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Citation: Epele, Luis B., Grech, Marta G., Williams-Subiza, Emilio A., Stenert, Cristina, McLean, Kyle, Greig, Hamish S., Maltchik, Leonardo, Pires, Mateus Marques, Bird, Matthew S., Boissezon, Aurelie, Boix, Dani, Demierre, Eliane, García, Patricia E., Gascón, Stephanie, Jeffries, Mike, Kneitel, Jamie M., Loskutova, Olga, Manzo, Luz M., Mataloni, Gabriela, Mlambo, Musa C., Oertli, Beat, Sala, Jordi, Scheibler, Erica E., Wu, Haitao, Wissinger, Scott A. and Batzer, Darold P. (2022) Perils of life on the edge: Climatic threats to global diversity patterns of wetland macroinvertebrates. *Science of the Total Environment*, 820. p. 153052. ISSN 0048-9697

Published by: Elsevier

URL: <https://doi.org/10.1016/j.scitotenv.2022.153052>
<<https://doi.org/10.1016/j.scitotenv.2022.153052>>

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1 **Abstract**

2 Climate change is rapidly driving global biodiversity declines. How wetland
3 macroinvertebrate assemblages are responding is unclear, a concern given their vital
4 function in these ecosystems. Using a data set from 769 minimally impacted depressional
5 wetlands across the globe (467 temporary and 302 permanent), we evaluated how
6 temperature and precipitation (average, range, variability) affects the richness and beta
7 diversity of 144 macroinvertebrate families. To test the effects of climatic predictors on
8 macroinvertebrate diversity, we fitted generalized additive mixed-effects models (GAMM)
9 for family richness, and generalized dissimilarity models (GDMs) for total beta diversity.
10 We found non-linear relationships between family richness, beta diversity and climate.
11 Maximum temperature was the main climatic driver of wetland macroinvertebrate richness
12 and beta diversity, but precipitation seasonality was also important. Assemblage responses
13 to climatic variables also depended on wetland water permanency. Permanent wetlands
14 from warmer regions had higher family richness than temporary wetlands. Interestingly,
15 wetlands in cooler and dry-warm regions had the lowest taxonomic richness, but both kinds
16 of wetlands supported unique assemblages. Our study suggests that climate change will
17 have multiple effects on wetlands and their macroinvertebrate diversity, mostly via
18 increases in maximum temperature, but also through changes in patterns of precipitation.
19 The most vulnerable wetlands to climate change are likely those located in warm-dry
20 regions, where entire macroinvertebrate assemblages would be extirpated. Montane and
21 high-latitude wetlands (i.e., cooler regions) are also vulnerable to climate change, but we do
22 not expect entire extirpations at the family level.

23

24 **Keywords:** depressional wetlands; freshwater; ponds; permanent wetlands; temporary
25 wetlands; water availability

26

27 **1. Introduction**

28 Wetlands are among the world's most valuable and threatened ecosystems
29 (Costanza et al. 2014, Davidson 2014, Reid et al. 2019) in which invertebrates play pivotal
30 ecological roles. Extensive data show how hydrology, water quality, aquatic plants,
31 predation and other local factors combine to influence wetland invertebrate diversity, but
32 more extensive climatic influences are rarely considered (Wiggins et al. 1980, Wellborn et
33 al. 1996, Batzer et al. 1999, Wissinger 1999, Euliss et al. 2004, Williams 2006, Batzer and
34 Boix 2016). While there is some recognition of the effects of extreme temperature or
35 drought on wetland biodiversity (Wiggins et al. 1980, Rader 1994, Wissinger 1999), the
36 dearth of studies assessing climate change effects on wetland invertebrates contrasts
37 markedly with those from other freshwater environments like lakes, rivers and streams
38 (Heino et al. 2015, Dodds et al. 2019, Haase et al. 2019, Patrick et al. 2019, Pound et al.
39 2021).

40 Recent meta-analyses of broad scale patterns in wetlands suggest that climate,
41 temperature, and precipitation are the principal controls on macroinvertebrate assemblages
42 (e.g. Ruhí et al. 2013, Kneitel 2016, Antón-Pardo et al. 2019). Batzer and Ruhí (2013)
43 assessed wetland invertebrates across North America, Europe, and Australia (and a few
44 sites in South America and Asia) and found that wetlands within regions were
45 compositionally similar, regardless of local factors (e.g., varying hydrologic and/or plant
46 conditions), while wetlands from regions with different climates tended to be
47 compositionally dissimilar. They also noted that wetlands with harsh climatic conditions

48 (alpine and desert environments) tended to have unique faunas. Boix and Batzer (2016)
49 similarly found that wetlands from harsh climates (unusually hot or cold) had low
50 invertebrate taxon richness compared to wetlands with more benign climates. Ruhí et al.
51 (2013) assessed a longitudinal gradient (spanning the Palearctic of Europe and Nearctic of
52 North America) and found that invertebrate assemblages differed based on broad ranges in
53 temperature and aridity. Stenert et al. (2020) analyzed a latitudinal gradient (spanning
54 North and South America) and found that climate zones (temperate vs subtropical)
55 controlled family-level composition and beta diversity. However, the simultaneous
56 influences of temperature and precipitation on wetland invertebrate assemblages has never
57 been directly assessed.

58 If climatic factors such as temperature and precipitation are the dominant drivers of
59 wetland invertebrate composition, as they are for other aquatic organisms (Dodds et al.
60 2019), then it would suggest that these organisms will be profoundly impacted by ongoing
61 climate change. Invertebrates residing in wetlands already subjected to harsh climatic
62 conditions (e.g., hot, frigid, and/or dry places) might be especially vulnerable to abiotic
63 stress under future climatic conditions (i.e. even hotter or drier). Because of the pivotal
64 ecological importance of invertebrates (Batzer and Wissinger 1996, Batzer and Boix 2016),
65 global warming could profoundly impact overall wetland ecosystem structure and
66 functioning. This could exacerbate the existing stress on threatened species (Amano et al.
67 2020), as well as wetland economic and ecosystem services, such as nutrient cycling, water
68 storage and purification, food production, and recreation (Zedler and Kercher 2005).
69 Concerns about climate change tend to focus on temperature increases, but precipitation
70 changes can dramatically alter hydrologic regimes and invertebrate communities of
71 wetlands as well (Calhoun et al. 2017). For example, studies in California vernal pools,

72 Andean ponds and Mediterranean wetlands, areas with seasonally dry periods, have
73 detected relationships between temporal shifts in precipitation regimes and regional
74 diversity (Boix et al. 2001, Kneitel 2014, Montemayor et al. 2017).

75 In this study, we compiled macroinvertebrate data from 769 depressional wetlands
76 across the globe, including all seven continents. Because precipitation and
77 evapotranspiration are major controls on the water budgets of depressional wetlands, this
78 class of wetlands is likely to be particularly vulnerable to climatic change (Dodds et al.
79 2019). Selected wetlands were relatively pristine (i.e., minimally impacted by human
80 activities), and occurred across a wide range of latitudes, elevations and precipitation
81 regimes, allowing us to assess the relative importance of different climate factors to
82 macroinvertebrate biodiversity. We aimed to tease apart which aspects of temperature and
83 precipitation (average, range, variability) exert the most influence macroinvertebrate
84 biodiversity on a global scale. We further assessed whether the effects of climatic controls
85 differ between permanent and temporary wetlands, an environmental dichotomy important
86 for the development of macroinvertebrate communities (Wellborn et al. 1996, Anton-Pardo
87 et al. 2019). Permanent wetlands transitioning to temporary wetlands (and vice versa; e.g.
88 McKenna et al. 2017) is a likely outcome of climate change (due to increased temperature
89 and/or precipitation regime shifts). The extent of our data set gives us the opportunity to
90 develop robust hypotheses about the impacts of on-going and future climate changes on the
91 biodiversity of depressional wetlands, which may also apply to a range of other habitats
92 (e.g. other wetlands, small streams).

93

94 **2. Material and methods**

95 **2.1 Data compilation**

96 We compiled a data set from 769 depressional wetlands (i.e., upland-embedded
97 wetlands, *sensu* Smith et al. 1995) distributed across a range of latitudinal, elevational, and
98 climatic gradients across the globe (Fig. 1). Based on wetlands location, we defined 22
99 regions, which we further used as a random intercept in Generalized Additive Mixed
100 Models (GAMM; see Statistical Analyses section) (Table S1, Appendix S1). The 22
101 regions varied greatly in temporal and spatial scale. For instance, some comprised a large
102 number of wetlands sampled only once, while others comprised a smaller number of
103 wetlands but they were sampled repeatedly (i.e. two or three times in a year). Thus, to
104 remove potential noise arising from these differences, and to reflect the range of natural
105 environmental conditions found at each wetland, we used only one year of data per region,
106 and when available, we pooled seasonal samples within the selected year into a single
107 observation. We were focused on individual wetland characteristics (i.e. local taxonomic
108 richness) rather than regional ones, which made standardization of the number of wetlands
109 per region less important. We set the minimum number of wetlands to ten per region. Our
110 goal was to generate a data set that could be viewed as being reasonable representative of
111 each of the assessed region. We categorized wetlands as permanent or temporary, defining
112 “*permanent wetlands*” as those that held some surface water continuously during both the
113 sampling year, and the prior one. Meanwhile “*temporary wetlands*”, were those that dried
114 during the sampling year, or the one immediately before sampling.

115 We used macroinvertebrate presence-absence data because it (1) removes noise
116 arising from differences in sampling techniques; (2) is useful for datasets covering wide
117 geographic ranges and across broad climatic gradients with high taxonomic turnover (or
118 beta diversity); and (3) has been shown to be a suitable surrogate for abundance in
119 biodiversity studies (Carneiro et al. 2010, Pires et al. 2021). As the level of taxonomic

120 resolution varied greatly among data sets and macroinvertebrate groups, we harmonized our
121 data by setting taxonomic resolution at the family level (or above for some groups), rather
122 than at sub-family, genus, or species levels. For aquatic invertebrates the family level (or
123 above) has been shown to be highly congruent with finer taxonomic resolution (i.e. genus
124 level) for calculations of diversity metrics (Mueller et al. 2013, Pires et al. 2021). To
125 corroborate this, we evaluated the concordance between ordinations produced using a
126 family level resolution (or lower) and ordinations produced with the finest possible
127 taxonomic level in six of the regions included in our study. We found that assemblage
128 structures were tightly correlated between higher and lower taxonomic levels ($r > 0.8$,
129 $p < 0.001$, Table S2), indicating the viability of using family-level metrics to assess biotic
130 metrics across all habitats. A focus on the family- rather than genus-level was also more
131 appropriate for the global scale of our study because, while many genera occur in relatively
132 small geographic areas, most families occur across broad (intercontinental) scales, enabling
133 valid global contrasts of presence-absence data (i.e. most taxa assessed could have occurred
134 in a specific wetland). We recognize that each contributing researcher had inherent biases
135 in developing their data sets, and so we do not focus on patterns within any single region,
136 but instead focus on robust patterns across climatic conditions for individual wetlands. For
137 nine Antarctica sites, no macroinvertebrates were recorded, and thus we excluded them
138 from further analyses (i.e. we retained a total of 760 wetlands to calculate biodiversity
139 metrics).

140 **2.2 Environmental predictors**

141 2.2.1 Geographical coordinates and elevations

142 The coordinates (latitude and longitude; WGS84 system) and elevation of each
143 wetland were provided by the contributors. For those sites lacking precise elevation data,

144 we derived values from a digital elevation model (www.worldclim.org; Fick and Hijmans
145 2017) using the R package ‘raster’ (Hijmans et al. 2020; see Table S1). We also calculated
146 regional centroid coordinates and elevations for each data set (Fig. 1; Table S1).

147 2.2.2 Climatic variables

148 We downloaded bioclimatic attributes from the WorldClim Global Climate Data
149 v2.1 (1970-2000 period; Fick and Hijmans 2017), at 30 seconds of arc resolution (~1 km²).
150 Using the R package ‘raster’ (Hijmans et al. 2020), we extracted 19 bioclimatic variables
151 for each site (Fig. S1), representing the major temperature and precipitation attributes.

152 2.3 Response variables

153 We used three diversity metrics: family richness (i.e. number of macroinvertebrate
154 families per wetland); local contribution to beta diversity (LCBD; i.e. contributions of each
155 site to total beta diversity); and total pairwise beta diversity (i.e. variation in community
156 composition across the whole array of 760 sites). We calculated the LCBD as the variance
157 of the Hellinger-transformed presence-absence data set (Legendre and De Cáceres 2013).
158 The LCBD index assesses the degree of uniqueness in assemblage composition from each
159 wetland, varying from 0 to 1, with higher values indicating higher singularity value of each
160 site. If high LCBD values coincide with low richness values, then low richness sites are
161 disproportionately contributing to regional beta diversity (Legendre and De Cáceres 2013).
162 We calculated the LCBD index using the R package ‘adespatial’ (Dray et al. 2020). We
163 used the Sørensen (incidence-based) index incorporated in the R package ‘betapart’
164 (Baselga et al. 2020), to calculate the total pairwise beta diversity following Baselga
165 (2010).

166 2.4 Statistical analyses

167 All statistical methods were conducted in R software v 4.0.0 (R Core Team, 2020); R codes
168 are available on figshare (<https://figshare.com/s/7c1a13466f8857f4b4bd>)

169 2.4.1 Climatic variable selection

170 We applied a nonparametric Spearman rank correlation to explore the relationships
171 among climatic variables. Based on those results we excluded 13 climatic variables that
172 were highly correlated over a pre-selected threshold of ± 0.6 , thereby retaining a total of six
173 variables: mean annual temperature; temperature seasonality (standard deviation $\times 100$);
174 maximum temperature of warmest month (hereafter referred as “maximum temperature”);
175 minimum temperature of coldest month (hereafter referred as “minimum temperature”);
176 annual precipitation (i.e. the sum of all total monthly precipitation values); and precipitation
177 seasonality (i.e. coefficient of variation that provides a percentage of precipitation
178 variability where larger percentages represent greater variability of precipitation). Although
179 some of these selected variables were still correlated over our threshold (see Fig. S1), we
180 kept them in order to assess whether any aspect (i.e. average, range, variability) had a
181 higher effect on response variables. Using the nonparametric Spearman rank correlations,
182 we also explored relationships between selected climatic variables and latitudes/elevations.

183 2.4.2 Taxonomic richness and LCBD relationships

184 Based on previous findings for other freshwater ecosystems (Heino and Grönroos
185 2017), we first tested if LCBD was explained by taxonomic richness at two scales: across
186 wetlands ($n = 760$) and across regions ($n = 22$). For the former, we fitted a generalized
187 linear mixed-effects model (GLMM) with region as a random intercept; and for the latter
188 we fitted a generalized linear model (GLM). We assumed a Gamma distribution of the
189 response variable and used a log link function for both models. We fitted the models using
190 the ‘lme4’ (Bates et al. 2015) R package. As LCBD and taxonomic richness were

191 negatively and significantly correlated (Table S3), we excluded LCBD from subsequent
192 models (i.e. generalized additive and linear mixed-effects models). However, we retained
193 LCBD to determine the vulnerabilities of different wetlands to possible climatic changes,
194 assuming that wetlands with high LCBD values would be more vulnerable to climate
195 change (i.e. they are unique in terms of macroinvertebrate assemblages).

196 2.4.3 Climatic predictors of taxonomic richness

197 We analyzed the effects of climatic predictors on family richness using generalized
198 additive mixed-effects models (GAMM), with a Poisson family distribution and log link
199 function. Since we expected different responses of macroinvertebrate assemblages to
200 climatic factors among permanent wetlands (n = 301) and temporary wetlands (n = 459),
201 we fitted separate models. Instead of including wetland type as a fixed effect, we decided to
202 fit models separately to avoid parameter estimation problems caused by the distribution of
203 wetland types across regions (i.e. some regions had only temporary or permanent wetlands;
204 Table S1). Moreover, as we aimed to tease apart the effects of different measures of
205 temperature and precipitation, we decided to fit univariate models (i.e. single predictor),
206 which allowed us to retain some highly correlated variables (e.g. mean annual temperature
207 and maximum temperature). We fitted 12 GAMMs (i.e. two wetland types vs six climatic
208 variables), calculating the effective degrees of freedom values, and including the effect of
209 region as a random intercept (with 21 levels for temporary and 17 levels for permanent
210 wetlands; see Table S1). Additionally, we fitted a third set of models (GAMMs) to test the
211 effect of maximum temperature, precipitation seasonality and their interaction on
212 taxonomic richness for temporary and permanent wetlands.

213 Adjusted R^2 values are provided for GAMMs as measures of how well a model fits
214 the data (i.e. the higher the value, the stronger the relationship among predictor and

215 response variables). Residual plots were examined for model validation following the
216 protocol described by Zuur et al. (2009). Modelling was performed using ‘itsadug’ (van Rij
217 et al. 2020), ‘mgcv’ (Wood 2017), ‘MuMIn’ (Bartoń 2019), ‘r2glmm’ (Jaeger 2017),
218 ‘lattice’ (Sarkar 2008) and ‘ggplot2’ (Wickham 2020) R packages.

219 2.4.4 Climatic predictors of pairwise beta diversity

220 We used generalized dissimilarity models (GDMs) for modelling beta diversity
221 patterns along climatic gradients (Ferrier et al. 2007). GDM is a nonlinear extension of
222 matrix regression for analyzing and predicting dissimilarity patterns in relation to
223 environmental gradients. In our study, we used it to model macroinvertebrate dissimilarities
224 across all possible pairs of sites (i.e. beta diversity) in relation to environmental gradients.
225 GDM takes into account the nonlinearity both in the relationship between ecological
226 separation and observed compositional dissimilarity (Gauch 1973, Faith et al. 1987) and in
227 the rate of compositional turnover along environmental gradients (Ferrier et al. 2007). We
228 fitted separate GDMs for temporary wetlands (n = 459) and permanent wetlands (n= 301),
229 based on total beta diversity. We used the default of three I-splines per predictor, with a
230 backward elimination procedure, retaining only significant GDMs ($p < 0.05$) and variables
231 that made a significant contribution to explained deviance ($p < 0.05$; 50 permutations). We
232 estimated the variable importance in each GDM model as the percent change in deviance
233 explained by the full model and the deviance explained by a model fit with that permuted
234 variable. We tested the full set of variables previously selected (i.e. mean annual
235 temperature, maximum temperature, minimum temperature, temperature seasonality,
236 annual precipitation, and precipitation seasonality) because we were particularly interested
237 in their relative effects. We did not remove any of the climatic variables from these
238 analyses since GDM is known to be robust to multicollinearity among predictor variables

239 (e.g. Heino et al. 2019). GDMs were conducted with the ‘gdm’ R package (Fitzpatrick et al.
240 2020).

241

242 **3. Results**

243 **3.1 Temperature effects on macroinvertebrate diversity**

244 The GAMMs indicated non-linear relationships between taxonomic richness per
245 wetland and all single temperature measures (except seasonality) (Table 1). We found that,
246 for both temporary and permanent wetlands, maximum temperature exerted the highest
247 effect on taxonomic richness (Table 1, Fig. 2a; Adjusted R²: 28% permanent and 12%
248 temporary, $p < 0.001$; see also Fig. S2), but richness responses were slightly different
249 between them. While both wetland types showed a relatively steady increase in richness as
250 maximum temperatures increased (note that the increase rate is particularly high at lower
251 temperatures), richness in temporary wetlands tended to decline at the highest maximum
252 temperatures values (but note that the uncertainty is high; Fig. 2a).

253 The GDMs exhibited similar patterns for macroinvertebrate beta diversity, with
254 maximum temperature exceeding the effects of the other climatic predictors (Table 2, Fig.
255 2b; Maximum temperature importance: 32.42 permanent and 36.04 temporary, $p < 0.001$;
256 see also Fig. S3). For permanent wetlands, beta diversity turnover across maximum
257 temperatures reached an asymptote around 25 °C (i.e. assemblages became similar). For
258 temporary wetlands an asymptote occurred at 20 °C, and the turnover increased again once
259 maximum temperatures reached 25 °C, but the uncertainty was higher for higher
260 temperatures (Fig. 2b).

261 **3.2 Precipitation as a secondary control on diversity**

262 Precipitation seasonality was also an important control, significantly associated with
263 taxonomic richness and beta diversity of temporary and permanent wetlands (Tables 1 and
264 2, Fig. 2; $p < 0.001$ and $p < 0.05$ for taxonomic richness and beta diversity, respectively), but
265 the relationships differed between them. Temporary wetlands' richness tended to decrease
266 as precipitation seasonality became higher (i.e. environments with long dry seasons). In
267 contrast, permanent wetlands' richness peaked at moderate and high precipitation
268 seasonality values (Fig. 2a). For permanent wetlands beta diversity turnover increased up to
269 a precipitation seasonality index of 60, and then reached a plateau. At that same point,
270 temporary wetlands turnover began to markedly increase, indicating larger differences
271 among assemblages (Fig. 2b).

272 **3.3 Macroinvertebrate diversity patterns across climatic regions**

273 In regions with maximum temperatures lower than 30°C and where precipitation is
274 evenly distributed throughout the year (i.e. low and medium precipitation seasonality index
275 values; Fig. 3), the number of permanent and temporary wetlands were similar. However,
276 temporary wetlands predominated in warm-dry climates (i.e. high precipitation seasonality;
277 Fig. 3a and Fig. S4), while permanent wetlands predominated in warm-humid climates
278 (Fig. 3c). Wetlands with low richness, such as montane, high latitude, and warm-dry
279 wetlands, often had unique assemblages of macroinvertebrate families, and so contributed
280 more to beta diversity than other wetland types (Fig. 3a, c; see Table S3 for taxonomic and
281 LCBD relationships). Moreover, maximum temperature and precipitation seasonality were
282 interacting drivers of temporary wetland richness ($p < 0.05$), but that pattern was not
283 significant for permanent ones ($p > 0.05$, Fig. 3b, d; Table S4). Thus, for low precipitation
284 seasonality values (i.e. 10, Fig. 3b), the richness of temporary wetlands increased with

285 increasing maximum temperatures (e.g. similar relationship as permanent wetlands), but
286 significantly decreased for precipitation seasonality values higher than 50.

287

288 **4. Discussion**

289 Our global analyses suggest that temperature (maxima) and precipitation (seasonality) are
290 major controls of macroinvertebrate diversity in wetlands. We found that macroinvertebrate
291 diversity of temporary wetlands is naturally constrained by the stressful combination of hot
292 and seasonally dry environmental conditions (drivers that also determine the duration of the
293 hydroperiods). Consequently, a shift in climate towards hotter or drier conditions may
294 exacerbate stress on these already taxon-poor communities. We also found that family
295 richness across all wetlands is naturally poor in climates with cooler summers (i.e. low
296 values of maximum temperature), and here climate warming may actually lead to increased
297 diversity. However, negative effects on the extant cold-adapted fauna are a major concern.
298 Finally, diversity in habitats not currently stressed (i.e. permanent habitats in warm
299 climates, temporary habitats in mild climates) may become more stressful with climate
300 change. Thus, we predict that wetland macroinvertebrate diversity in both stressed and
301 benign environments will further decline.

302 **4.1 Temperature as the primary control of wetland macroinvertebrate biodiversity**

303 Our expansive data set allowed us to test whether geographic patterns in
304 macroinvertebrate diversity, which previously have only been assessed at small scales (e.g.,
305 Rosset et al. 2010), are consistent at a global scale. We found that maximum temperatures
306 explained more variation than mean annual temperature in the diversity of wetland
307 macroinvertebrates globally, especially in temporary habitats. We used air temperature as a
308 surrogate of water temperature. Although it is well known that water temperature is not

309 linearly related with air temperature (e.g., water temperatures depend on water depth,
310 canopy cover, ice cover, among others), we assumed that daily and seasonal water
311 temperature extremes varied predictably with climate (Dodds et al. 2019).

312 Maximum temperature rather than averages, was a strong predictor of
313 macroinvertebrate diversity in wetlands because it captures seasonality in contrast to
314 average annual temperatures. Macroinvertebrates are ectotherms (i.e. the regulation of body
315 temperature depends on external sources) that require a certain amount of temperature
316 degree days to complete their life cycles, and therefore are especially likely to be
317 vulnerable to extremes in climate warming (Woodward et al. 2010). Episodic stresses from
318 high temperatures may only occur over a certain threshold (Vasseur et al. 2014). Despite
319 many macroinvertebrates displaying a wide variety of physiological adaptations to cope
320 with thermal extremes, warming can alter their distribution, morphology, phenology,
321 genetics, and lastly their survival (Scheffer et al. 2016). Additionally, stronger negative
322 effects might be produced when climate warming alters other water quality parameters (i.e.
323 apart from just rising water temperature), leading to local or regional anoxic conditions,
324 salinization, or cyanobacterial blooms (Reid et al. 2019, Cantonati et al. 2020). These
325 effects are likely to be accentuated in temporary wetlands where shallow depths may allow
326 a more rapid response to extreme heat events (Boix et al. 2020).

327 Our study suggests that global warming could trigger complex diversity changes in
328 wetlands, depending on the wetland type, the geographical region, and the relationship with
329 precipitation regimes. Across wetlands under cool or mild temperature summers, we
330 detected a positive relationship between maximum temperature and diversity metrics,
331 suggesting that diversity in these habitats is constrained by low temperatures (e.g. Stenert et
332 al. 2020). However, in temporary wetlands where summers were hot, richness declined

333 (although beta diversity turnover increased because they hosted some macroinvertebrate
334 specialists; e.g., anostracan crustaceans). We acknowledge a lack of data from tropical
335 depressional wetlands, which could bias some of our conclusions. However, as maximum
336 temperature was consistently a very strong driver of macroinvertebrate diversity across the
337 wetland types assessed, we believe our findings could be extrapolated to even warmer
338 locations. Thus, as maximum temperatures continue to rise (NASA, Global Climate
339 Change 2021), we expect that macroinvertebrate biodiversity will be negatively affected
340 across a range of wetlands.

341 **4.2 Precipitation seasonality as a secondary control of wetland macroinvertebrate** 342 **diversity**

343 The hydrology of depressional wetlands is largely dependent on precipitation, and
344 in turn, hydrology controls many environmental variables (e.g. electrical conductivity, pH,
345 organic matter) and biological assemblages (Batzer and Boix 2016). Given that the wetland
346 permanence gradient is considered a key factor in determining macroinvertebrate
347 assemblages (Wellborn et al. 1996, Wissinger 1999, Williams 2006), we anticipated that
348 annual precipitation would exert a pronounced influence on macroinvertebrate diversity.
349 Unexpectedly, we found a significant effect of precipitation seasonality on taxonomic
350 diversity, but it did not depend on total annual precipitation. Precipitation seasonality is a
351 measure of the tendency for a site or region to have more rainfall in certain months or
352 seasons than others (i.e. the higher the coefficient of variation, the greater the temporal
353 fluctuation in rainfall). Studies in other freshwater ecosystems, such as streams (e.g.,
354 Vinson and Hawkins 2003), suggest that precipitation seasonality is a surrogate for
355 biological disturbance, and this association likely holds true for wetlands.

356 We found that in temporary wetlands, precipitation seasonality tended to increase
357 concurrently with maximum temperature. The synergy between these two environmental
358 factors creates stressful hot, dry seasons, resulting in low-richness macroinvertebrate
359 assemblages comprised of taxa with adaptations for seasonal drying (i.e. desiccation-
360 tolerant stages); these assemblages were remarkably similar in family compositions across
361 broad geographical regions. In contrast, taxonomic richness in permanent wetlands was
362 somewhat independent of precipitation seasonality. The fact that permanent habitats retain
363 water year-round, regardless of seasonal changes in precipitation, likely limits the influence
364 of precipitation on macroinvertebrate diversity. However, if a permanent habitat is
365 converted into a temporary one in the future, precipitation will likely impose an important
366 control.

367 **4.3 Linking climate change and wetland diversity**

368 Surprisingly, the categorization of wetlands according to water permanency was not
369 a major driver of macroinvertebrate diversity (see Fig. S5, Tables S5-S7). Permanent
370 wetlands supported only modestly higher family richness than temporary wetlands, and
371 beta diversity was similar in both wetland types. However, we found that regions with high
372 precipitation seasonality and warm conditions supported mostly temporary wetlands, which
373 had unique macroinvertebrate assemblages (Fig. 4a). Because evapotranspiration is
374 typically the largest cause of water loss from precipitation-based depressional wetlands
375 (some montane wetlands excepted), permanent wetlands in arid regions like California
376 (US), Mendoza (Argentina), and the Mediterranean are rare (Kneitel 2016, Boix et al.
377 2020). The recently published global distribution of non-perennial rivers and streams
378 supports our findings, showing that permanent freshwaters are quite rare in arid regions
379 (Messenger et al. 2021). We recognize that our findings could be biased due to the

380 distribution of study wetlands (and regions), but the inclusion of 22 locations across seven
381 continents represents significant scope (and many landscapes of the world lack depressional
382 wetlands of any kind; Jackson et al. 2014).

383 Climate change is affecting water availability by exacerbating extremes in seasonal
384 precipitation (e.g. some arid regions are becoming drier for longer periods of time). Among
385 the regions included in our study, we have detected varying shifts in wetland types
386 associated with precipitation seasonality changes. The semi-arid North Dakota Prairie
387 Potholes wetlands, for example, have become wetter and many wetlands have shifted from
388 being temporary to permanent (McKenna et al. 2017; Fig. 4b). The opposite is happening in
389 the Argentinian Patagonia, which is becoming drier (Masiokas et al. 2020), and formerly
390 permanent habitats have become temporary. These changes are strongly dependent on the
391 interactions between the distribution of precipitation and the extremes in summer
392 temperatures (Fig. 4).

393 Our study suggests that macroinvertebrate diversity in depressional wetlands varies
394 over a continuum of temperature and precipitation seasonality. The most vulnerable
395 wetlands to global warming are likely those located in warm-dry regions. Moreover, we
396 predict that increased precipitation seasonality (e.g. Patagonia) will exert stress on more
397 macroinvertebrate taxa than decreased precipitation seasonality (e.g. North Dakota). Warm
398 and seasonally dry habitats in California, Mendoza and the Mediterranean may be similarly
399 vulnerable, and these may be places where climate change could lead to extirpations of
400 entire families (IPCC 2007, Ferri et al. 2020, Boix et al. 2020). Wetlands located in cooler
401 regions (e.g. montane and high latitude wetlands), which are often considered vulnerable to
402 climate change (Rosset and Oertli 2011, Montemayor et al. 2017), would also experience
403 compositional changes, but probably not from extirpations of families. Instead it seems

404 likely that entirely new families may colonize previously cold places as the climate warms,
405 meanwhile species composition within existing families are already changing (Shepard et
406 al. 2021). Further, climate change may also negatively influence diversity in many wetlands
407 that do not currently appear to be stressed. These are particularly concerning impacts since
408 wetlands are hotspots of biodiversity and ecosystem function. Our analyses provide new
409 context for global risk assessment of wetland degradation under climate change.

410

411

412 **ACKNOWLEDGEMENTS**

413 LBE, MGG, EAW-S and LMM were funded by CONICET. The contribution by Olga
414 Loskutova was done within the framework of the State Task of the Animal Ecology
415 Department of the Institute of Biology, Komi SC, Ural Branch, Russian Academy of
416 Sciences. Data collection efforts at the North Dakota study areas are supported by the US
417 Geological Survey's Climate Research and Development Program. Any use of trade, firm,
418 or product names is for descriptive purposes only and does not imply endorsement by the
419 US Government. We also thank Dr. Sarah French for her constructive review of the
420 manuscript. We finally express our gratitude to all of the people that helped with data
421 collection and invertebrate identifications including: M Archangelsky, C Brand, C di
422 Prinzio, J Compte, D Cunillera-Montcusí, ML Miserendino, A Ruhí, I Tornero, among
423 others.

424

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597

598 **Data availability**

599 Data used in this publication can be downloaded from figshare

600 (<https://figshare.com/s/7c1a13466f8857f4b4bd>).

601 U.S. Federally funded data generated during this study are available from the USGS at

602 <https://www.sciencebase.gov/catalog/item/599d9555e4b012c075b964a6> (Mushet et al.

603 2015 and 2017).

604 **Table 1.** Generalized additive mixed-effects models (GAMM) results for the effects of
 605 climatic predictors on family richness of temporary and permanent wetlands. Predictor
 606 variables, effective degrees of freedom values (edf), f- and p-values, and adjusted R^2 are
 607 shown for each model. Predictor variables with significant effects are highlighted in bold.

Wetland type	Predictor variables	edf	f-value	p-value	Adjusted R^2
Temporary	s(MAT)	2.4	6.1	0.001**	-R^2
	s(MAXT)	3.3	10	1.2e⁻⁶***	12%
	s(MINT)	7.1	5.8	8.5e⁻⁷***	9.4%
	s(TSE)	1	1.1	0.3	2%
	s(AP)	1.4	0.3	0.7	- R^2
	s(PSE)	7	5.5	2.3e⁻⁶***	6%
Permanent	s(MAT)	3	14.1	1.2e⁻⁸***	-R^2
	s(MAXT)	4	16.5	2.6e⁻¹²***	28%
	s(MINT)	6.1	5.2	3.3e⁻⁵***	12%
	s(TSE)	1	6.5	0.01 *	-R^2
	s(AP)	1.4	0.3	0.5	2%
	s(PSE)	4.6	4.5	0.001**	4%

608 MAT: mean annual temperature; MAXT: maximum temperature; MINT: minimum temperature; TSE:
 609 temperature seasonality; AP: annual precipitation; PSE: precipitation seasonality. Significance codes: 0 '***'
 610 0.001 '**'. Negative R^2 : means the explanation towards response is very low or negligible.

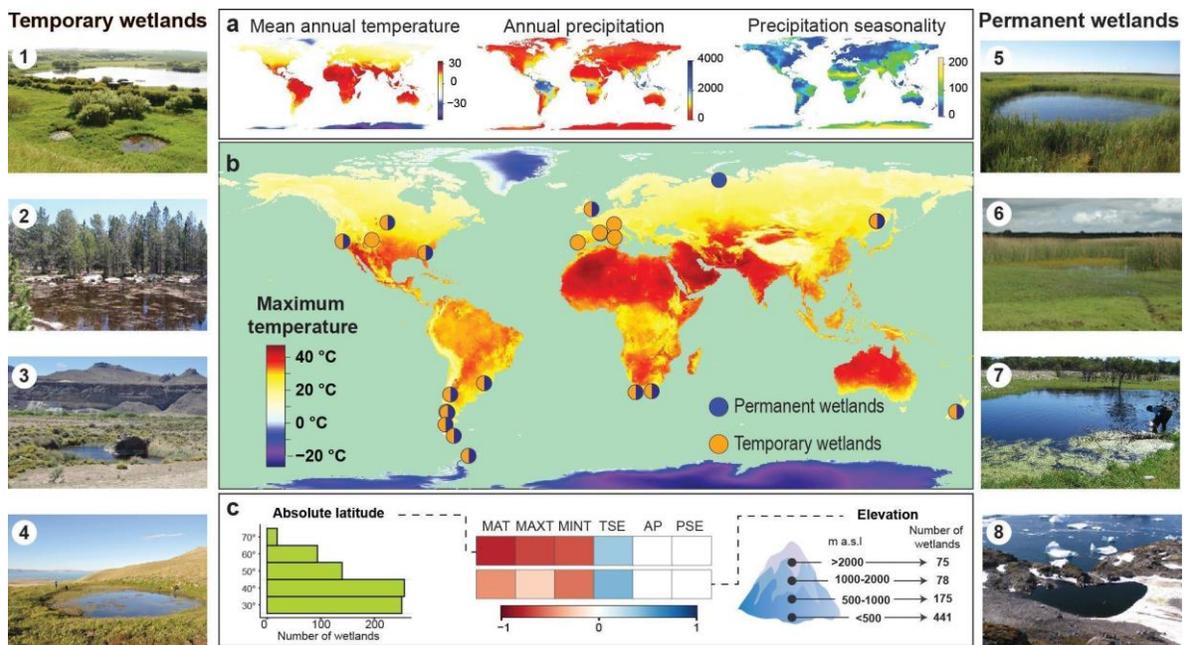
611

612 **Table 2.** Summary of the GDMs for each wetland type and beta diversity (Sørensen index).
 613 Variable importance was measured as the percent change in deviance explained by the full
 614 model and the deviance explained by a model fit after 50 permutations. All variables were
 615 significant ($p < 0.05$).

	Temporary wetlands	Permanent wetlands
<i>Variables importance</i>		
Mean annual temperature		20.21
Maximum temperature	36.04	32.42
Minimum temperature	9.43	
Temperature seasonality		
Annual precipitation	10.87	
Precipitation seasonality	15.51	10.61
<i>GDM summary</i>		
Model deviance	12137	3880
Percent deviance explained	15.58	22.42
Model p-value	0.000	0.000

616

617 **Figure 1.** Global distribution of the 22 study regions, and main climatic drivers of wetland
 618 macroinvertebrates diversity. (a) Global patterns of three WorldClim v2.1 bioclimatic variables. (b)
 619 Maximum temperature and study region centroids. (c) Distribution of the 769 depressional wetlands
 620 across absolute latitudinal and elevation gradients, and their correlations with selected climatic
 621 variables (MAT: mean annual temperature; MAXT: maximum temperature; MINT: minimum
 622 temperature; TSE: temperature seasonality; AP: annual precipitation; PSE: precipitation
 623 seasonality). Photographs 1-4 show temporary wetlands from the United Kingdom (credit: Michael
 624 Jeffries), Spain (credit: Jordi Sala) and Patagonia (credit: Luis B. Epele), respectively. Photographs
 625 5-8 show permanent wetlands from Russia (credit: Olga Loskutova), Brazil (credit: Cristina
 626 Stenert), South Africa (credit: Matthew Bird) and Antarctica (credit: Gabriela Mataloni),
 627 respectively.

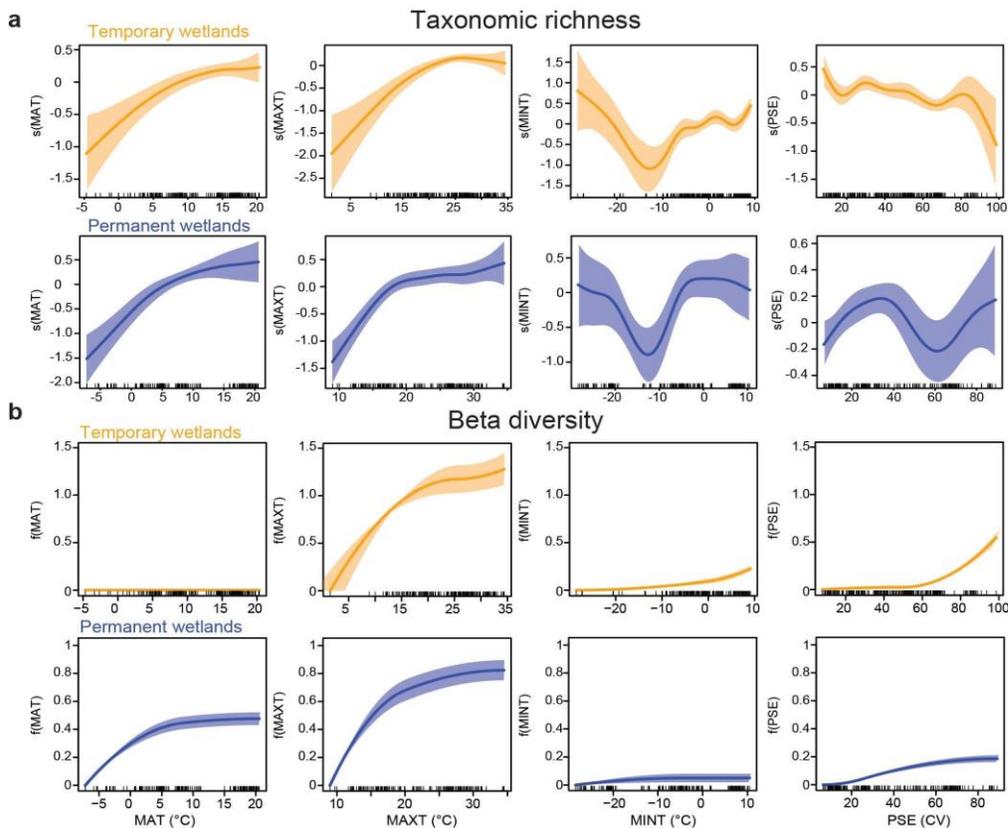


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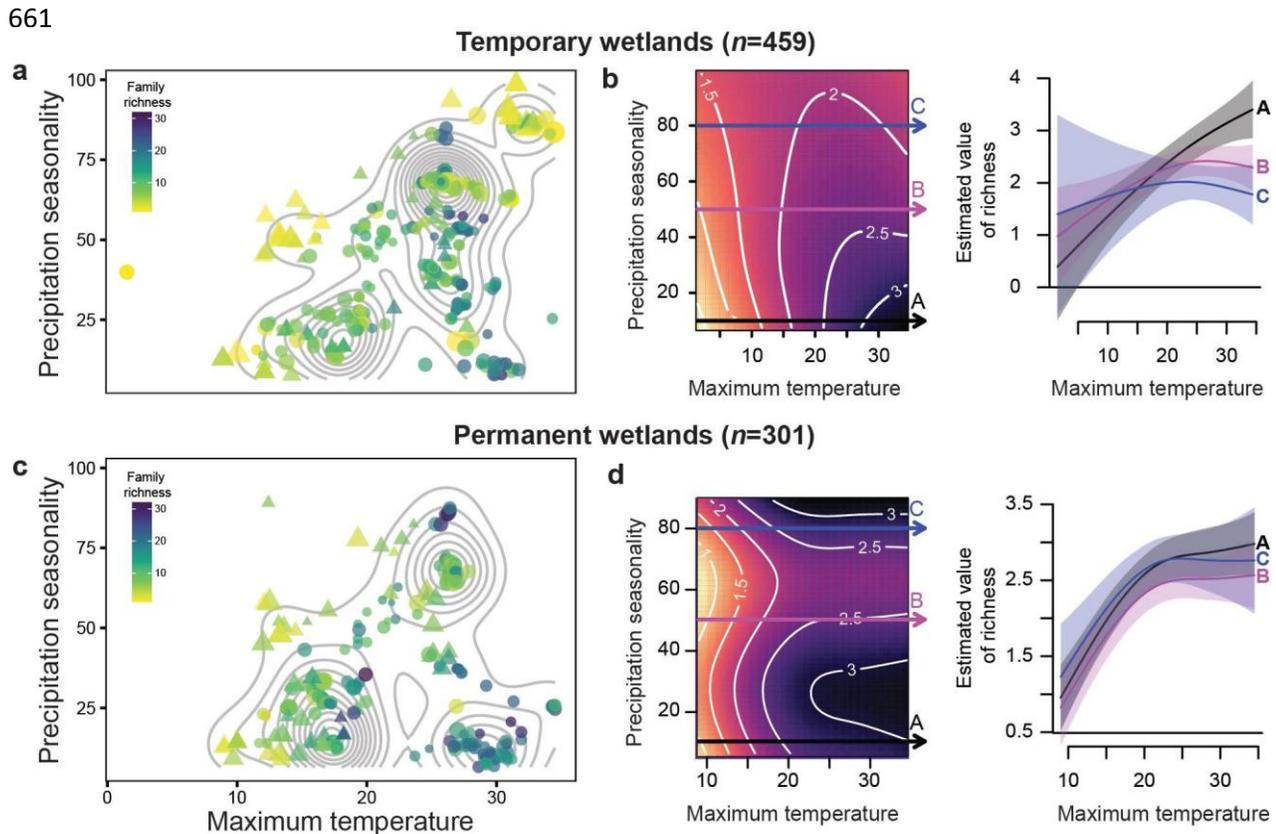
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635 **Figure 2.** Relationships between macroinvertebrates and selected climatic variables from 459
 636 temporary (orange) and 301 permanent (blue) depressional wetlands (each location is represented
 637 with a black tick mark over the x-axis). (a) Graphical results for the effects of climatic predictors on
 638 family richness modelled with generalized additive mixed-effects models (GAMM). The y-axes
 639 represent the estimated smoothing curve and the 95% confidence bands (*s*) obtained from fitted
 640 GAMMs. (b) Graphical results for the effects of climatic predictors on total beta diversity modelled
 641 with generalized dissimilarity modelling (GDM). GDMs are represented by fitted (*f*) I-splines
 642 (partial regression fits), displaying their error bands (+/- one standard deviation). The maximum
 643 height reached by each curve indicates the total amount of compositional turnover associated with
 644 that variable, and the relative importance of that variable in explaining beta diversity. The shape of
 645 each function indicates how the rate of compositional turnover varies along the gradient. MAT:
 646 mean annual temperature; MAXT: maximum temperature; MINT: minimum temperature; PSE:
 647 precipitation seasonality.

648



649 **Figure 3.** Interactions between maximum temperature and precipitation seasonality. (a, c) Density
650 distribution (grey lines) of wetland types (circles=non-montane wetlands, triangles=montane
651 wetlands) and their macroinvertebrate family richness (color gradient) and local contribution to beta
652 diversity (LCBD; size), based on maximum temperature and precipitation seasonality. (b, d)
653 Graphical results for generalized additive mixed-effects models (GAMM) using maximum
654 temperature, precipitation seasonality and their interactions as predictor variables of taxonomic
655 richness (interactions are only significant for temporary wetlands, Table S4). Contour lines (white)
656 in the contour plots (left plots) are representing the estimated richness across the precipitation
657 seasonality and maximum temperature relationships. Arrows “A” (black), “B” (pink) and “C”
658 (blue), are used to represent the estimated macroinvertebrate richness with the 95% confidence
659 bands at low, medium and high values of precipitation seasonality (i.e., 10, 50, and 80) , and across
660 the maximum temperature gradient (right plots).



662 **Figure 4.** Summary of the main results. (a) Hypothetical distribution of depressional wetlands
 663 across global maximum temperature and precipitation seasonality. The maximum temperature could
 664 be interpreted as an elevational gradient (i.e. the coldest wetlands would be those located at the
 665 highest elevations) or latitudinal gradient (i.e. the coldest wetlands would be those located at higher
 666 latitudes). The color of the circles represents temporary (orange) and permanent (blue) wetland
 667 assemblages, while the number of macroinvertebrate icons is used as surrogate of taxonomic
 668 richness. With the bars at the bottom and right, we are showing the assemblages/regions most likely
 669 to be vulnerable to climate change. Note that the coldest and warmest regions are most vulnerable
 670 to climate change (i.e. temperature rise), as well as the seasonally driest ones (e.g. regional
 671 precipitation shifts due to climate change, would lead to permanent wetlands becoming temporary).
 672 (b) Two contrasting examples of the consequences of precipitation shifts on wetlands water
 673 availability. This figure is linked with Fig. 4a, since “Precipitation seasonality” and “Vulnerability
 674 to climate change” axis can be used to interpret precipitation shift effects. The upper tier of aerial
 675 images is showing a decrease in precipitation seasonality (i.e. higher dispersion across the year) for
 676 a Prairie Pothole wetland (47°5’23.81”N, 99° 6’22.09”W; North Dakota, US), illustrating the shift
 677 from temporary to permanent wetlands. In the lower tier of images the opposite is illustrated for a
 678 Patagonian wetland (42°57’39.60”S, 71°10’58.80”W; Patagonia, Argentina) that was permanent
 679 until 2007 and after precipitation seasonality increased, became temporary.

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 681

