1 # Anthropogenic stress alters community concordance at the river-

2 # riparian interface

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4 **Running head**: River-riparian community concordance

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Abstract

Organisms often respond in similar ways to environmental or spatial gradients, particularly at

large spatial scales, but patterns at finer scales and across ecotones are less certain. It is

important to understand these relationships at multiple spatial scales, as managers often need

suitable surrogate taxa for conservation and monitoring purposes. We explored whether

community concordance at the river-riparian interface was decoupled by increasing

anthropogenic stress (a gradient of local land-use intensity) at 15 sites over three years within

the LTER site, Rhine-Main Observatory, a low mountain river system in central Germany

We assessed concordance between four organism groups: riparian spiders and carabid

beetles, benthic macroinvertebrates, and combined aquatic macrophytes and riparian plants.

This represented three different linkages: (1) predator-prey, (2) direct competition, and (3)

habitat associations. While there were no correlations in richness patterns, multivariate

community structure was highly concordant between all groups. Anthropogenic stress

strongly reduced links between riparian spiders and carabid beetles, likely resulting from

their shared resource requirements. However, increasing concordance occurred between

plants and other groups. We posit that patterns may be resulting from two processes: (1)

linkages between directly competing species decouple with increasing anthropogenic stress,

and (2) stronger coupling may occur between habitat providers and dependent species when

overall habitat complexity is reduced. These results highlight the complex manner in which

anthropogenic stress can influence ecosystems and the importance of considering community

structure when exploring biodiversity patterns in basic and applied ecological research,

particularly at small scales and for surrogate taxa development.

Introduction

44

45 Biodiversity often responds to environmental or spatial gradients in a consistent manner over

46 large spatial scales (Lamoreux et al., 2006; Qian and Ricklefs, 2008). The concordance in

47 pattern between multiple taxon groups, also termed cross-taxon congruence, is important for

48 both fundamental and applied reasons (Heino, 2010; Howard et al., 1998; Kati et al., 2004),

49 such as understanding multi-organism responses to environmental gradients, and surrogacy

50 for conservation planning and biomonitoring purposes. In fact, much of the research on cross-

51 taxon congruence has emerged out of the sheer complexity of ecosystems. This complexity

52 results in an inability to adequately describe biodiversity in many systems, through lack of

53 financial resources or expertise. Consequently, much of this research has focused on the

54 development of surrogate or indicator taxa for applied purposes. However, while

55 concordance has been found in a variety of systems and between a wide range of organisms

56 (Bilton et al., 2006; Heino, 2002; Lund and Rahbek, 2002; Su et al., 2004), linkages may be

57 weaker at smaller spatial scales (Kati et al., 2004; Paavola et al., 2006).

58 Concordance in patterns between organism groups at finer spatial scales should

59 theoretically depend on the levels of ecological and physical connectivity between these

60 groups. Spatial subsidies between habitats, for instance, can significantly influence many

61 ecosystem properties and the dynamics of receiving food-webs (Anderson and Polis, 1999;

62 Polis et al., 1997), and dissimilar habitat types have as much potential for cross-boundary

63 transfer of material as do similar habitats (Talley et al. 2006). Freshwater and terrestrial

64 ecosystems are a prime example of such an inter-habitat connection, being strongly linked

65 through the riparian ecotone (Gregory et al., 1991; Talley et al., 2006). Running water

66 ecosystems in particular are highly connected to adjacent riparian zones through flows of

67 nutrients (Gende et al., 2002), organic matter (Wallace et al., 1997), and organisms (Nakano

68 et al., 1999). The flow of energy through this transition zone is reciprocal, strongly

69 influencing the functioning of these systems, but these processes are vulnerable to

70 anthropogenic stressors (Baxter et al. 2005).

71   While ecosystems spanning the globe are currently subjected to a suite of global

72 change related stressors (Tylianakis et al., 2008), rivers in particular are under significant

73 threat (Dudgeon et al., 2006; Vörösmarty et al., 2010). In fact, recent work has highlighted

74 that human-derived stressors can have contrasting influences to natural stressors on diversity

75 of riverine organisms (Gutiérrez-Cánovas et al., 2013), and can also alter the co-occurrence

76 patterns of stream invertebrates through changes in community assembly patterns (Larsen

77 and Ormerod, 2014). Given, for example, pulses of marine-derived nutrient subsidies in the

78 form of spawning salmon carcasses can temporarily decouple the detrital resource-consumer

79 relationship in streams (Zhang et al., 2003), it is likely that other processes and community

80 linkages decouple with external influences at the river-riparian interface.

81   Riparian zones represent a unique ecotone with strong interactions and dynamic

82 communities, as well as often harbouring high levels of biodiversity (Naiman and Henri,

83 1997). As a transitional area from aquatic to terrestrial, river-riparian interfaces provide an

84 ideal focal area to test concordance between taxon groups across an ecological boundary that

85 is subject to metaecosystem flows (*sensu* Loreau et al., 2003). Strong linkages have been

86 found between aquatic insects and riparian arthropod predators (Hering and Plachter, 1997;

87 Sanzone et al., 2003). Therefore, given the importance of understanding linkages between

88 multiple organism groups at fine spatial scales and across ecotones, we assessed cross-taxon

89 congruence / community concordance of riparian spiders and carabid beetles, benthic

90 invertebrates, and riparian and in-stream plants in the Rhine-Main Observatory, a low-

91 mountain river system in central Germany, over three consecutive years. This provides us

92 with three different linkages to compare between in the form of: (1) predator-prey (riparian

93   predators-benthic invertebrates), (2) direct competition (spiders-beetles), and (3) habitat

94   associations (i.e. flora-fauna associations such as beetles using plants as habitat).

95   Specifically, given that land use change related stressors form a major component of

96   the threats to freshwater biodiversity (Dudgeon et al., 2006; Vörösmarty et al., 2010), we

97   assessed whether the degree of concordance of richness and community structure at fifteen

98   sites, each sampled consecutively over three years, differed between three levels of

99   anthropogenic stress (a local land use gradient). We developed the following set of

100   hypotheses: 1) due to the small spatial scale, concordance between richness and community

101   patterns of different organism groups would be weak in general; 2) highest concordance

102   would be between beetles and spiders, given their shared habitat/resources, and previously

103   reported similarity in important environmental conditions (Lambeets et al., 2008); 3)

104   concordance would decrease between different organisms with increasing anthropogenic

105   stress, resulting from more impaired communities and lower functional connectivity; 4) due

106   to the buffering capacity of rivers, and the distance across the aquatic-terrestrial interface, the

107   weakest concordance would occur between benthic invertebrates and the remaining groups.

108

109   **Materials and methods**

110   **Study site**

111   Fifteen sites were sampled along the Kinzig River as part of the Rhine-Main Observatory

112   (RMO), a long-term ecological research (LTER) site (Fig. S1). The Kinzig River is a low-

113   mountain river catchment situated in central Germany and flows through a mosaic of

114   different land uses, including forested, agriculture and urban areas. The sampling design was

115   set up to maximise the coverage of sites across a land use intensity gradient. Sampling sites

116   were situated in one of three land use types, which represented a clear gradient in

117   anthropogenic stress (five replicates of each category), ranging from low to high stress.

118 Forest represented the low stress sites, open agricultural land was medium and urban zones

119 represented high stress sites. Sampling was performed annually in summer 2010-2012 at each

120 of the 15 sites. Each site covers a 100-m river reach and spans 30 m laterally from the centre

121 of the river (area = 6000 m^2).

122

Vegetation mapping

124 Riparian vegetation and in-stream macrophytes were mapped at each of the sites in a two-

125 step approach. First, areal coverage of vegetation types according to Oberdorfer (Oberdorfer,

126 1992) was mapped in a field survey supported by aerial photographs using GIS. Second, for

127 each vegetation type determined at each of the sites, three replicate assessments of individual

128 species abundances (relevés) were performed using the Braun-Blanquet scale (Braun-

129 Blanquet, 1964). For vegetation types comprising predominantly herbaceaous species, each

130 assessment covered an area on 10 m²; for vegetation types including woody plants larger

131 areas of 100 m² each were assessed. Sampling took part in summer, when the vegetation was

132 fully developed. Only forested sites were visited twice, in spring and summer, to also cover

133 the geophytes that are only visible in spring.

134

Riparian spiders and carabid beetles

136 Riparian spiders (Order: Araneae) and carabid beetles (Order: Coleoptera; Family:

137 Carabidae) were sampled using 5.5-cm diameter pitfall traps in the riparian zone. Eight pitfall

138 traps were used at each site, covering the range of microhabitat conditions available (i.e. bare,

139 mown grass, unmown grass, annuals, shrubs, low forest ground cover, high forest ground

140 cover, garden, hard substrate, deadwood). Each year, traps were left *in situ* for a period of

141 two weeks in August, and were filled with Renner solution to kill and preserve the

142 specimens. Juvenile spiders were excluded from the analysis.

143

Benthic macroinvertebrates

145   Benthic macroinvertebrates were sampled following the official EU Water Framework

146   Directive (WFD) multi-habitat sampling protocols (Haase et al., 2004a). This process

147   involves 20 sub-samples being taken from multiple locations covering the range of

148   microhabitats present at a site (i.e. seven substrate size classes, two artificial substrate classes,

149   algae, submerged macrophytes, emergent macrophytes, terrestrial plants, deadwood, CPOM,

150   FPOM, saprobic, non-woody debris), to accurately represent the sample reach. Samples were

151   then stored in 70% ethanol and later identified in the laboratory to the level of the EU WFD-

152   compliant operational taxon list (Haase et al., 2004a, 2004b).

153

Statistical analysis

155   All statistical analyses were performed in R version 3.0.2 (R Core Team, 2013).

156   To assess differences in taxonomic richness between the three stress levels and years,

157   we used two-way analysis of variance (ANOVA) using the 'aov' function the package 'stats'.

158   To assess whether species richness patterns were congruent between the four organism

159   groups across all sites and years we performed Pearson's correlations between all groups

160   using the 'rcorr' function in the Hmisc package (Harrell Jr, 2014). We also correlated

161   richness associations for each local land use separately to assess if richness congruence was

162   stronger for certain stress levels.

163   For multivariate community analyses, we used presence-absence data to best enable

164   standardised between-group comparisons. To visualise differences in community structure

165   between the three stress categories and years, we used non-metric multidimensional scaling

166   (nMDS) ordination, with the function 'metaMDS' in Vegan (Oksanen et al., 2013). We also

167   compared ordination stress scores with those from ordinations on log-transformed data and

168   these remained similar to presence-absence data (stress for log-transformed data increased for

169   beetles, decreased for invertebrates, and remained the same for spiders and plants). We used

170   Bray-Curtis as the distance measure and fit vectors to compare year-to-year changes in

171   community structure between the groups and stress levels. To statistically assess differences

172   in community structure between the three stress levels and years, we used two-way

173   PERMANOVA, using the 'adonis' function in Vegan. Again we used Bray-Curtis distances

174   and performed 9999 permutations.

175   To assess pairwise community concordance between the four groups we compared the

176   two-dimensional nMDS ordination structures using a Procrustes superimposition approach

177   (Gower, 1971). This process attempts to minimise the sum-of-squared residuals of points

178   (sites) on two ordination structures by scaling and rotating ordination structures. This is

179   essentially similar to the Mantel test but dealing only with the two-dimensional ordination

180   structure rather than the entire distance matrix. Thus, it has the advantage over Mantel tests of

181   reducing dimensionality of the original data and allowing a visual inspection of the compared

182   structures (Peres-Neto and Jackson, 2001).

183   We then tested for significant associations between these structures on a pairwise

184   basis using a PROTEST permutation procedure (Jackson, 1995) implemented with the

185   'protest' function in Vegan using 9999 permutations. This approach uses randomisation to

186   test the significance of the Procrustean fit (Jackson, 1995; Peres-Neto and Jackson, 2001).

187   Finally, to test our hypothesis that anthropogenic stress influences community

188   concordance, we assessed pairwise differences in ordination structures between the four

189   groups. To do this, we extracted residual differences between individual ordination points

190   resulting from the Procrustean rotations and tested for differences in residuals between the

191   three stress categories using one-way ANOVA. Where significant differences were evident,

192 we assessed individual differences between stress levels using Tukey's HSD post-hoc test

193 with the 'TukeyHSD' function.

194

195 **Results**

196 **Richness patterns**

197 Richness of plants and benthic invertebrates did not differ either between the three stress

198 levels or between years (Fig. 1). Riparian beetle richness was higher at the medium compared

199 to high stress sites (Tukey's HSD: $P < 0.01$), but there were no other pairwise differences

200 between stress categories (Tukey's HSD: $P > 0.05$; Fig. 1). Further, beetle richness was

201 significantly lower in 2012 than both 2010 and 2011 (Tukey's HSD: $P < 0.05$; Fig. 1). Spider

202 richness was significantly higher at medium compared to both low and high stress sites

203 (Tukey's HSD: $P < 0.0001$), with no difference between low and high stress sites (Tukey's

204 HSD: $P > 0.05$; Fig. 1).

205   There was no correlation between taxonomic richness of any of the organism groups

206 within each anthropogenic stress level or for all stress categories combined (Fig. 2).

207

208 **Multivariate structure**

209 Multivariate structure of all organism groups differed strongly between stress levels, but only

210 spiders and invertebrates differed between years (Fig. 3; Table 1). Plants had the lowest

211 variation from year to year (Fig. 3; Table 1)

212   All pairwise ordination similarities were highly significantly related, with correlations

213 ranging between 0.431 and 0.711 (Fig. 4). Plant and spider ordinations were the most similar,

214 whereas the least similar structures were those between invertebrates and both beetles and

215 spiders (Fig. 4). Benthic invertebrates had the lowest concordance with other groups (Fig. 4).

216   Anthropogenic stress had variable influences shaping concordance between organism

217   groups (Fig. 4). Extracted pairwise ordination residuals between the four organism groups

218   exhibited significant differences between stress types for plants-spiders, plants-invertebrates,

219   beetles-invertebrates and beetles-spiders comparisons. Residuals between plant and spider

220   assemblage ordinations were greater (implying lower concordance) at low than medium, but

221   not high stress sites (Fig. 4), and the same trend was apparent for the beetles-invertebrates

222   comparison. Concordance between plant and benthic invertebrate assemblages increased with

223   increasing stress (i.e. residuals reduced), with intermediate concordance at medium stress

224   sites (Fig. 4). Concordance decreased between riparian beetles and spiders with increasing

225   stress, with significantly higher residuals at high compared to low and medium stress sites

226   (Fig. 4).

227

228   **Discussion**

229   Cross-taxon congruence is of fundamental importance for the selection of indicator (or

230   surrogate) taxa, often with the focus on whether or not surrogate taxa are able to predict

231   spatial patterns in other taxa. This topic has received significant attention in conservation

232   biology and applied ecology (Fattorini et al., 2012; Heino, 2010; Kati et al., 2004), stemming

233   from the lack of resources to effectively monitor every component of highly complex

234   ecosystems. We examined the congruence in species richness and community structure

235   between four organism groups in a river-floodplain system, and whether or not these linkages

236   were influenced by anthropogenic stress. While there was no evidence of concordance in

237   taxonomic richness between organisms at the river-riparian interface in this study,

238   community structure was strongly linked between all groups. We hypothesised concordance

239   would decrease between different organisms with increasing anthropogenic stress, resulting

240   from more impaired communities and lower functional connectivity. However, the influence

241 of stress shaping concordance of community structure varied between pairwise comparisons.

242 We posit that two processes are operating to reveal these relationships: (1) increasing

243 anthropogenic stress leads to decoupling of directly competing species (e.g. riparian beetles

244 and spiders), whereas (2) stronger coupling occurs between habitat providers (i.e. plants) and

245 other species when overall habitat complexity is reduced.

246   Due to both groups being active ground hunters and competing for the same

247 resources, we hypothesised riparian beetles and spiders would exhibit the most concordant

248 patterns at the community level. A previous study examining lowland river bank spider and

249 carabid beetle assemblages found similarities in the predominant environmental variables

250 influencing their structure (Lambeets et al., 2008). While the strongest link for multivariate

251 structure was between spiders and plants, riparian beetles and spiders exhibited strongly

252 concordant patterns at the community level. The association between these two groups was

253 most clearly affected by anthropogenic stress, with a strong decoupling with increasing

254 stress, which we hypothesise is a function of their shared resource requirements. In low-stress

255 environments, species interactions shape community structure, resulting in a strong coupling

256 between different taxonomic groups, particularly those with shared resource requirements

257 such as riparian spiders and carabid beetles. With increasing stress, this species network that

258 is structured by competitive interactions and limiting similarities is broken up and

259 communities are increasingly shaped by abiotic controls. Nonetheless, a recent meta analysis

260 showed that increasing stress may facilitate positive species interactions, but this paper

261 focused solely on plant communities (He et al., 2013).

262   In line with our hypothesis, whilst being significantly linked, benthic invertebrates

263 had consistently the lowest concordance with the remaining groups. This is likely a result of

264 two key factors: first, contrary to riparian communities, in-stream communities are buffered

265 from the influence of the immediately surrounding terrestrial zone and are shaped by the

266   entire upstream catchment processes (Allan, 2004). Second, benthic invertebrates were the

267   only purely aquatic taxonomic group in our analyses and consequently were the most

268   disconnected of the groups across the aquatic-terrestrial boundary. Nevertheless, patterns

269   remained strongly concordant with other groups, reflecting the importance of reciprocal

270   aquatic-terrestrial connectivity in stream ecosystems (Baxter et al., 2005), which can occur in

271   many forms, including energy, materials, and organisms (Talley et al., 2006).

272   As plants in the present study were combined riparian vegetation and in-stream

273   macrophytes and thus spanned the river-riparian boundary, it is not surprising they were the

274   most strongly linked grouped with benthic invertebrates. Nonetheless, studies have found

275   strong associations between benthic invertebrates and riparian communities (Burdon and

276   Harding, 2008; Sabo and Power, 2002; Sanzone et al., 2003). For instance, stream insect

277   biomass was found to be strongly associated with riparian spider biomass and web densities

278   in New Zealand streams (Burdon and Harding, 2008), and this association weakened with

279   distance from the stream for spider webs. Riparian web-building spiders derive a significant

280   proportion of their carbon from aquatic sources (Collier et al., 2002; Sanzone et al., 2003),

281   and riparian carabid beetles also largely feed on aquatic insects, particular those that emerge

282   through crawling (Hering and Plachter, 1997). However, the use of aquatic subsidies by

283   riparian ground beetles and spiders can be separated seasonally, likely as a result of their life-

284   history characteristics (Paetzold et al., 2006), and our study was based on one-off sampling in

285   late summer/autumn. Finally, as we included both mero- and hololimnic benthic invertebrate

286   species (i.e. those with and without an adult flight stage) in our analyses, and the fact that

287   riparian predators feed predominantly on emerging insects, it may be assumed that the link

288   between riparian predators and benthic invertebrates would be stronger with merolimnic

289   species alone.

290   Contrary to expectation, concordance between plants and other groups increased with

291   increasing stress. This trend likely reflects the habitat provision role that plants have for

292   associated groups, rather than direct competition as per beetles and spiders. For beetles and

293   spiders, concordance increased mostly from low to both medium and high stress sites. This

294   pattern is challenging given the contrasting richness trends between medium and high stress

295   sites for these communities. That is, richness of both beetles and spiders was highest in the

296   medium stress sites and lower in high stress sites. Despite these variable richness patterns, it

297   appears there is an increased dependence on plant structure with increasing local habitat

298   stress. Greater concordance at high stress sites, in particular, likely results from reduced

299   richness leading to a strengthening of the link of remaining species on plant habitat. Habitat

300   loss is one of the principal causes of biodiversity decline worldwide (Brookes et al., 2002),

301   and riverine habitats are particularly vulnerable to land-use change (Allan, 2004; Vörösmarty

302   et al., 2010). Remaining species under these stressed conditions are likely those able to cope

303   under conditions of reduced habitat complexity. Vegetation is one important aspect of

304   habitat, and habitat complexity can mediate species interactions such as predation and

305   competition (Beukers and Jones, 1997; Grabowski, 2004). In fact, habitat modification can

306   influence food-web structure without altering conventional community metrics (Tylianakis et

307   al., 2007).

308   The increased coupling of remaining benthic invertebrates and beetles to plants with

309   increasing environmental stress, is likely a result of the overall reduction of site-wide habitat

310   complexity leading to an increased dependence on remaining vegetation habitat; a trend that

311   may also be operating for the riparian communities. Furthermore, while invertebrate richness

312   did not change with stress level, community structure fluctuated the least year-to-year in the

313   high-stress sites. This trend, coupled with the high plant temporal stability, helps to further

314   explain this strengthened invertebrate-plant association. While spiders were more

315 spatiotemporally variable, they followed the same general pattern as the other two animal

316 groups.

317 Our finding of weak congruence between richness of all groups, but strong

318 concordance of community structure has important management implications, particularly for

319 identifying surrogates or indicator taxa. A variety of previous studies spanning a range of

320 organism sizes, habitat types and trophic levels have reported similar patterns (Bilton et al.,

321 2006; Su et al., 2004). For instance, Su et al. (2004) found highly varied associations between

322 richness of birds, butterflies and vascular plants, but consistent and strong when assessing

323 community similarity. Moreover, Bilton et al. (2006) found weak richness associations but

324 strong similarity in community patterns for pond inhabiting macroinvertebrates. These

325 examples and our results exemplify the importance of not overlooking more complex

326 responses to environmental variables and relying on richness as a measure of congruence,

327 particularly at small spatial scales. Global change not only operates on communities by

328 directly influencing richness, but by altering species interactions (Tylianakis et al., 2008).

329 The lack of association of richness between groups likely reflects the small spatial

330 scale of observation in this study. While biodiversity often corresponds with environmental

331 or spatial variation similarly over large spatial scales (Qian and Ricklefs, 2008), the link is

332 less clear at smaller spatial scales (e.g. Kati et al., 2004; Paavola et al., 2006). The spatial

333 scale of observation is critical with regard to many relationships in nature, such as the

334 response of biodiversity to productivity (Chase and Leibold, 2002; Tonkin and Death, 2013).

335 For instance, in boreal streams, Paavola et al. (2006) found weaker concordance patterns

336 within individual stream drainages compared to between drainages and ecoregions. In

337 general, cross-taxon congruence has been too weak to find reliable predictors of biodiversity

338 in freshwater ecosystems (Heino, 2010). Our results suggest that these relationships are

339 highly dependent on anthropogenic stress and underlying processes. First, increasing

340 anthropogenic stress decouples the link between directly competing organisms, and second,

341 when overall habitat complexity is reduced, the link between habitat providers (i.e. plants)

342 and other species will strengthen. Future work seeking to find appropriate surrogate or

343 indicator taxa for conservation or biomonitoring purposes would benefit from focusing on

344 multiple spatial scales and the community rather than individual species level, particularly at

345 finer spatial scales.

346

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353

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482

483   **Tables**

484   **Table 1:** Results of two-way PERMANOVA tests comparing community structure of four

485   different organism groups collected from the Kinzig River, Hesse, Germany from 2010-2012

486   between three stress levels and years. Degrees of freedom for all factors are 2,40.

Factor	Sums sq.	Mean sq.	F Model	R^2	P
Plants					
Stress	2.923	1.462	13.57	0.387	< 0.0001
Year	0.314	0.157	1.46	0.042	0.131
Beetles					
Stress	2.527	1.263	4.77	0.183	< 0.0001
Year	0.686	0.343	1.30	0.050	0.142
Spiders					
Stress	2.331	1.166	7.97	0.267	< 0.0001
Year	0.574	0.287	1.96	0.066	0.032
Invertebrates					
Stress	1.009	0.504	3.45	0.137	< 0.0001
Year	0.495	0.248	1.69	0.067	0.035

487

Figure legends

Figure 1: Taxonomic richness for each organism group for three stress levels collected from 15 sites annually between 2010 and 2012 on the Kinzig River, Hesse, Germany.

Figure 2: Pairwise comparisons of species richness between each organism group for three stress levels and all land uses combined for data collected between 2010 and 2012 on the Kinzig River, Hesse, Germany. Results on right are Pearson's correlations. Note p values have not been corrected for multiple comparisons, but there were no significant values.

Figure 3: nMDS ordinations on presence-absence community data of four organism groups collected between 2010 and 2012 on the Kinzig River, Hesse, Germany. The arrow represents community shifts from 2010 to 2012. Two-dimensional stress value: plants - 0.12; beetles - 0.20; spiders = 0.17; invertebrates = 0.20. Differences between stress levels and years can be found in Table 1.

Figure 4: Results of Procrustes rotations and PROTEST permtutation tests on nMDS ordination plots from Fig. 3 on presence-absence community data of four organism groups collected between 2010 and 2012 on the Kinzig River, Hesse, Germany. Bottom left plots show Procrustes superimposition plots indicating the level of rotation required to align pairwise ordinations between different organism groups and lines indicate shifts in individual site points between the two ordinations, colour coded for each stress level. $M12^2$ is the sum of squares of the symmetric Procrustes analysis and Cor represents the correlation between the two ordinations. All Procrustes tests were significant at $P < 0.0001$. The top right box plots represent residual differences between points on pairwise Procrustes rotations for each stress level. One-way ANOVA results for residual differences are displayed above the plots and where significant differences were evident, Tukey's HSD results, where $P < 0.05$, are displayed on the graphs.

513   Figure 1

Plants

Stress : $F_{2,40} = 2.37$, $P = 0.107$
Year : $F_{2,40} = 0.239$, $P = 0.788$

Beetles

Stress : $F_{2,40} = 4.23$, $P = 0.022$
Year : $F_{2,40} = 4.83$, $P = 0.013$

Spiders

Stress : $F_{2,40} = 21.55$, $P < 0.0001$
Year : $F_{2,40} = 0.22$, $P < 0.808$

Invertebrates

Stress : $F_{2,40} = 0.18$, $P = 0.833$
Year : $F_{2,40} = 1.4$, $P = 0.258$

Stress   Low   Medium   High

514

Plants

All: $r = -0.28$ $p = 0.06$
Low: $r = -0.16$, $p = 0.56$
Medium: $r = -0.38$, $p = 0.16$
High: $r = -0.14$, $p = 0.61$

All: $r = -0.03$, $p = 0.86$
Low: $r = 0.01$, $p = 0.98$
Medium: $r = 0.15$, $p = 0.60$
High: $r = 0.11$, $p = 0.69$

All: $r = 0.18$, $p = 0.24$
Low: $r = 0.18$, $p = 0.51$
Medium: $r = 0.21$, $p = 0.45$
High: $r = 0.26$, $p = 0.36$

Beetles

All: $r = 0.24$, $p = 0.12$
Low: $r = -0.01$, $p = 0.71$
Medium: $r = 0.10$, $p = 0.74$
High: $r = 0.01$, $p = 0.97$

All: $r = -0.15$, $p = 0.32$
Low: $r = -0.22$, $p = 0.43$
Medium: $r = -0.07$, $p = 0.80$
High: $r = -0.33$, $p = 0.23$

Spiders

All: $r = -0.11$, $p = 0.48$
Low: $r = -0.34$, $p = 0.22$
Medium: $r = -0.11$, $p = 0.69$
High: $r = -0.25$, $p = 0.37$

Invertebrates

Richness

Richness

Stress ● Low ▲ Medium ■ High

519   Figure 4

520