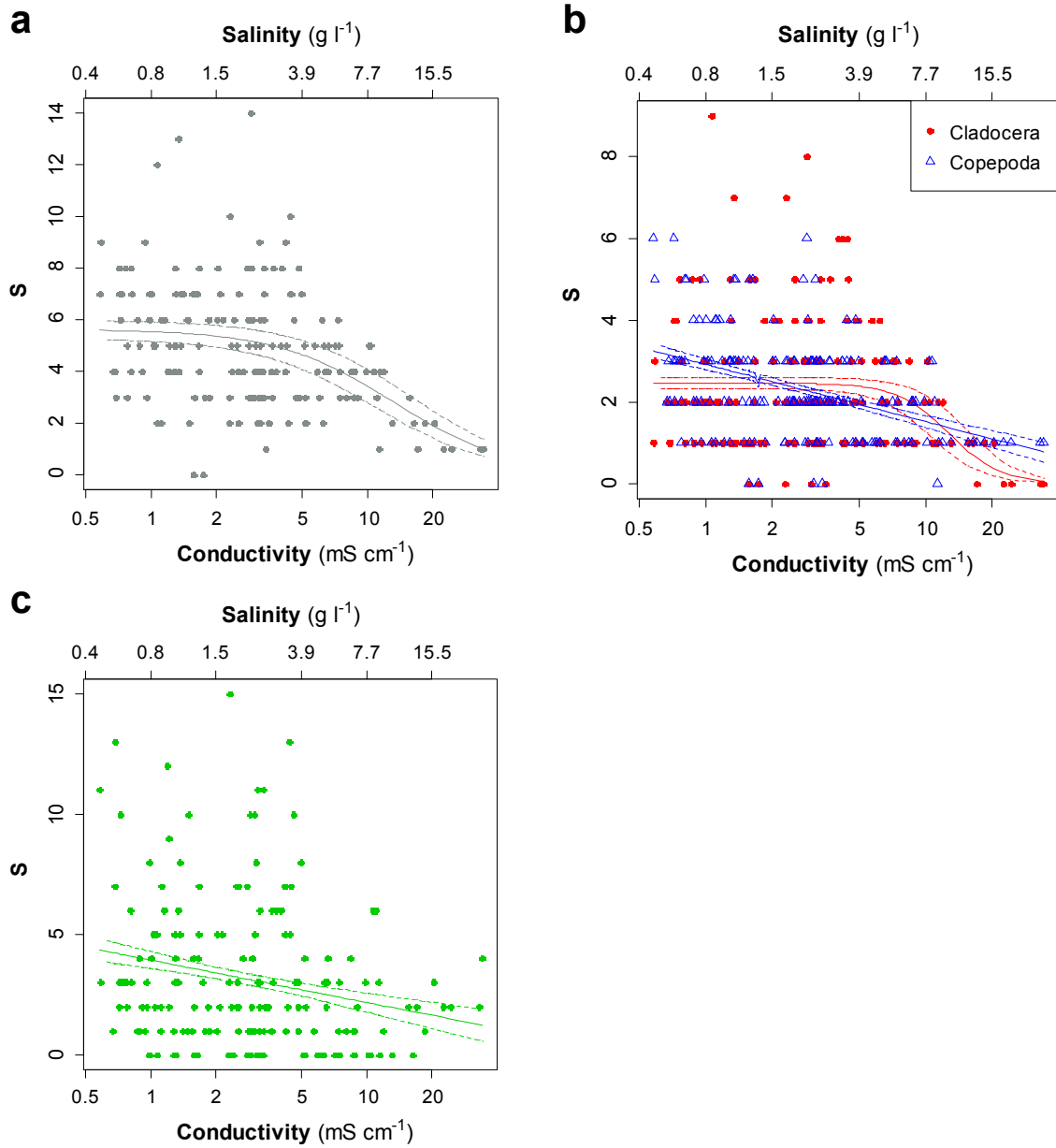
614   314: 787–790.

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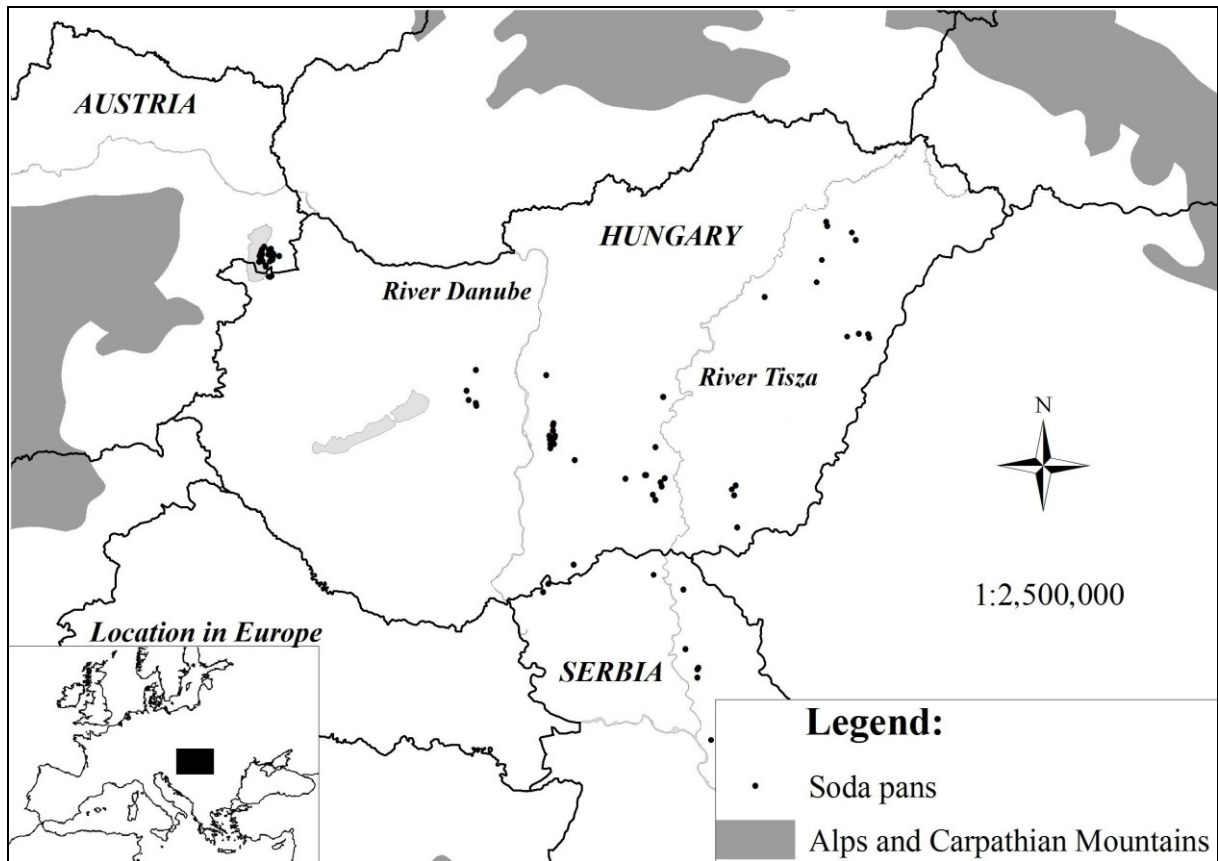
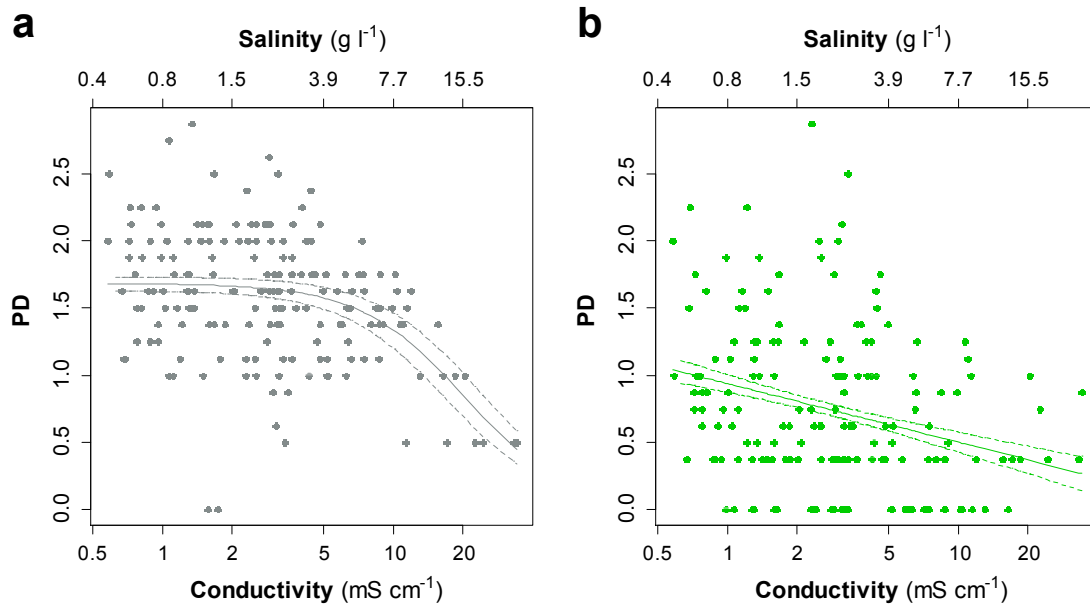**Figure 1.** Location of the 89 sampling sites in the three countries

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Figure 2. Local species richness (S) of crustaceans (Copepoda, Anostraca, Cladocera) (**a**),

Copepoda and Cladocera (**b**) and Rotifera (**c**) related to the conductivity and salinity of the

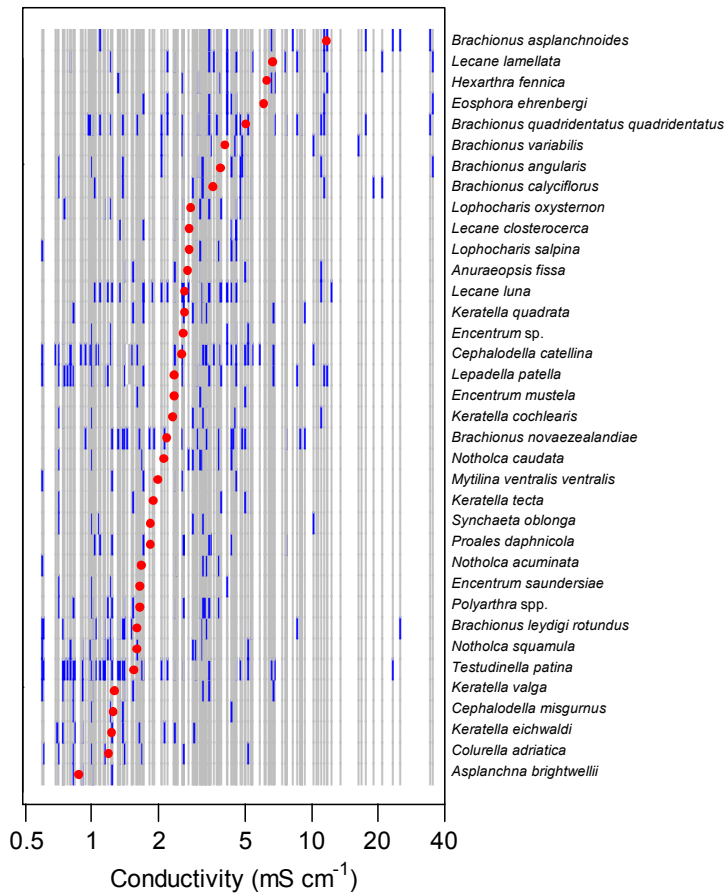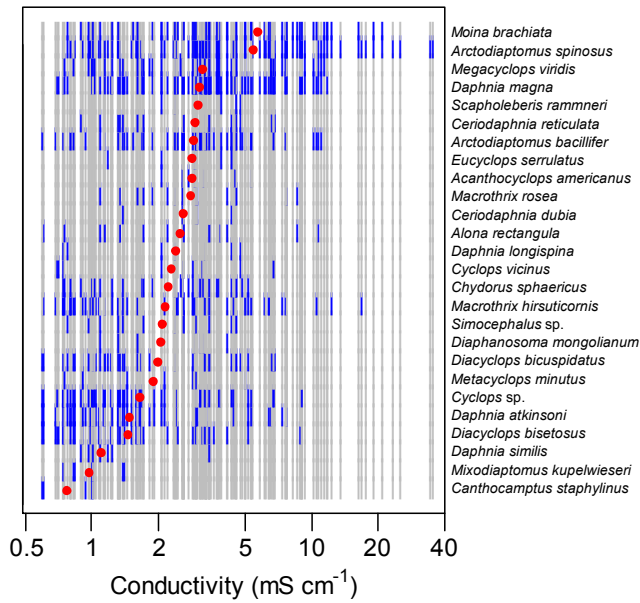pans (solid lines show the fitted logistic link functions or LMs, while dashed lines indicate ±

SE)

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

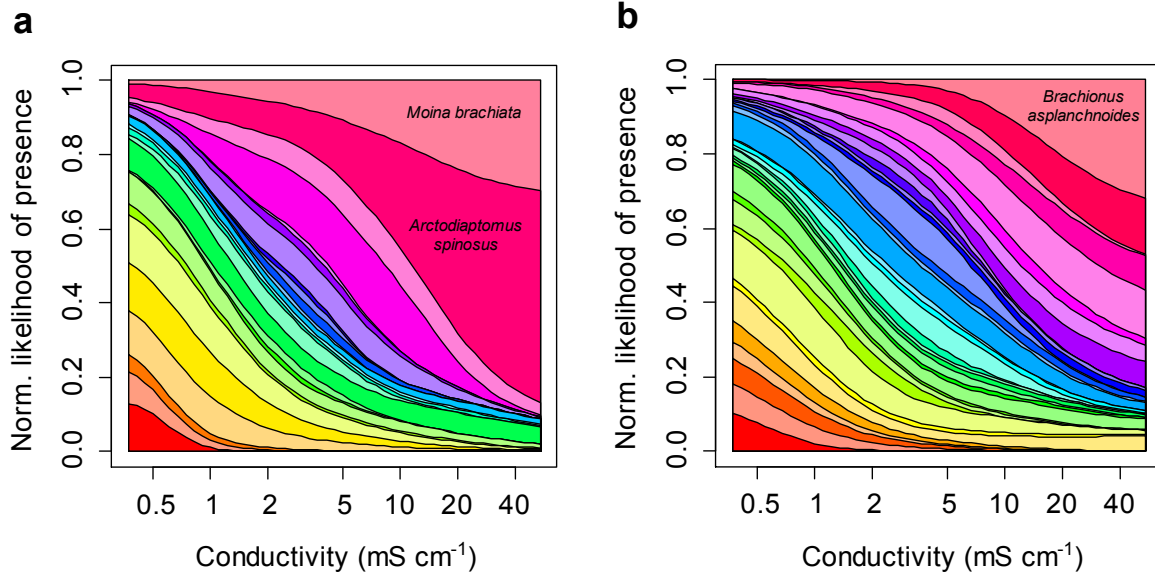**Figure 4.** Rank of microcrustacean (above) and Rotifera species (below) regarding their occurrence on the salinity scale, based on spring and summer data together (blue columns: all occurrences, grey columns: conductivity of unoccupied pans, dots: mean conductivity for each species)

Figure 5. Prevalence of microcrustaceans (**a**) and Rotifera (**b**), depending on the conductivity of the pans
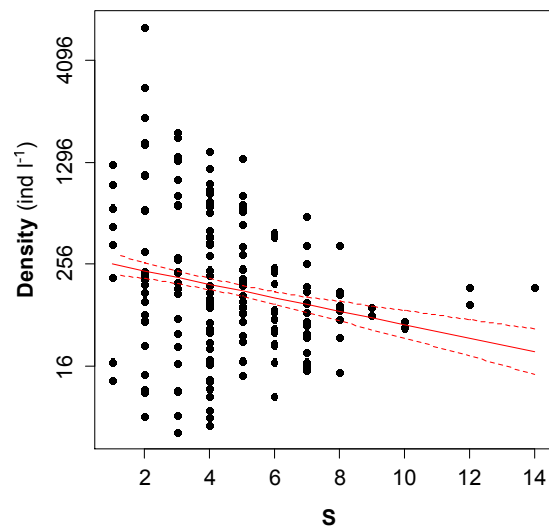
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643 **Figure 6**. Microcrustacean density (double square root transformed) related to

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 1^{-1})	0.05−72.5 mS cm^{-1}	decrease	-	-	-	East Africa	Green 1993
0.3−343 g 1^{-1}	(0.45–511.9 mS cm^{-1})	decrease	abiotic stress (salinity)	-	-	Victoria, Australia	Williams et al. 1990
(0.21–84.3 g 1^{-1})	0.32−125.8 mS cm^{-1}	decrease	abiotic stress (salinity)	-	-	South Africa	McCulloch et al. 2008
(0.4–3.4 g 1^{-1})	0.6−5.0 mS cm^{-1}	decrease	abiotic stress (salinity and hydroperiod)	-	-	South France	Waterkeyn et al. 2008
0.6−43.7 g 1^{-1}	(0.9–65.2 mS cm^{-1})	decrease	-	-	-	Spain	Alonso 1990
0.03−328 g 1^{-1}	(0.04–489.6 mS cm^{-1})	decrease	-	-	-	Western Australia	Pinder et al. 2005
0.1−85.2 g 1^{-1}	(0.15–127.2 mS cm^{-1})	decrease	-	-	-	New South Wales, Australia,	Timms 1993
(0.07–69.7 g 1^{-1})	0.1–104 mS cm^{-1}	decrease	abiotic stress (salinity)	-	-	Central Spain	Boronat et al. 2001
(37.5–90.7 g 1^{-1})	56–135.4 mS cm^{-1}	decrease	abiotic stress (salinity, pH), absence of macrophytes	-	-	Uganda	Rumes et al. 2011
0−5 g 1^{-1}	(0–7.5 mS cm^{-1})	decrease	-	decrease	-	New Zealand	Schallenberg et al. 2003
(4.2–36.5 g 1^{-1})	6.2–54.4 mS cm^{-1}	decrease	abiotic stress (salinity)	decrease	abiotic stress (salinity) and depth (probably indirect effect through salinity)	Spain	Green et al. 2005
2.8−269 g 1^{-1}	(4.2–401.5 mS cm^{-1})	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 (ln$Z$), Secchi disc transparency (lnZs), conductivity (ln$Cond$), 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 ($p < 0.05$)

	ln$Z$	lnZs	ln$Cond$	lnTSS	lnDO	rHet
lnZs	**0.579**					
	<0.001					
ln$Cond$	**-0.427**	-0.142				
	<0.001	0.059				
lnTSS	**-0.500**	**-0.928**	0.111			
	<0.001	**<0.001**	0.146			
lnDO	0.095	0.111	-0.007	-0.080		
	0.211	0.142	0.924	0.296		
rHet	**-0.436**	-0.081	**0.402**	0.047	**-0.172**	
	<0.001	0.280	**<0.001**	0.539	**0.022**	
pH	**-0.425**	**-0.174**	**0.306**	**0.152**	0.045	**0.226**
	<0.001	**0.023**	**<0.001**	**0.048**	0.556	**0.003**

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

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

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

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

	Estimate	Std. error	t-value	p
Intercept	1.428	0.372	3.835	<0.001
ln*Cond*	0.887	0.102	8.700	<0.001
S	0.044	0.040	1.070	0.286
Trophic state (ln*TSS*)	0.184	0.043	4.271	<0.001