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River drying lowers the diversity and alters the composition of an assemblage of desert riparian arthropods

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1 **River drying lowers diversity and alters composition of a desert riparian**
2 **arthropod community**

3

4 Running title: Riparian arthropods along a drying river

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12 Keywords: River drying, drought, riparian, arthropod, water availability

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15 **Summary**

16 1. Many studies have shown negative effects of river drying on in-stream animals.

17 However, the influence of river drying on riparian animals remains poorly studied.

18 2. We examined ground-dwelling riparian arthropod assemblages along a drying section of
19 the semi-arid San Pedro River in southeastern Arizona, USA.

20 3. We found strong differences in assemblage composition, taxon diversity and the
21 abundance of key taxa between dry and flowing sites, with higher diversity and
22 abundance of most taxa at flowing sites.

23 4. Changes in assemblage composition, taxon diversity, and abundance of representative
24 taxa were associated with a combined measure of water availability that included distance
25 to water and type of water. Other environmental variables showed a weaker association
26 with changes in these arthropod assemblages.

27 5. Thus, we found evidence that desert riparian arthropods are sensitive to river drying and
28 to reduction in water resources. Increases in drying along this river may reduce diversity
29 and the abundance of many groups of ground-dwelling arthropods leading to marked
30 shifts in community composition.

31

32 ***Introduction***

33 Rivers around the world are drying with increasing frequency, including large rivers,
34 such as the Yellow River in China and the Colorado in the USA (e.g. Zusman, 2000; Tockner &
35 Stanford, 2002; Gleick, 2003; Pearce, 2006; Stone & Jia, 2006). Droughts related to climate
36 change and increased human appropriation of water resources have led to declining ground and
37 surface waters in many regions, contributing to river drying (e.g. Pool & Coes, 1999).

38 Much recent research has concentrated on the effects of river drying on in-stream aquatic
39 communities and ecosystems (e.g. Stanley *et al.*, 1994; Feminella, 1996; Baldwin & Mitchell,
40 2000; Arthington *et al.*, 2010; Larned *et al.*, 2010; Ludlam & Magoulick, 2010). This work has
41 documented strong effects of river drying on the dynamics of aquatic macroinvertebrates, and
42 their taxonomic richness, abundance and community composition (e.g. Clarke *et al.*, 2010), as
43 well as on ecosystem processes such as litter decomposition (e.g. Leberfinger, Bohman &
44 Herrmann, 2010). Some research has suggested that, after rewetting, previously dry reaches are
45 quickly re-colonized from nearby perennial reaches (Clarke *et al.*, 2010) or potentially from
46 underground refugia or resistant life-stages (Stubbington *et al.*, 2009), minimizing long-term
47 effects, whereas others have found lasting effects of drying events (Sponseller *et al.*, 2010). One
48 recent study has implicated river permanence as a key factor controlling aquatic food chain
49 length, with much shorter food chains in rivers that dried at some point within the last decade
50 (Sabo *et al.*, 2010). Clearly, and as one might expect, river communities and ecosystems are
51 greatly influenced by river drying.

52 Terrestrial organisms living near the river may also be strongly linked to declining
53 surface and groundwater. For example, changes in riparian plant community composition and
54 diversity in the southwestern US are associated with altered flow regimes (Stromberg, Tiller &

55 Richter, 1996; Baird, Stromberg & Maddock, 2005; Lite, Bagstad & Stromberg, 2005; Lite &
56 Stromberg, 2005; Stromberg *et al.*, 2005; Stromberg *et al.*, 2007a). The composition of
57 dominant woody species shifts from cottonwood (*Populus* spp.) and willow (*Salix* spp.) to
58 tamarisk (*Tamarix* spp.), as spring floods are reduced by flow regulation, groundwater drops and
59 rivers dry (Rood & Mahoney, 1990; Stromberg *et al.*, 2007b; Stromberg & Tellmann, 2009).
60 The diversity of herbaceous plants is also affected by these changes in flow (Stromberg *et al.*,
61 2005).

62 Recent research has sought to relate changes in riparian arthropod assemblages with
63 floods, river regulation and other changes in flow regime (Ellis, Crawford & Molles, 2001;
64 Cartron *et al.*, 2003; Paetzold, Yoshimura & Tockner, 2008). For example, Lambeets *et al.*
65 (2008) explored the associations between a suite of environmental factors and spider and carabid
66 beetle assemblages along the Meuse River in N. Europe, finding that the composition of these
67 assemblages varied with flooding disturbance, vegetation density and siltation. Direct
68 examination of the effects of *river drying* on riparian arthropods is still needed.

69 In contrast to the rich literature showing effects of reduced flows and drying on aquatic
70 organisms and riparian plants, and some research relating the flood regime with riparian animal
71 communities, less is known about the effects of drying on riparian animals. Since the aquatic
72 and terrestrial components of riverine landscapes are strongly connected and riparian consumers
73 often depend on aquatic subsidies (Nakano & Murakami, 2001; Baxter, Fausch & Saunders,
74 2005), one would expect drying to influence riparian animal communities. However this effect
75 may be reduced compared to aquatic communities, considering the high productivity of
76 terrestrial riparian zones (National_Research_Council, 2002) and the ability for some riparian
77 consumers to switch to terrestrial prey (Sabo & Power, 2002). Additionally, in dryland regions,

78 river drying may directly influence riparian communities through a decrease in water
79 availability—decreases have direct consequences for animal physiology (Hadley, 1994),
80 behaviour (Davis & Denardo, 2006) and trophic interactions (McCluney & Sabo, 2009). One
81 recent study also showed a decline in the abundance of riparian fishing spiders with river drying
82 in New Zealand (Greenwood & McIntosh, 2010). Drying was associated with a decline in
83 aquatic, but not terrestrial, prey. In the laboratory, these spiders were shown to be intolerant to
84 desiccation, which was alleviated by access to moist prey (similar to McCluney & Sabo, 2009).
85 Thus, the river provided this species with important food and water resources.

86 Here we ask how the distribution and diversity of riparian arthropods varies along a
87 drying section of the San Pedro River, a desert river in semi-arid southeastern Arizona, USA.
88 We expected that riparian arthropod assemblages would be influenced by river drying, but that
89 the magnitude of effects would vary among taxonomic groups. More specifically, riparian
90 predators that are known to rely on subsidies of aquatic invertebrates are likely to be most
91 strongly influenced by river drying, but the composition of the entire arthropod community could
92 also be altered through combinations of changes in water availability and trophic interactions.
93 Therefore, we (1) compared arthropod assemblage composition, diversity and abundance along
94 dry and flowing sections of a 6 km section of the river (Fig 1) and (2) examined associations
95 between biological responses and several environmental factors, including availability of river-
96 derived resources.

97

98 ***Methods***

99 *Study System*

100 The San Pedro River is one of the last free-flowing rivers in the western US, originating
101 in northern Mexico and flowing north across the US border for over 100 km until reaching the
102 Gila River, part of the Colorado River drainage. The San Pedro River experiences seasonal
103 periods of drying that have been exacerbated by recent droughts and increased withdrawals of
104 groundwater (Pool & Coes, 1999). Our research was conducted along a section that has dried
105 with increasing frequency in recent years, partly due to municipal pumping from the regional
106 aquifer and local climate change (Pool & Coes, 1999). Floodplain habitats along the San Pedro
107 are characterized by cottonwood (*Populus fremontii* S. Watson) and willow (*Salix gooddingii*
108 C.R. Ball) trees, whereas uplands are characterized by plants of the Chihuahuan desert scrub to
109 the south and Sonoran desert to the north. In places where surface water permanence has
110 declined and groundwater tables have fallen substantially, the floodplain is often dominated by
111 introduced Tamarisk (*Tamarix chinensis* Lour). The river is subject to dramatic changes in
112 stream flow and experiences severe floods in the late-summer rainy season. A wide floodplain
113 has developed along much of the river, which is often covered by riparian trees and a forest floor
114 blanketed with leaf litter.

115 The San Pedro River valley harbours a high diversity of birds (~100 breeding species and
116 another 250 migratory), mammals (~80 species), and reptiles and amphibians (~65 species),
117 including endangered species, such as the southwestern willow flycatcher (*Empidonax traillii*
118 *extimus* Phillips) (Stromberg & Tellmann, 2009). This river and other riparian areas in the
119 southwest appear to be important stop-over points for migrating birds (Skagen *et al.*, 1998).
120 Thus, this region has been identified as particularly important for conservation purposes by The
121 Nature Conservancy. A large section of the riparian corridor in the upper basin is designated as a
122 national conservation area and is managed by the US Bureau of Land Management. However,

123 the San Pedro is affected by land-use changes outside the conservation area, through effects of
124 regional groundwater pumping on baseflows within the river (Pool & Coes, 1999).
125 Understanding the effects of groundwater pumping on this river is a high priority (Stromberg &
126 Tellmann, 2009). Our study took place along the upper San Pedro, including both flowing and
127 drying sections of the river channel adjacent to Boquillas Ranch House (31°41'50.95" N,
128 110°10'57.15" W), near the town of Tombstone, AZ (Fig 1). This portion of the San Pedro, in
129 particular, is thought to be influenced by municipal groundwater pumping (Pool & Coes, 1999).

130 *Methods*

131 We collected pitfall trap samples in the dry portion of the active channel along a 6 km
132 section of the river (Fig 1: see Supporting Information Text S1 for details of construction).

133 While most of the samples were collected in unmanipulated areas, 10 of the sampling locations
134 were near artificially constructed and maintained pools measuring approximately 1 m in diameter
135 (Fig 1; Text S1). The river was flowing at all sites on 14 May 2006, but had dried near many of
136 the sites by 25 June 2006. There were a total of 62 sites over the entire experimental period, but
137 only 35 sites on the final sampling date (25 June 2006; see Supporting Information Table S1).

138 While our initial sampling design was intended to include sites near the flowing river, natural
139 pools, artificial pools and dry sites, the river dried more quickly and completely than anticipated,
140 so we were forced to chose new natural pool and flowing sites over the course of the sampling
141 period, while abandoning some of our previous sites (due to sampling constraints).

142 Two pitfall traps were set at each site, with one within 0.5 m on either side of the water
143 body that was present at initial placement. Within a week of each sampling event (in between
144 each sampling event), we recorded the distance between each trap and the nearest water body
145 (flowing river, natural pool, artificial pool). We did not measure distances beyond 55 m,

146 considering these locations to be dry. Once a site had dried, it stayed dry, with no reinstatement
147 of flows during the study period. We also measured the distance from each trap to the nearest
148 channel bank, as our traps were generally located in the dry portion of the river channel with low
149 cover of litter and vegetation. This variable may be of importance, because arthropods may
150 inhabit banks or floodplain habitats with more litter and vegetation during the day, but move into
151 the channel at night. For instance, we have observed field crickets (*Gryllus alogus* Rehn)
152 moving from channel banks into the dry portion of the channel at sunset. We also measured the
153 percent cover of herbaceous vegetation within a 1 m diameter circle of the trap by visual
154 approximation in 5% categories. Further, we classified the substratum near the trap by visual
155 approximation of soil type and rock size classes. Later, these descriptors were categorized into a
156 structural rating between 0 and 5 (see Table 1). On the final sampling date, we also measured
157 the relative cover of leaf litter in four categories (none, low, medium or high). On this date, we
158 recorded the presence of cottonwood or willow trees near the traps.

159 Arthropods were collected in pitfall traps lined with Tangle-trap™ (The Tanglefoot
160 Company, Grand Rapids, MI, USA) on the bottom 4 cm of 473 mL (16 oz) party cups and left
161 open for 24 hours. Traps were processed by freezing, thawing, soaking in mineral oil and
162 filtering (0.5 µm) (see Text S1). Due to biases inherent in our collection and processing, we
163 excluded all arthropods less than 1 mm in length from our analysis as well as all mites and
164 Collembola. All remaining arthropods were typically identified to family. Ground beetles
165 (family: Carabidae) were identified to genus. We used Borrer *et al.* (1992), Ubick *et al.* (2005)
166 and Arnett & Thomas (2000) to identify our samples. We also categorized arthropods into
167 feeding guilds using Arnett & Thomas (2000), Hamback *et al.* (2009), Hering (1998) and general
168 knowledge (e.g. all spiders in our samples were assumed to be predators).

169 *Statistical analysis*

170 GENERAL DESCRIPTION—To assess the effect of river drying, we first quantified differences in
171 the riparian arthropod community between locations that were dry or adjacent to flowing river
172 (Fig 1). We then examined associations between environmental factors (Table 1) and the
173 arthropod community. This second analysis included additional sites near natural and artificial
174 pools (Fig 1; Table S1). In all cases, we conducted analyses at two taxonomic levels. First, we
175 examined all arthropod families collected in traps, including flying insects. Second, we
176 conducted analyses for genera in the ground beetle family Carabidae. We also examined total
177 abundance of all arthropods, arthropods known to be predators and those known to consume
178 some animal material (this included omnivores). Similar techniques were used for analyses of
179 both taxonomic groups. We note any differences below.

180 We typically collected two traps per sampling location, but for statistical analyses we
181 calculated mean values for each location. Levels of environmental characteristics measured for
182 each trap were also averaged. Thus we obtained single values for the abundance and
183 environmental characteristics of each location. Due to difficulties in maintaining our desired
184 river state categories in the face of rapid river drying, we sampled some sites repeatedly for all
185 four collections, while other sites were sampled only once, twice, or thrice. Statistical
186 approaches that dealt adequately with this incomplete repeated sampling were not available.
187 Thus, we chose only the final sampling date for all our statistical analyses (when there was
188 substantial variation in stream flow across sites).

189 We assessed and eliminated multi-collinearity using variance inflation factors (VIF)
190 following Meyers (1990) (see Text S1). Our environmental variables representing leaf litter and
191 the presence of riparian trees were collinear and leaf litter was removed from all analyses in

192 favour of presence of trees, which was likely to control the distribution of leaf litter, as well as
193 the availability of greenfall (freshly fallen moist green leaves). Distance to water and type of
194 water were also collinear. Rather than remove one of these variables from the analyses, we used
195 principal components analysis (PCA) in R v. 2.9.0 to combine these two factors into a single
196 factor representing river resources more generally (PC1). However, to improve interpretability,
197 we used the normalized inverse of the original values (max value – actual value) of distance to
198 water and created numerical categories of water type with dry sites equal to 1, artificial pools
199 equal to 2, natural pools equal to 3, and stream sites equal to 4. Thus, in general, most types of
200 river resources (i.e. drinking water and emergent insects) should increase with increasing values
201 of PC1.

202 ANALYSING MULTIVARIATE RESPONSES—We tested for differences in community composition
203 between dry and flowing sites, as well as for associations between environmental factors and
204 community composition using non-parametric permutational multivariate ANOVA (*adonis*) in
205 the VEGAN package of R v. 2.9.0 (4999 permutations; see Text S1 for additional details). Data
206 were natural log-transformed prior to all multivariate analyses.

207 To display differences in assemblage composition between flowing and dry sites, or
208 associations of assemblages with environmental variables, we used non-metric multidimensional
209 scaling (*metaMDS*) with the *envfit* vector plotting function in the VEGAN package of R v. 2.9.0.
210 For environmental association graphs, we calculated proximity to channel bank instead of
211 distance by taking the normalized inverse of the original values (max value – actual value). This
212 approach improved simplicity of interpretation of graphs, by making the direction of increase
213 correspond to increasing proximity to the channel bank (increasing proximity to leaf litter,
214 vegetation, etc). Thus taxonomic groups aligned along an environmental axis could be

215 interpreted as associated with this factor more clearly. All multivariate community composition
216 techniques employed Bray-Curtis distances.

217 ANALYSING UNIVARIATE RESPONSES—Next, we tested for differences in total abundance,
218 diversity, the abundance of predators, the abundance of consumers known to eat at least some
219 animal material and the abundance of key taxa, between flowing and dry sites, using general
220 linear modelling (*glm*) in R v.2.9.0. We then performed similar analyses examining associations
221 between environmental factors (Table 1) and these same responses. We employed Shannon’s
222 diversity and Pielou’s evenness, in addition to richness, as our estimates of diversity. Pielou’s
223 evenness is a good measure for our type of dataset and study question because it is relatively
224 insensitive to the effects of rare taxa (Beisel *et al.*, 2003). Tests of mean total abundance and
225 diversity assumed a Gaussian distribution, whereas tests of taxa or functional group abundance
226 assumed a quasi-Poisson distribution, since these datasets often contained a large number of
227 zeros and this distribution is better for modelling such datasets (Potts & Elith, 2006). Total
228 abundance data were natural log transformed prior to analysis, whereas taxon abundance data
229 were rounded to the nearest integer prior to analysis (for the use of a quasi-Poisson distribution).
230 In all tests, we evaluate differences assuming a Type-I error rate of $\alpha = 0.1$ given our low sample
231 sizes and our goal of identifying patterns rather than testing causal relationships; however, we
232 report exact *P* values so that patterns at the more conservative Type-I error rate ($\alpha = 0.05$) can be
233 easily assessed.

234 *Spatial autocorrelation*

235 Due to the varying distances between our sampling locations, spatial correlation could be
236 an important source of variation in our study. Currently, no good methods exist for detecting and
237 correcting for spatial autocorrelation with multivariate community data (Gilbert & Bennett,

238 2010). However, for significant univariate responses (diversity, abundance), we report results of
239 Moran's I test for spatial autocorrelation (using the ape package of R v. 2.9.0), thus detecting
240 spatial effects that could be mechanistically investigated by future studies.

241 **Results**

242 *Total abundance and abundance of functional groups*

243 We found significantly higher abundance of all known predators at flowing sites than at
244 dry sites (Table 2; Table S3) and predators were positively associated with river resources (i.e.
245 water and/or aquatic invertebrates) and negatively associated with distance to the nearest channel
246 bank (higher near channel bank; Table 3; Table S4). Significant spatial autocorrelation was
247 apparent for these relationships (Tables S5 and S6). There were no significant differences in the
248 total abundance of all arthropods, or the abundance of consumers known to consume at least
249 some animal material, nor did we find any association of predators with other environmental
250 variables (Table S3, Table S4).

251 *Arthropod families*

252 Shannon's diversity and familial richness were higher at flowing than dry sites (Table 2,
253 Table S3) and there was a significant positive association between familial richness and river
254 resources, but no other associations (Table 3, Table S4). These relationships did not show spatial
255 autocorrelation (Tables S5 and S6).

256 Assemblage composition also differed significantly between dry and flowing sites ($F =$
257 2.23 , $df = 1,16$, $P = 0.021$; Fig 2; Table 2; Table S7) and there was a significant association
258 between assemblage composition and river resources (Fig 3; Table 3; Table S7). These
259 community differences seem to have been driven by higher abundances of field crickets
260 (Gryllidae), wolf spiders (Lycosidae), rove beetles (Staphylinidae) and shore bugs (Saldidae) at

261 flowing sites (Table 2, Table S8) and positive associations of shore bugs (Saldidae), pygmy mole
262 crickets (Tridactylidae), and pygmy grasshoppers (Tetrigidae) with river resources (Table 3,
263 Table S9).

264 In addition to associations with river drying and river resources, several taxa showed
265 significant associations with other environmental factors. Wolf spiders (Lycosidae) and shore
266 bugs (Saldidae) were more abundant nearer to the channel bank, but pygmy grasshoppers
267 (Tetrigidae) were more abundant farther from the channel bank (Table 3, Table S9). Both
268 pygmy mole crickets (Tridactylidae) and pygmy grasshoppers (Tetrigidae) were more abundant
269 with less herbaceous ground cover (Table 3, Table S9), but pygmy grasshoppers were also more
270 abundant where cottonwood and willow trees were in close proximity. Pygmy grasshoppers
271 were the only family to respond to substrate complexity, with greater abundance at intermediate
272 complexity (e.g. coble bars with small to medium sized rocks and sand or gravel, see Table 1;
273 Table 3; Table S9). There were no significant associations between environmental factors and
274 the abundance of Gryllidae, Carabidae, Formicidae, Elateridae, Noctuidae, Linyphiidae,
275 Anthicidae, Staphylinidae and Rhabdophoridae (Table S9). Only the relationship between
276 wolf spiders (Lycosidae) and distance to the channel bank showed significant spatial
277 autocorrelation (Table S6).

278 *Carabid genera*

279 Similarly to the results for the diversity of arthropod families, Shannon's diversity and
280 the richness of carabid beetle genera were higher at flowing sites than at dry sites (Table 2, Table
281 S11) and there was a positive association between river resources and generic richness.
282 Differing from the family-level results, Shannon's diversity and Pielou's evenness of carabid
283 genera were additionally positively related to river resources. Shannon's diversity and generic

284 richness were also higher near the channel bank (Table 3, Table S12). All of these relationships
285 showed significant spatial influence except for the difference in Shannon's diversity between dry
286 and flowing sites and the association between Pielou's evenness and water resources.

287 Like for the patterns of familial assemblage composition (and carabid diversity), we
288 found a significant difference in carabid assemblage composition between dry and flowing sites
289 ($F = 33.78$, $df = 1, 16$, $P = 0.000$; Fig 4; Table 3; Table S10) and significant associations between
290 carabid assemblages and river resources (Fig 5, Table 3, Table S10). River related differences in
291 carabid assemblages were likely driven by higher abundances of the carabid beetle genera
292 *Brachinus*, *Agonum*, *Lachnophorus*, *Chlaenius* and *Bembidion* at flowing than dry sites (Table 2,
293 Table S13), along with positive associations of these genera with river resources (Table 3, Table
294 S14). Lower abundance of the genus *Syntomus* at flowing sites (Table 2, Table S13) and
295 negative associations of this genus with river resources (Table 3, Table S14) also contributed to
296 differences in carabid assemblages. Differences in *Lachnophorus*, *Bembidion* and *Syntomus*
297 between dry and flowing sites showed significant spatial autocorrelation, as did associations of
298 *Brachinus*, *Agonum*, *Lachnophorus*, *Chlaenius*, *Bembidion* and *Syntomus* with river resources.

299 Differing from the results for familial assemblage composition, carabid genera
300 assemblage composition was found to be additionally associated with distance from the channel
301 bank and substratum complexity (Fig 5, Table 3, Table S10). The significant influence of the
302 channel bank on composition was likely driven by higher abundances of *Brachinus*, *Agonum*,
303 *Lachnophorus*, *Chlaenius*, *Bembidion* and *Schizogenius* near the channel bank (Table 3, Table
304 S14). Additionally, the higher abundance of *Lachnophorous* at low to intermediate substratum
305 complexity (e.g. sand or gravel and small rocks, see Table 1; Table S14) likely contributed to the
306 relationship between this factor and carabid assemblage composition. Some carabid genera were

307 related to environmental variables in ways that did not manifest in assemblage differences.
308 *Schizogenius*, *Chlaenius* and *Agonum* were found to be negatively associated with percent
309 herbaceous ground cover (Table 3, Table S14) and *Schizogenius* was higher without cottonwood
310 or willow trees present (Table 3, Table S14). All of these relationships showed significant
311 spatial influence (Table S6).

312 **Discussion**

313 Recent global changes are drastically altering the distribution of water resources. One
314 result has been dewatering of rivers around the world (Gleick, 2003; Pearce, 2006). Little
315 information is available about how these drying events influence riparian animal communities.
316 Here we show that river drying is associated with alterations of riparian arthropod assemblage
317 composition, a decline in taxon diversity and reductions in the abundance of several taxa.
318 Further, direct access to river-related resources (e.g. water, aquatic food) may help explain these
319 patterns, since this factor is more strongly correlated with differences in these arthropod
320 communities than other habitat characteristics. These associations are apparent for riparian
321 arthropod families and appear strong when focussing on genera within the ground beetle family
322 (Carabidae). Thus, this study suggests that many desert riparian arthropods are sensitive to river
323 drying events and changes in water availability and thus may require the existence of at least
324 some perennial flows within a river network for persistence.

325 While we cannot separate whether drinking water or emergent insects were more
326 important in driving the response of arthropods to river resources, insect emergence from rivers
327 in this region has been found to be relatively low at the end of June, with peak emergence
328 generally occurring earlier in the year (Hagen, 2010). This suggests water may be directly
329 important as a resource for this arthropod community in June when dry conditions prevail, in

330 addition to the important effects of emergence of aquatic insects documented in other systems
331 (e.g. Paetzold, Bernet & Tockner, 2006) and likely still important here. For example, pygmy
332 grasshoppers in the family Tetrigidae are known to eat mostly moist, recently stranded algae
333 (Bastow *et al.*, 2002) and bombardier beetles in the carabid genus *Brachinus* are known to have
334 ectoparasitic larvae of aquatic diving beetles in the family Dytiscidae (Juliano, 1985). Both of
335 these taxa were positively associated with river resources in our study. These examples highlight
336 the important roles rivers play as both water and food resources for riparian arthropods.

337 *Desert riparian zones harbour cosmopolitan species*

338 Drying may be particularly common along desert rivers (Kingsford, 2006). Many species
339 living in desert uplands (Noy-Meir, 1974; Polis & Seely, 1990; Davis & DeNardo, 2007) or
340 within rivers (Meffe & Minckley, 1987; Beche, McElravy & Resh, 2006; Kingsford, 2006) have
341 traits that help them cope with the challenges of highly variable desert environments. Therefore,
342 one might be tempted to predict that desert riparian zones contain species that are well adapted
343 and relatively insensitive to drying events. However, many of the riparian arthropods in our
344 study are distributed along rivers throughout North America. For instance, the most common
345 large spider collected in our study, the beach wolf spider, *Arctosa litorallis* Hentz, is widely
346 distributed across North America (Ubick *et al.*, 2005; Punzo, 2006). Most of the carabid beetle
347 genera we found are also widely distributed throughout North America, although individual
348 species within these genera may or may not be widely distributed. For instance, bombardier
349 beetles (Carabidae: *Brachinus*) and the genus *Syntomus*, which contains only one species in
350 North America, *Syntomus americanus* Dejean, are widely distributed across the continent (Arnett
351 & Thomas, 2000). Thus, desert riparian zones often harbour a cosmopolitan fauna dominated by
352 taxonomic groups also found in more mesic environments. This result is consistent with

353 previous evidence that riparian zones contain different species than uplands (Sabo *et al.*, 2005b).

354 In fact, floodplain forests along desert rivers may act as oases, showing more mesic

355 environmental characteristics than do adjacent uplands (Skagen *et al.*, 1998; Sabo *et al.*, 2008).

356 The mixture of widely and locally distributed taxa among those collected, suggests the

357 intriguing hypothesis that the relative endemism of each taxonomic group may be a good

358 predictor of the degree to which it is influenced by river drying or to which it is associated with

359 measures of water availability, with more endemic species being less influenced by drying.

360 However, our data do not support this hypothesis. For example, the beach wolf spider

361 (*Lycosidae: A. littoralis* Hentz), which made up most of the individuals collected in the family

362 *Lycosidae*, is widespread (Punzo, 2006), but the family *Lycosidae* did not show a significant

363 association with river resources (though abundance was higher overall at flowing sites).

364 Similarly, the carabid beetle, *S. americanus* Dejean, is found throughout North America (Arnett

365 & Thomas, 2000), but its abundance was higher at dry sites and farther from water bodies. On

366 the other hand, the carabid beetle *Lachnophorus elegantulus* Dejean (the only representative of

367 this genus in this area) is most commonly found in the southwestern US (Arnett & Thomas,

368 2000), but its abundance was lower at dry locations and farther from water bodies. Therefore,

369 the responses of each taxonomic group to river drying and the association with environmental

370 characteristics are not strictly predictable by regional distribution. This suggests a) some species

371 most abundant in desert regions are still sensitive to river drying (e.g. *L. elegantulus* Dejean),

372 particularly along historically perennial rivers like the San Pedro and b) that species interactions

373 (e.g. McCluney & Sabo, 2009) or life history constraints (e.g. Juliano, 1985) may be modulating

374 the observed response to river drying.

375 *Floodplain versus dry channel habitats*

376 Generally, we found that predator abundance, some metrics of diversity, and abundance
377 of some families and carabid genera were higher nearer the channel bank (Table 3). This
378 suggests an important positive aspect of the transition zone between floodplain and channel, such
379 as the availability of increased structure or vegetation, the overlap of species between these two
380 habitat types, or decreased danger of flow-related disturbance. However, we observed some taxa
381 that were more abundant farther from the channel bank, with less herbaceous cover, or without
382 cottonwood trees nearby. While these preferences for more open environments may be due to
383 energy balance requirements or predator avoidance (e.g. wolf spiders were higher near channel
384 banks), the preference may also reflect our choice of study location. Our research focussed on
385 the river channel itself and did not sample the wide floodplains that occur along this river. These
386 floodplains probably harbour a different suite of arthropods that may be better suited to habitats
387 with leaf litter, herbaceous vegetation and shade. For instance, the large wolf spider *A. littoralis*
388 Hentz, is abundant in the river channel along the San Pedro, but is rarely found in floodplain
389 habitats, which instead are dominated by the wolf spider *Hogna antelucana* Montgomery, which
390 in turn is rarely found in the river channel (K. McCluney and J. Sabo, personal observations).

391 *Spatial autocorrelation*

392 Significant spatial autocorrelation was observed for some of our responses, but not
393 others, with spatial effects more commonly observed for the abundance of particular taxa and
394 less commonly for patterns of diversity and predator abundance (Table S5 and S6). In some
395 cases, local migration may cause spatial autocorrelation and may explain patterns instead of the
396 relevant site characteristics. However, we note that, in comparisons between dry and flowing
397 sites, all four flowing sites were clumped together and separated from dry sites (Fig 1). Thus,
398 significant spatial autocorrelation would be likely to occur, even if differences in responses were

399 completely associated with river drying. However, our analysis was concerned with identifying
400 patterns of variation of riparian arthropods along this drying river rather than testing for causal
401 relationships. A related study that manipulated water resources along this river segment as it
402 dried, and avoided these spatial issues, found similar patterns for diversity, composition, and
403 biomass of some of these taxa (McCluney, 2010).

404 *Conclusion*

405 Overall, we found evidence that short-term river drying can substantially influence
406 riparian arthropod communities and that direct access to the resources associated with river water
407 may be an important part of the effect. In general, we found a decrease in diversity and in
408 abundance of many taxa associated with river drying, with an increase in only one carabid beetle
409 genus. Riparian arthropods make up an important component of the diet of higher consumers,
410 such as birds, skunks and foxes (Sabo, Soykan & Keller, 2005a; Soykan, 2007). Thus, they are
411 important in the conservation of the entire suite of organisms living along the river. Achieving a
412 balance between human and non-human water needs in this region and other similar regions will
413 require an understanding of the connections between groundwater pumping and in-stream and
414 riparian ecology. Our study helps provide some of the first information linking groundwater
415 withdrawals to the invertebrate resource base of riparian animal communities.

416

417

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426

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- 590

591 **Tables**

592

TABLE 1. Description of each environmental factor measured.

Factor	Description
Substratum Complexity	Score out of 5: Sand/Clay/Silt = 1, Gravel = 2, Rocks<10cm = 3, Rocks 10-40 cm = 4, Rocks>40 cm = 5 (If the rocks were in clay, it lowered the score by 1)
Distance to Water	Distance between the trap and the nearest water source (up to 55 m)
Type of Water	Classification into categories of flowing stream, natural pool, artificial pool, dry site.
Water Resources	Principal component 1 from principal components analysis (PCA) of distance to water and type of water. However, original factors were converted so that water resources increase with increasing values of PC1 (see Methods).
Distance to Channel Bank	Distance between the trap and the nearest channel bank. Proximity to channel bank was calculated for interpretability in graphs (see Methods).
Percent Herbaceous Cover	Visual estimates of herbaceous ground cover within 1 m diameter of each trap, divided into 5% categories
Litter	Not examined due to collinearity with other factors.
Presence of Cottonwood or Willow Trees	Whether or not cottonwood or willow trees were found near the trap (close enough for leaves to commonly fall near the trap)

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TABLE 2. Significant results for differences between flowing and dry sites on 25 June 2006. Grey highlighting indicates significance only at $\alpha = 0.1$, while all other reported metrics are significant at $\alpha = 0.05$.

Metric	Type of site with higher level of metric	F	df	p
Abundance of known predators	Flowing	24.352	1, 16	0.000
<u>Families</u>				
Community composition	NA	2.234	1, 16	0.021
Shannon's diversity	Flowing	5.350	1, 16	0.034
Richness	Flowing	5.983	1, 16	0.026
Gryllidae abundance	Flowing	5.062	1, 16	0.039
Lycosidae abundance	Flowing	10.023	1, 16	0.005
Staphylinidae abundance	Flowing	4.780	1, 16	0.044
Saldidae abundance	Flowing	23.822	1, 16	0.000
<u>Carabid Genera</u>				
Community composition	NA	33.777	1, 16	0.000
Shannon's diversity	Flowing	12.0829	1, 16	0.003
Richness	Flowing	27.346	1, 16	0.000
<i>Brachinus</i> abundance	Flowing	8.042	1, 16	0.012
<i>Agonum</i> abundance	Flowing	48.13	1, 16	0.000
<i>Lachnophorus</i> abundance	Flowing	48.13	1, 16	0.000
<i>Bembidion</i> abundance	Flowing	8.033	1, 16	0.012
<i>Syntomus</i> abundance	Dry	17.418	1, 16	0.001
<i>Chlaenius</i> abundance	Flowing	4.197	1, 16	0.057

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599

TABLE 3. Significant associations between environmental factors and response variables on 25 June 2006. Grey highlighting indicates significance only at $\alpha = 0.1$, while all other reported metrics are significant at $\alpha = 0.05$. For F and df see Tables S4, S7, S9, S10, S12 and S14.

Response Metric	Environmental Factor	Relationship direction	p
Abundance of known predators	Water Resources	Positive	0.074
Abundance of known predators	Distance to Channel Bank	Negative	0.011
<u>Families</u>			
Community composition	Water Resources	NA	0.020
Richness	Water Resources	Positive	0.090
Lycosidae abundance	Distance to Channel Bank	Negative	0.025
Saldidae abundance	Water Resources	Positive	0.003
Saldidae abundance	Distance to Channel Bank	Negative	0.005
Tridactylidae abundance	Water Resources	Positive	0.034
Tridactylidae abundance	Percent Herbaceous Cover	Negative	0.036
Tetrigidae abundance	Water Resources	Positive	0.000
Tetrigidae abundance	Distance to Channel Bank	Positive	0.003
Tetrigidae abundance	Percent Herbaceous Cover	Negative	0.001
Tetrigidae abundance	Presence of Trees	Positive	0.046
Tetrigidae abundance	Substrate Complexity	Intermediate	0.020
<u>Carabid Genera</u>			
Community composition	Water Resources	NA	0.000
Community composition	Distance to Channel Bank	NA	0.072
Community composition	Substrate Complexity	NA	0.002
Shannon's diversity	Water Resources	Positive	0.000
Shannon's diversity	Distance to Channel Bank	Negative	0.007
Richness	Water Resources	Positive	0.000
Richness	Distance to Channel Bank	Negative	0.000
Pielou's Evenness	Water Resources	Positive	0.014
<i>Brachinus</i> abundance	Water Resources	Positive	0.004
<i>Brachinus</i> abundance	Distance to Channel Bank	Negative	0.077
<i>Agonum</i> abundance	Water Resources	Positive	0.000
<i>Agonum</i> abundance	Distance to Channel Bank	Negative	0.000
<i>Agonum</i> abundance	Percent Herbaceous Cover	Negative	0.000
<i>Lachnophorus</i> abundance	Water Resources	Positive	0.000

<i>Lachnophorus</i> abundance	Distance to Channel Bank	Negative	0.000
<i>Lachnophorus</i> abundance	Substratum Complexity	Intermediate	0.095
<i>Bembidion</i> abundance	Water Resources	Positive	0.006
<i>Bembidion</i> abundance	Distance to Channel Bank	Negative	0.054
<i>Syntomus</i> abundance	Water Resources	Negative	0.075
<i>Chlaenius</i> abundance	Water Resources	Positive	0.001
<i>Chlaenius</i> abundance	Distance to Channel Bank	Negative	0.000
<i>Chlaenius</i> abundance	Percent Herbaceous Cover	Negative	0.027
<i>Schizogenius</i> abundance	Distance to Channel Bank	Negative	0.063
<i>Schizogenius</i> abundance	Percent Herbaceous Cover	Negative	0.001
<i>Schizogenius</i> abundance	Presence of Trees	Negative	0.002

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602

603 **Figure Legends**

604 FIG 1. Maps of the region of Southeastern AZ, USA where the study took place and the
605 distribution of sampling sites along the river on the final sampling date. The direction of flow is
606 from south to north. Sampling regions are noted by broader lines following the river course,
607 with narrow solid lines indicating dry sites, broad dashed lines indicating a mix of dry sites,
608 natural pools, and artificial pools, and broad solid lines indicating flowing stream sites. The
609 Sierra Vista metropolitan area, a region of groundwater withdrawal, is just upstream of the
610 sampling locations.

611

612 FIG 2. Non-metric multi-dimensional scaling plot of the difference in familial assemblage
613 composition between flowing and dry sites (D = Dry, S = Flowing Stream). Grey text and
614 symbols refer to each family in the analysis. Only families with greater than one individual
615 across all sites are labelled.

616

617 FIG 3. Non-metric multi-dimensional scaling plot showing the association between each
618 environmental factor and familial assemblage composition. The rays show the direction and
619 importance of variation of each factor along the first two axes (WaterR = Water Resources,
620 ProxBank = Proximity to the Channel Bank, Pcov = Percent Herbaceous Ground Cover,
621 SubstrScore = Structural Complexity of the Substratum; the variable indicating the presence of
622 trees near the trap is not shown since the labels overlapped with the origin and were
623 uninformative). Grey text and symbols refer to each family in the analysis. See Table S7 for R^2
624 values for each factor. Only families with greater than one individual across all sites are labelled.
625

626 FIG 4. Non-metric multi-dimensional scaling plot of the difference in carabid genera assemblage
627 composition between flowing and dry sites (D = Dry, S = Flowing Stream). Grey text refers to
628 each genus in the analysis. Only genera with greater than one individual across all sites are
629 labelled.
630

631 FIG 5. Non-metric multi-dimensional scaling plots showing the association between each
632 environmental factor and carabid genera assemblage composition. The rays show the direction
633 and importance of variation of each factor along the first two axes (WaterR = Water Resources,
634 ProxBank = Proximity to the Channel Bank, Pcov = Percent Herbaceous Ground Cover,
635 SubstrScore = Structural Complexity of the Substratum, CWoWNear = Presence of Cottonwood
636 or Willow Trees Near the Trap, with the suffix -Y indicating yes, -N indicating no, and no suffix
637 representing a single site with missing information). Grey text refers to each genus in the
638 analysis. See Table S10 for R^2 values for each factor. Only families with greater than one
639 individual across all sites are labelled.









