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Perils of life on the edge: Climatic threats to global diversity patterns of wetland macroinvertebrates

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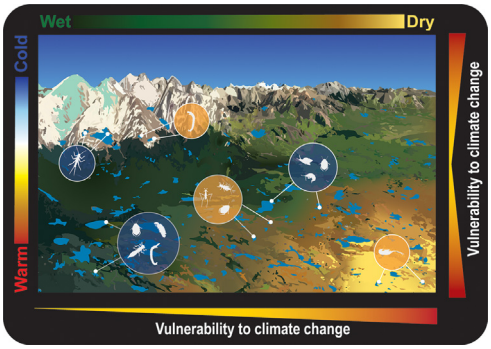
HIGHLIGHTS

- Assemblage responses to climatic variables depend on water permanency.
- Maximum temperature is the main climatic driver of wetland macroinvertebrate diversity.
- Precipitation seasonality is also an important control.
- Cooler and warm-dry regions have low richness, but support unique assemblages.
- Wetlands from warm-dry regions are the most vulnerable to climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

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

1. Introduction

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

Recent meta-analyses of broad scale patterns in wetlands suggest that climate, temperature, and precipitation are the principal controls on macroinvertebrate assemblages (e.g., Ruhí et al., 2013; Kneitel, 2016; Anton-Pardo et al., 2019). Batzer and Ruhí (2013) assessed wetland invertebrates across North America, Europe, and Australia (and a few sites in South America and Asia) and found that wetlands within regions were compositionally similar, regardless of local factors (e.g., varying hydrologic and/or plant conditions), while wetlands from regions with different climates tended to be compositionally dissimilar. They also noted that wetlands with harsh climatic conditions (alpine and desert environments) tended to have unique faunas. Boix and Batzer (2016) similarly found that wetlands from harsh climates (unusually hot or cold) had low invertebrate taxon richness compared to wetlands with more benign climates. Ruhí et al. (2013) assessed a longitudinal gradient (spanning the Palearctic of Europe and Nearctic of North America) and found that invertebrate assemblages differed based on broad ranges in temperature and aridity. Stenert et al. (2020) analyzed a latitudinal gradient (spanning North and South America) and found that climate zones (temperate vs subtropical) controlled family-level composition and beta diversity. However, the simultaneous influences of temperature and precipitation on wetland invertebrate assemblages has never been directly assessed.

If climatic factors such as temperature and precipitation are the dominant drivers of wetland invertebrate composition, as they are for other aquatic organisms (Dodds et al., 2019), then it would suggest that these organisms will be profoundly impacted by ongoing climate change. Invertebrates residing in wetlands already subjected to harsh climatic conditions (e.g., hot, frigid, and/or dry places) might be especially vulnerable to abiotic stress under future climatic conditions (i.e., even hotter or drier). Because of the pivotal ecological importance of invertebrates (Batzer and Wissinger, 1996; Batzer and Boix, 2016), global warming could profoundly impact overall wetland ecosystem structure and functioning. This could exacerbate the existing stress on threatened species (Amano et al., 2020), as well as wetland economic and ecosystem services, such as nutrient cycling, water storage and purification, food production, and recreation (Zedler and Kercher, 2005). Concerns about climate change tend to focus on temperature increases, but precipitation changes can dramatically alter hydrologic regimes and invertebrate communities of wetlands as well (Calhoun et al., 2017). For example, studies in California vernal pools, Andean ponds and Mediterranean wetlands, areas with seasonally dry periods, have detected relationships between temporal shifts in precipitation regimes and regional diversity (Boix et al., 2001; Kneitel, 2014; Montemayor et al., 2017).

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

2. Material and methods

2.1. Data compilation

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

We used macroinvertebrate presence-absence data because it (1) removes noise arising from differences in sampling techniques; (2) is useful for datasets covering wide geographic ranges and across broad climatic gradients with high taxonomic turnover (or beta diversity); and (3) has been shown to be a suitable surrogate for abundance in biodiversity studies (Carneiro et al., 2010; Pires et al., 2021). As the level of taxonomic resolution varied greatly among data sets and macroinvertebrate groups, we harmonized our data by setting taxonomic resolution at the family level (or above for some groups), rather than at sub-family, genus, or species levels. For aquatic invertebrates the family level (or above) has been shown to be highly congruent with finer taxonomic resolution (i.e., genus level) for calculations of diversity metrics (Mueller et al., 2013; Pires et al., 2021). To corroborate this, we evaluated the concordance between ordinations produced using a family level resolution (or lower) and ordinations produced with the finest possible taxonomic level in six of the regions included in our study. We found that assemblage structures were tightly correlated between higher and lower taxonomic levels ($r > 0.8$, $p < 0.001$, Table S2), indicating the viability of using family-level

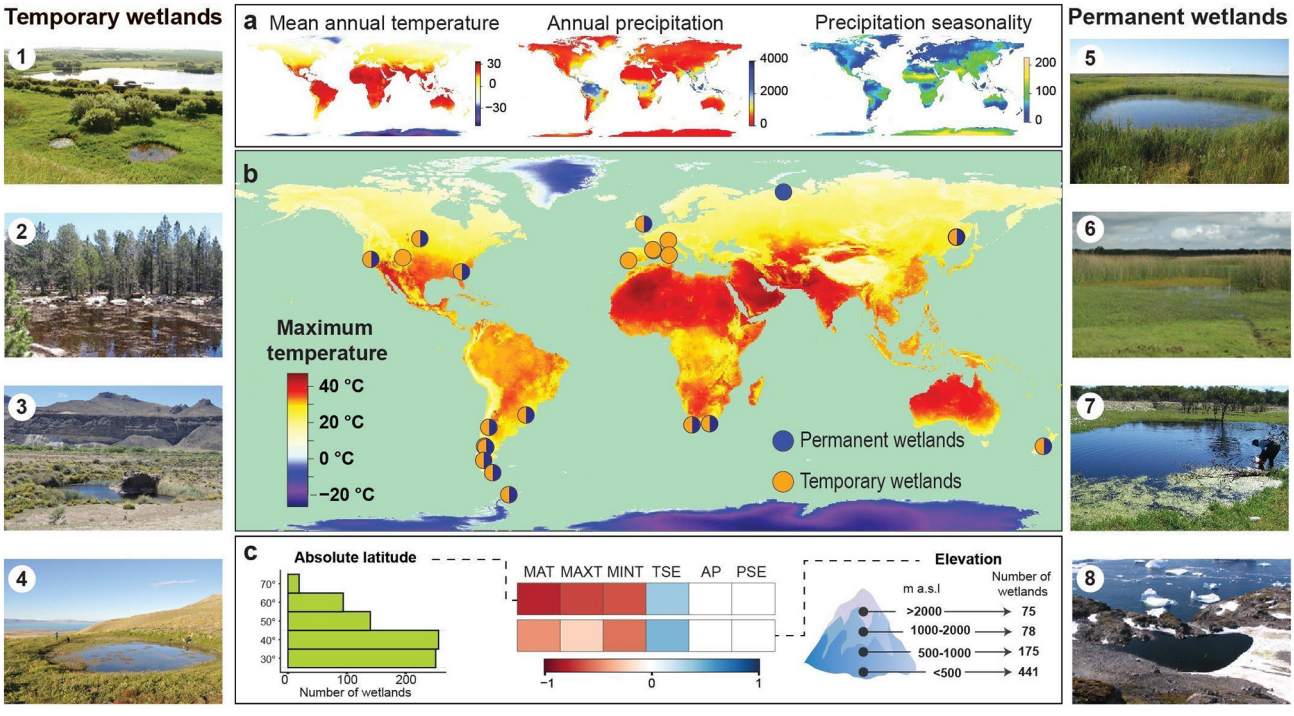

Fig. 1. Global distribution of the 22 study regions, and main climatic drivers of wetland macroinvertebrates diversity. (a) Global patterns of three WorldClim v2.1 bioclimatic variables. (b) Maximum temperature and study region centroids. (c) Distribution of the 769 depressional wetlands across absolute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

metrics to assess biotic metrics across all habitats. A focus on the family- rather than genus-level was also more appropriate for the global scale of our study because, while many genera occur in relatively small geographic areas, most families occur across broad (intercontinental) scales, enabling valid global contrasts of presence-absence data (i.e., most taxa assessed could have occurred in a specific wetland). We recognize that each contributing researcher had inherent biases in developing their data sets, and so we do not focus on patterns within any single region, but instead focus on robust patterns across climatic conditions for individual wetlands. For nine Antarctica sites, no macroinvertebrates were recorded, and thus we excluded them from further analyses (i.e., we retained a total of 760 wetlands to calculate biodiversity metrics).

2.2. Environmental predictors

2.2.1. Geographical coordinates and elevations

The coordinates (latitude and longitude; WGS84 system) and elevation of each wetland were provided by the contributors. For those sites lacking precise elevation data, we derived values from a digital elevation model (www.worldclim.org; Fick and Hijmans, 2017) using the R package 'raster' (Hijmans et al., 2020; see Table S1). We also calculated regional centroid coordinates and elevations for each data set (Fig. 1; Table S1).

2.2.2. Climatic variables

We downloaded bioclimatic attributes from the WorldClim Global Climate Data v2.1 (1970–2000 period; Fick and Hijmans, 2017), at 30 s of arc resolution (~1 km^2). Using the R package 'raster' (Hijmans et al., 2020), we extracted 19 bioclimatic variables for each site (Fig. S1), representing the major temperature and precipitation attributes.

2.3. Response variables

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

2.4. Statistical analyses

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

2.4.1. Climatic variable selection

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

2.4.2. Taxonomic richness and LCBD relationships

Based on previous findings for other freshwater ecosystems (Heino and Grönroos, 2017), we first tested if LCBD was explained by taxonomic richness at two scales: across wetlands (n = 760) and across regions (n = 22). For the former, we fitted a generalized linear mixed-effects model (GLMM) with region as a random intercept; and for the latter we fitted a generalized linear model (GLM). We assumed a Gamma distribution of the response variable and used a log link function for both models. We fitted the models using the 'lme4' (Bates et al., 2015) R package. As LCBD and taxonomic richness were negatively and significantly correlated (Table S3), we excluded LCBD from subsequent models (i.e., generalized additive and linear mixed-effects models). However, we retained LCBD to determine the vulnerabilities of different wetlands to possible climatic changes, assuming that wetlands with high LCBD values would be more vulnerable to climate change (i.e., they are unique in terms of macroinvertebrate assemblages).

2.4.3. Climatic predictors of taxonomic richness

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

Adjusted R^2 values are provided for GAMMs as measures of how well a model fits the data (i.e., the higher the value, the stronger the relationship among predictor and response variables). Residual plots were examined for model validation following the protocol described by Zuur et al. (2009). Modelling was performed using 'itsadug' (van Rij et al., 2020), 'mgcv' (Wood, 2017), 'MuMIn' (Bartoń, 2019), 'r2glmm' (Jaeger, 2017), 'lattice' (Sarkar, 2008) and 'ggplot2' (Wickham et al., 2020) R packages.

2.4.4. Climatic predictors of pairwise beta diversity

We used generalized dissimilarity models (GDMs) for modelling beta diversity patterns along climatic gradients (Ferrier et al., 2007). GDM is a nonlinear extension of matrix regression for analyzing and predicting dissimilarity patterns in relation to environmental gradients. In our study, we used GDMs to model macroinvertebrate dissimilarities across all possible pairs of sites (i.e., beta diversity) in relation to environmental gradients. GDMs account for nonlinearity both in the relationship between ecological separation and observed compositional dissimilarity (Gauch, 1973; Faith et al., 1987) and in the rate of compositional turnover along environmental gradients (Ferrier et al., 2007). We fitted separate GDMs for temporary wetlands (n = 459) and permanent wetlands (n = 301), based on total beta diversity. We used the default of three I-splines per predictor, with a backward elimination procedure, retaining only significant GDMs (p < 0.05) and variables that made a significant contribution to explained

deviance ($p < 0.05$; 50 permutations). We estimated the variable importance in each GDM model as the percent change in deviance explained by the full model and the deviance explained by a model fit with that permutated variable. We tested the full set of variables previously selected (i.e., mean annual temperature, maximum temperature, minimum temperature, temperature seasonality, annual precipitation, and precipitation seasonality) because we were particularly interested in their relative effects. We did not remove any of the climatic variables from these analyses since GDM is known to be robust to multicollinearity among predictor variables (e.g., Heino et al., 2019). GDMs were conducted with the 'gdm' R package (Fitzpatrick et al., 2020).

3. Results

3.1. Temperature effects on macroinvertebrate diversity

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

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

3.2. Precipitation as a secondary control on diversity

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

Table 1
Generalized additive mixed-effects models (GAMM) results for the effects of climatic predictors on family richness of temporary and permanent wetlands. Predictor variables, effective degrees of freedom values (edf), f- and *p*-values, and adjusted R^2 are 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%**

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

3.3. Macroinvertebrate diversity patterns across climatic regions

In regions with maximum temperatures lower than 30 °C and where precipitation is evenly distributed throughout the year (i.e., low and medium precipitation seasonality index values; Fig. 3), the number of permanent and temporary wetlands were similar. However, temporary wetlands predominated in warm-dry climates (i.e., high precipitation seasonality; Figs. 3a and S4), while permanent wetlands predominated in warm-humid climates (Fig. 3c). Wetlands with low richness, such as montane, high latitude, and warm-dry wetlands, often had unique assemblages of macroinvertebrate families, and so contributed more to beta diversity than other wetland types (Fig. 3a, c; see Table S3 for taxonomic and LCBD relationships). Moreover, maximum temperature and precipitation seasonality were interacting drivers of temporary wetland richness ($p < 0.05$), but that pattern was not significant for permanent ones ($p > 0.05$, Fig. 3b, d; Table S4). Thus, for low precipitation seasonality values (i.e., 10, Fig. 3b), the richness of temporary wetlands increased with increasing maximum temperatures (e.g., similar relationship as permanent wetlands), but significantly decreased for precipitation seasonality values higher than 50.

4. Discussion

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

4.1. Temperature as the primary control of wetland macroinvertebrate biodiversity

Our expansive data set allowed us to test whether geographic patterns in macroinvertebrate diversity, which previously have only been assessed at small scales (e.g., Rosset et al., 2010), are consistent at a global scale. We found that maximum temperatures explained more variation than mean annual temperature in the diversity of wetland macroinvertebrates globally, especially in temporary habitats. We used air temperature as a surrogate of water temperature. Although it is well known that water temperature is not linearly related with air temperature (e.g., water temperatures depend on water depth, canopy cover, ice cover, among others), we assumed that daily and seasonal water temperature extremes varied predictably with climate (Dodds et al., 2019).

Maximum temperature rather than averages, was a strong predictor of macroinvertebrate diversity in wetlands because it captures seasonality in contrast to average annual temperatures. Macroinvertebrates are ectotherms (i.e., the regulation of body temperature depends on external

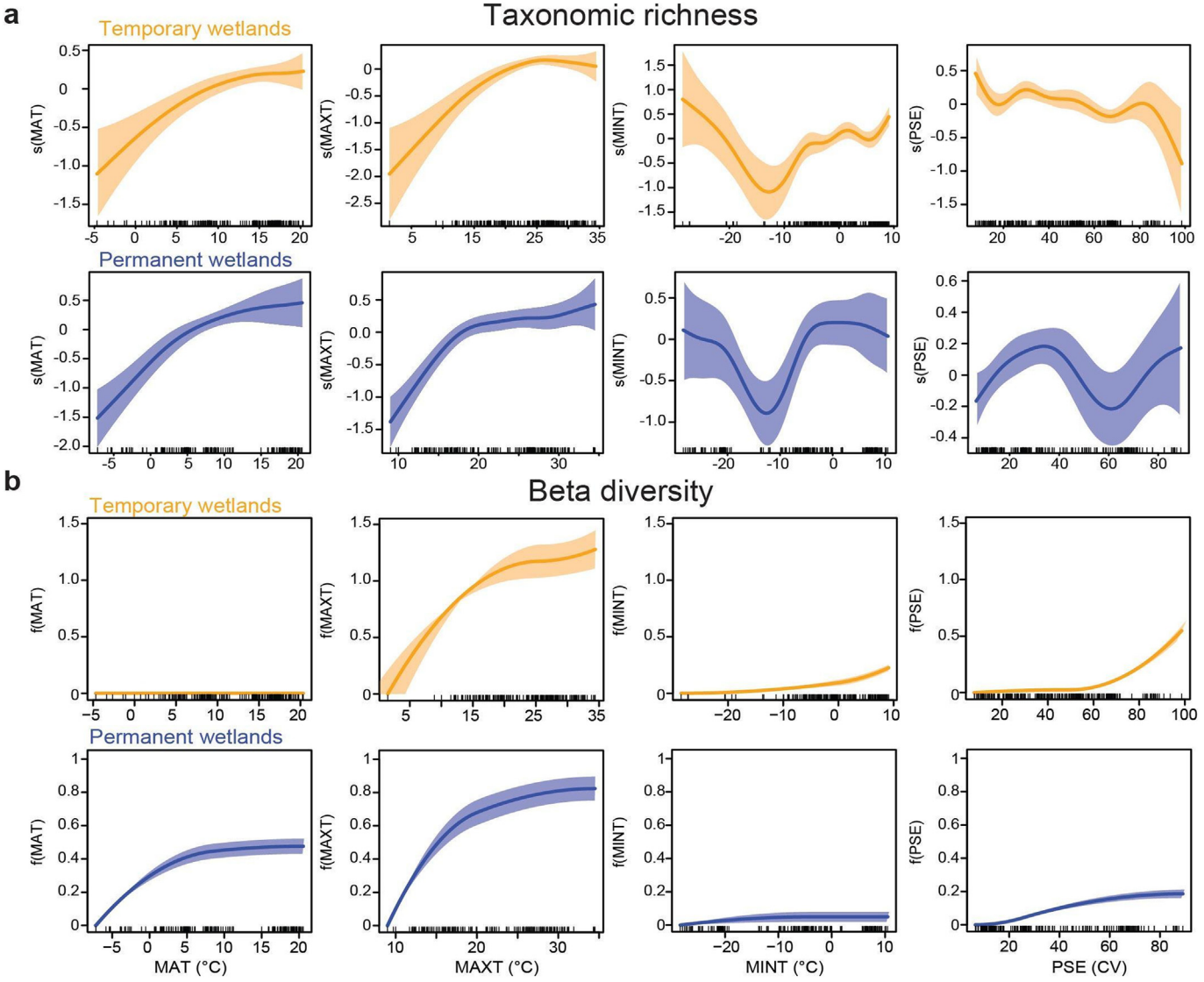

Fig. 2. Relationships between macroinvertebrates and selected climatic variables from 459 temporary (orange) and 301 permanent (blue) depressional wetlands (each location is represented with a black tick mark over the x-axis). (a) Graphical results for the effects of climatic predictors on family richness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

sources) that require a certain amount of temperature degree days to complete their life cycles, and therefore are especially likely to be vulnerable to extremes in climate warming (Woodward et al., 2010). Episodic stresses from high temperatures may only occur over a certain threshold (Vasseur et al., 2014). Despite many macroinvertebrates displaying a wide variety of physiological adaptations to cope with thermal extremes, warming can alter their distribution, morphology, phenology, genetics, and lastly their survival (Scheffers et al., 2016). Additionally, stronger negative effects might be produced when climate warming alters other water quality parameters (i.e., apart from just rising water temperature), leading to local or regional anoxic conditions, salinization, or cyanobacterial blooms (Reid et al., 2019; Cantonati et al., 2020). These effects are likely to be accentuated in temporary wetlands where shallow depths may allow a more rapid response to extreme heat events (Boix et al., 2020).

Our study suggests that global warming could trigger complex diversity changes in wetlands, depending on the wetland type, the geographical region, and the relationship with precipitation regimes. Across wetlands under cool or mild temperature summers, we detected a positive relationship between maximum temperature and diversity metrics, suggesting that diversity in these habitats is constrained by low temperatures (e.g., Stenert et al., 2020). However, in temporary wetlands where summers were hot, richness declined (although beta diversity turnover increased because they hosted some macroinvertebrate specialists; e.g., anostracan crustaceans). We acknowledge a lack of data from tropical depressional wetlands, which could bias some of our conclusions. However, as maximum temperature was consistently a very strong driver of macroinvertebrate diversity across the wetland types assessed, we believe our findings could be extrapolated to even warmer locations. Thus, as maximum temperatures continue to rise (NASA, 2021), we expect that macroinvertebrate biodiversity will be negatively affected across a range of wetlands types.

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

	Temporary wetlands	Permanent wetlands
Variables importance		
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
GDM summary		
Model deviance	12,137	3880
Percent deviance explained	15.58	22.42
Model p-value	0.000	0.000

4.2. Precipitation seasonality as a secondary control of wetland macroinvertebrate diversity

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

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

4.3. Linking climate change and wetland diversity

Surprisingly, the categorization of wetlands according to water permanency was not a major driver of macroinvertebrate diversity (see Fig. S5, Tables S5-S7). Permanent wetlands supported only modestly higher family richness than temporary wetlands, and beta diversity was similar in both

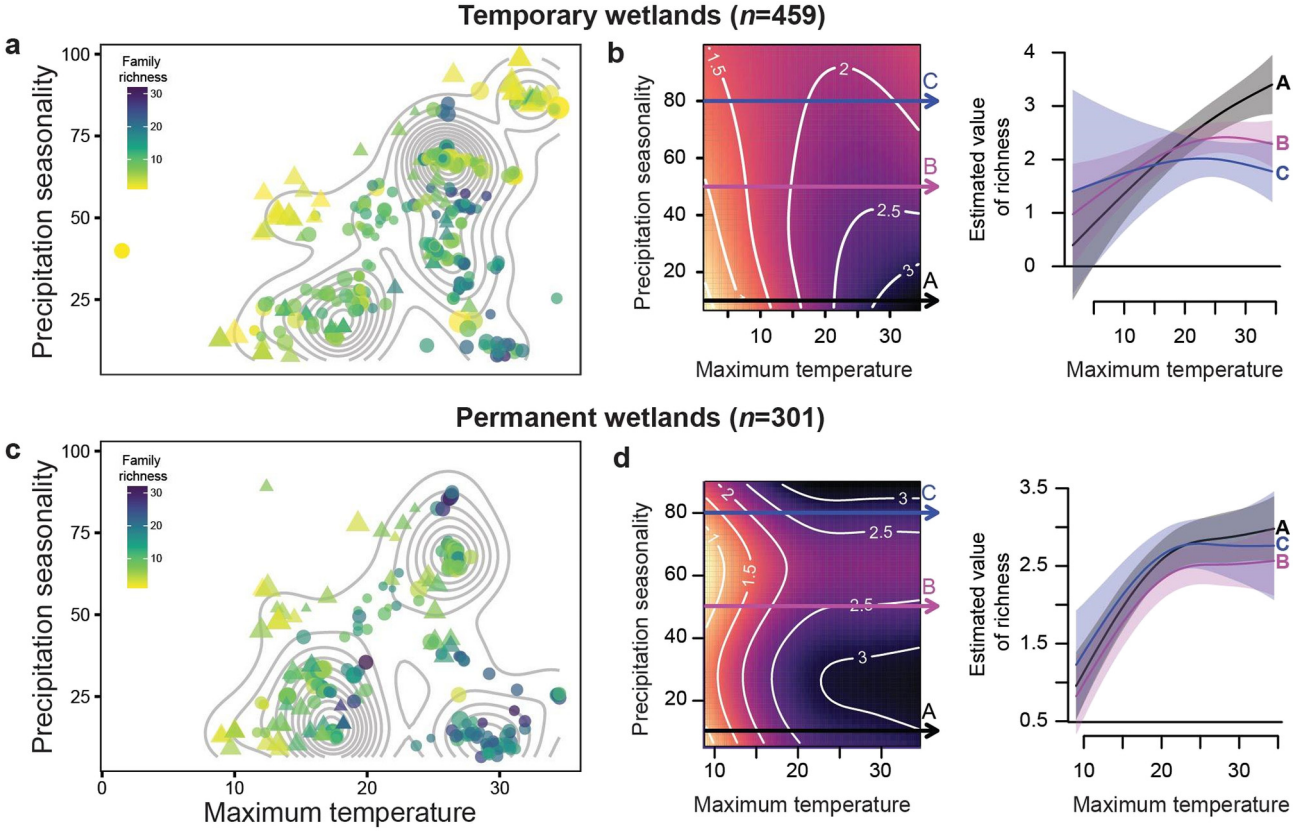

Fig. 3. Interactions between maximum temperature and precipitation seasonality. (a, c) Density distribution (grey lines) of wetland types (circles = non-montane wetlands, triangles = montane wetlands) and their macroinvertebrate family richness (color gradient) and local contribution to beta diversity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

wetland types. However, we found that regions with high precipitation seasonality and warm conditions supported mostly temporary wetlands, which had unique macroinvertebrate assemblages (Fig. 4a). Because evapotranspiration is typically the largest cause of water loss from precipitation-based depressional wetlands (some montane wetlands excepted), permanent wetlands in arid regions like California (US), Mendoza (Argentina), and the Mediterranean are rare (Kneitel, 2016; Boix et al., 2020). The recently published global distribution of non-perennial rivers and streams supports our findings, showing that permanent freshwaters are quite rare in arid regions (Messager et al., 2021). We recognize that our findings could be biased due to the distribution of study wetlands (and regions), but the inclusion of 22 locations across seven continents represents significant scope (and many landscapes of the world lack depressional wetlands of any kind; Jackson et al., 2014).

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

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

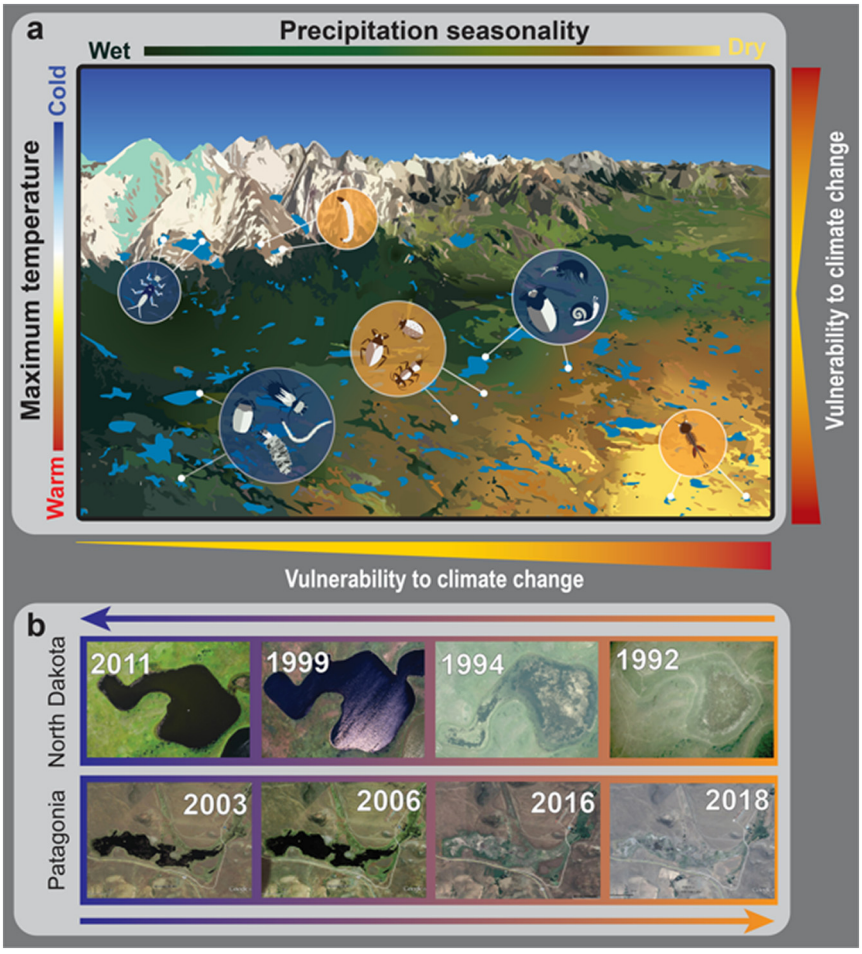

Fig. 4. Summary of the main results. (a) Hypothetical distribution of depressional wetlands across global maximum temperature and precipitation seasonality. The maximum temperature could be interpreted as an elevational gradient (i.e., the coldest wetlands would be those located at the highest elevations)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

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

Data availability

The R code and data used in this publication can be downloaded from figshare (https://figshare.com/s/7c1a13466f8857f4b4bd). U.S. Federally funded data generated during this study are available as a USGS data release (Mushet et al., 2017) and Appendix 5 in Mushet et al. (2015).

CRediT authorship contribution statement

LBE, MGG, CS, KM, HSG, LM, MMP and DPB conceived the manuscript. LBE and DPB, assembled the team and gathered the data. LBE, MGG and EAW-S performed the analyses. LBE, MGG and DPB drafted the manuscript. All authors contributed with data and edited the manuscript.

Declaration of competing interest

We have no conflicts of interest to disclose.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.153052.

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