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RESEARCH ARTICLE

A global assessment of environmental and climate influences on wetland macroinvertebrate community structure and function

Luis B. Epele[1] | Emilio A. Williams-Subiza[1] | Matthew S. Bird[2] | Aurelie Boissezon[3] | Dani Boix[4] | Eliane Demierre[3] | Conor G. Fair[5] | Patricia E. García[6] | Stephanie Gascón[4] | Marta G. Grech[1] | Hamish S. Greig[7,8] | Michael Jeffries[9] | Jamie M. Kneitel[10] | Olga Loskutova[11] | Leonardo Maltchik[12] | Luz M. Manzo[1] | Gabriela Mataloni[13] | Kyle McLean[14] | Musa C. Mlambo[15,16] | Beat Oertli[3] | Mateus Marques Pires[17] | Jordi Sala[4] | Erica E. Scheibler[18] | Cristina Stenert[12] | Haitao Wu[19] | Scott A. Wissinger[8,20,21,†] | Darold P. Batzer[5]

Correspondence
Luis B. Epele, Centro de Investigación Esquel de Montaña y Estepa Patagónica (CONICET-UNPSJB), Roca 780, Esquel, Chubut, Argentina.
Email: luisbepele@comahue-conicet.gob.ar

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Abstract

Estimating organisms' responses to environmental variables and taxon associations across broad spatial scales is vital for predicting their responses to climate change. Macroinvertebrates play a major role in wetland processes, but studies simultaneously exploring both community structure and community trait responses to environmental gradients are still lacking. We compiled a global dataset (six continents) from 756 depressional wetlands, including the occurrence of 96 macroinvertebrate families, their phylogenetic tree, and 19 biological traits. Using Bayesian hierarchical joint species distribution models (JSDMs), we estimated macroinvertebrate associations and compared the influences of local and climatic predictors on both individual macroinvertebrate families and their traits. While macroinvertebrate families were mainly related to broad-scale factors (maximum temperature and precipitation seasonality), macroinvertebrate traits were strongly related to local wetland hydroperiod. Interestingly, macroinvertebrate families and traits both showed positive and negative associations to the same environmental variables. As expected, many macroinvertebrate family occurrences were positively associated with temperature, but a few showed the opposite pattern and were found in cooler or montane regions. We also found that wetland macroinvertebrate communities would likely be affected by changing climates through alterations in traits related to precipitation seasonality, temperature seasonality, and wetland area. Temperature increases may negatively affect collector and shredder functional groups. A decrease in precipitation could lead to reductions in wetland area benefiting drought-tolerant macroinvertebrates, but it may negatively affect macroinvertebrates lacking those adaptations. Wetland

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[†] Deceased.

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processes may be compromised through broad-scale environmental changes altering macroinvertebrate family distributions and local hydroperiod shifts altering organism traits. Our complementary family-based and trait-based approaches elucidate the complex effects that climate change may produce on wetland ecosystems.

KEYWORDS
biotic associations, climate change, depressional wetlands, ecosystem change, freshwater biodiversity, joint species distribution models (JSDMs), trait-based model, wetland processes

1 | INTRODUCTION

Climate change is already altering natural systems all around the globe, and its effects on freshwater biodiversity are beginning to be documented (Balik et al., 2023; Reid et al., 2019; Rosset et al., 2010; Sabater et al., 2023; Stewart et al., 2013; Timoner et al., 2021; Woodward et al., 2010). For example, anomalously long dry periods can significantly modify assemblage composition and metacommunity dynamics in depressional wetlands, ponds, and other small lentic habitats (e.g., Euliss et al., 2004; Sim et al., 2013; Wellborn et al., 1996). Climatic factors are the dominant drivers of freshwater biodiversity at continental scales (Dodds et al., 2019; Epele et al., 2022; García-Girón et al., 2020; Ruhí et al., 2013), while local factors (e.g., water chemistry or hydroperiod length) have more relevance at smaller spatial scales (e.g., Batzer et al., 2004; Bird & Day, 2016; Heino et al., 2017; Hill et al., 2019; Knauth et al., 2019; McLean et al., 2021; Pires, Maltchik, et al., 2021). Anticipating how climate change affects aquatic communities will benefit from understanding interactions among current environmental gradients (i.e., water quality, topography, bioregion), the duration and frequency of water permanence (i.e., hydroperiod), and the traits of resident taxa (Dodds et al., 2019; Ruhí et al., 2013).

The current global context of changing temperatures and increasing water scarcity requires an understanding of the biodiversity responses (i.e., taxa) and adaptations (e.g., taxa traits) of taxa to the environment at different scales (Bellard et al., 2012; Calapez et al., 2018; Weiskopf et al., 2020). Community dynamics across different spatial scales have been traditionally studied through taxonomic-based approaches (i.e., community structure and composition) (McGill, 2019; Rapacciuolo & Blois, 2019). Recently, trait-based approaches have been adopted by ecologists, as they often help to elucidate the mechanistic basis of taxon–environment relationships (e.g., Bonada et al., 2007; Verberk et al., 2013) and overcome differences in taxa occurrence across coarse biogeographic scales (e.g., the differences in macroinvertebrate families or genera between southern and northern hemisphere wetlands; Ruhí et al., 2013). This is because it is the characteristics of organisms (i.e., traits) that determine their response to environmental change, not their taxonomic identity (e.g., Cunillera-Montcusí et al., 2020; Green et al., 2022; Menezes et al., 2010; Mouillot et al., 2013).

Joint species distribution models (JSDMs) have emerged as a valuable tool for effectively capturing the inherent complexity in taxon responses to changing environments (Norberg et al., 2019). These models can simultaneously incorporate organismal data (occurrence or abundance, traits, and phylogenetic relationships), environmental factors, and random effects to unravel environment–biodiversity relationships (Guzman et al., 2022; Leibold et al., 2022; Tikhonov et al., 2020), which enables the exploration of drivers of biological communities across different ecosystems and spatio-temporal scales (Ovaskainen et al., 2017, 2019). Several novel questions in wetland macroinvertebrate ecology could be answered using JDSMs. For example, these models can be used to determine inter-taxon interactions (i.e., species-to-species or family-to-family associations). This nuanced level of analysis helps in setting a base layer of knowledge that could be used to compare current wetland macroinvertebrate co-occurrence patterns with future associations that might be altered due to global environmental changes. Furthermore, exploring macroinvertebrate responses to environmental gradients by combining both taxon-based and trait-based approaches should improve our understanding of their influence on macroinvertebrate structure and function at a global scale.

We gathered a dataset of macroinvertebrate taxa (96 families) collected across the globe from 756 depressional wetlands (upland-embedded wetlands, sensu Smith et al., 1995), categorized 19 biological traits, measured a set of environmental factors, and modeled the data using the JSDMs workflow proposed in Ovaskainen and Abrego (2020; Figure 1). The aim of our study is to evaluate global-scale family-to-family macroinvertebrate associations at different hierarchical spatial scales and test macroinvertebrate community responses to environmental gradients using both taxonomy-based and trait-based data. We hypothesized that (H_1) the number of detectable family-to-family associations will be greater at the local scale than at larger spatial scales because interactions among individuals typically play out within individual wetlands. We also hypothesized that (H_2) environmental factors will exert contrasting effects on the macroinvertebrate community when comparing taxonomy-based (each family) versus trait-based responses because many traits operate across multiple families. Moreover, we explored the potential phylogenetic-dependent responses to local and climatic environmental factors, hypothesizing that (H_3) phylogenetically closer families will respond similarly to the environmental factors because of evolved, shared affinities. Finally, we examined the predicted responses of macroinvertebrate traits to environmental gradients to understand the potential

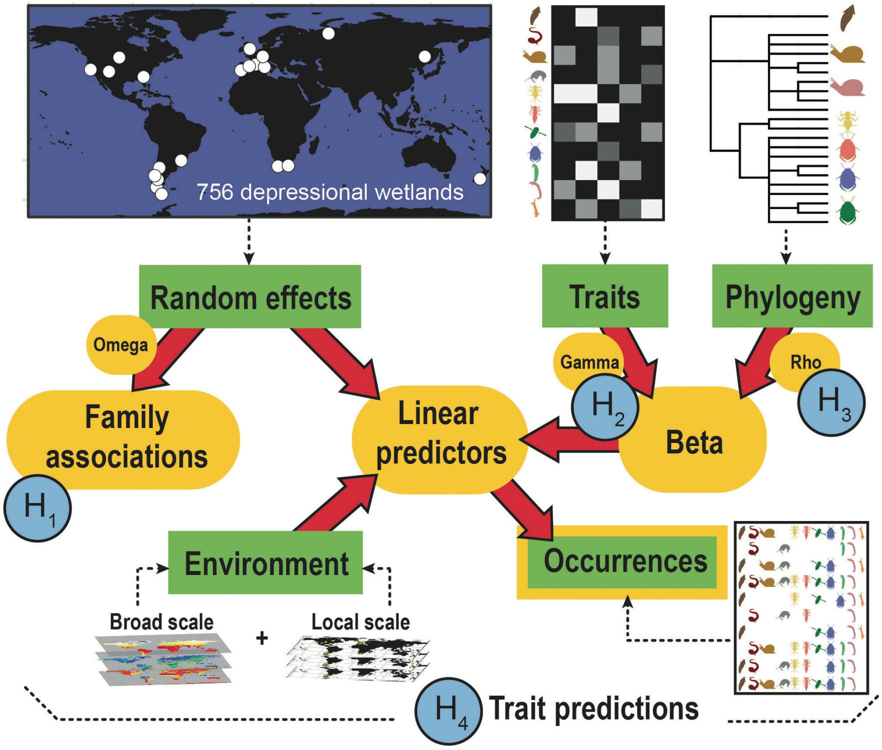


FIGURE 1 Joint species distribution model (JSDM) simplified workflow representation for global assessment of environmental and climate influences on wetland macroinvertebrate community structure and function (adapted from Ovaskainen & Abrego, 2020). Input data are represented with green squares, including a map showing the centroid of each study region (21 regions that included 756 depressional wetlands), environmental variables, and macroinvertebrates family measures (occurrence of 96 families, 19 traits, and the phylogenetic tree). Model outputs and parameters are represented in yellow large and small ellipses, respectively. Light blue circles are used to represent our four hypotheses. Black dotted arrows are used to connect data input representations with their corresponding concept. Red arrows are used to represent the flow direction of the JSDM. See that macroinvertebrate occurrence is represented with both yellow and green colors, since it can be both input data (i.e., raw macroinvertebrate occurrences) and output data (i.e., modeled macroinvertebrate occurrence after fitting the JSDM).

effects of current changing environmental conditions, hypothesizing that (H_4) predicted trait variation will depend primarily on temperature and precipitation, two climatic factors likely to be altered due to current climate change.

2 | MATERIALS AND METHODS

2.1 | Macroinvertebrate data

Using data from our own field surveys, we compiled a dataset of macroinvertebrate communities from 756 pristine or minimally impacted depressional wetlands (field methods and sampling design are explained in Appendix S1). Our records spanned six continents (excluding Antarctica) and covered a wide range of latitudinal, elevational, and climatic variation (Figure 1, Table S1). Most macroinvertebrate taxa were identified to family level, with the exception of a few taxonomically difficult groups that were identified to sub-class or order (Table S2). As families tend to occur across broad (intercontinental) scales, family-level data allow the analysis of global-scale biodiversity patterns, which would be otherwise impossible at infra-family levels given that most genera and species are typically restricted to small geographic areas. In addition, family-level data are sufficient to describe broad-scale functional diversity and trait composition patterns in macroinvertebrate communities, as reported in previous studies (e.g., Beketov et al., 2009; Gayraud et al., 2003; Sotomayor et al., 2022). After removing families with fewer than five records, a total of 96 families (36 orders, 8 classes, and 5 phyla) were retained for statistical analysis (Table S2). Macroinvertebrate abundances (when available) were converted to occurrence data (i.e., presence–absence) because it removes noise arising from differences in sampling techniques among the different surveys, is useful for datasets covering wide geographic ranges and across broad climatic gradients, and is often used in biodiversity studies (Brito et al., 2018; Carneiro et al., 2010; Mueller et al., 2013; Pires, Grech, et al., 2021).

2.2 | Trait data

Biological traits are intrinsic characteristics of species that influence their fitness (de Bello et al., 2021). Related traits are typically categorized into *grouping features*, as proposed by Schmera et al. (2015). We considered six biological grouping features with

TABLE 1 List of the six grouping features (i.e., group of related traits), 19 traits, and one wetland macroinvertebrate family as example (Merritt et al., 2019; Thorp et al., 2010). For more information, see Appendix S1 and Table S3.

Grouping feature	Trait	Example
Functional feeding group	Collector	Chironomidae
	Scraper	Lymnaeidae
	Shredder	Limnephilidae
	Predator	Aeshnidae
Respiration strategy	Water oxygen (gills–integument)	Chirocephalidae
	Atmospheric oxygen (siphon–air bubbles–plastron–plant aerenchyma)	Dytiscidae
Aquatic stage	Immature	Coenagrionidae
	Adult	Hirudinidae
Drought tolerance	Intolerant	Baetidae
	Resistant eggs or cysts	Streptocephalidae
	Diapause	Naididae
	Drought avoider	Notonectidae
Dispersal ability	Flightless	Planorbidae
	Weak flyer	Caenidae
	Strong flyer	Corixidae
Body size	Very small (<0.5 cm)	Lynceidae
	Small (0.5–1 cm)	Haliplidae
	Medium (1–2 cm)	Libellulidae
	Large (>2 cm)	Belostomatidae

a total of 19 different traits (Table 1; see also Appendix S2 for an explanation behind the selection of each grouping feature). Some of the selected features describe macroinvertebrate taxa profiles in terms of resilience or resistance ability (e.g., drought tolerance, dispersal ability), whereas others, like functional feeding groups and body size, potentially reflect important ecosystem processes (e.g., nutrient cycling, biomass accumulation). We described the affinity of each taxon for each trait using a fuzzy coding approach (Chevenet et al., 1994). The score for each taxon belonging to each trait ranged from 0 to 3, with 0 indicating no affinity with the trait, 1 indicating weak affinity, 2 indicating moderately strong affinity, and 3 indicating strong affinity (Table S3). All traits were allowed to co-occur (e.g., a certain family may include both predator and collector species). Many available macroinvertebrate trait databases primarily describe riverine macroinvertebrates (e.g., Merritt et al., 2019; Pennak, 1989; Poff, 1997; Tachet et al., 2010; Thorp et al., 2010), and thus do not acknowledge some unique wetland characteristics. This may result in categorizations of limited discriminatory value for wetlands. We therefore adapted the available trait data, using literature and our own observations, to reflect the unique ecological constraints known to affect macroinvertebrate taxa in this type of environment (e.g., varying wet–dry cycles, periodically low dissolved oxygen levels, different degrees of habitat isolation, etc.) (Batzer & Boix, 2016). For example, we split aerial colonizers into weak and strong flyers because this difference might affect assemblages able to access geographically isolated wetlands (Borthagaray et al., 2015; Cunillera-Montcusí et al., 2020; Heino, 2013).

2.3 | Phylogenetic tree

We used taxonomy identities based on Linnaean hierarchy as a surrogate for true phylogenetic information that is not available for our data (Ovaskainen & Abrego, 2020). We obtained the phylogenetic tree using the R-package *ape* (Paradis & Schliep, 2019). The phylogenetic tree was based on four taxonomic categories (i.e., family, order, class, and phylum; Table S2), setting the same distance for each branch of the tree.

2.4 | Environmental variables

To model macroinvertebrates families and trait distributions, we selected a set of environmental covariates known to influence freshwater macroinvertebrate occurrences (e.g., Dodds et al., 2019; Epele et al., 2022), including wetland geographical and morphological features such as area and elevation, as well as hydroperiod, climate, and a composite measure of different human pressures.

Wetland area (m^2) and elevation (meters above sea level, m a.s.l.) were measured in situ in most cases, but also via satellite imaging and digital elevation models. We log transformed wetland area to achieve a more homogeneous distribution. We also classified study sites into *montane* and *non-montane* based on whether they were located above or below the tree line (Wissinger et al., 2016). We also classified sites into two groups according to their hydroperiod: *permanent wetlands* were those that held surface water continuously during both the sampling year and the previous one, while *temporary wetlands* were those that dried during either the sampling year or the previous one.

We obtained mean annual temperature, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, and precipitation seasonality (~1 km^2 resolution) from the WorldClim 2.1 database (Fick & Hijmans, 2017) based on the 5-year data leading up to each sampling event. Temperature seasonality expressed the amount of temperature variation over five averaged years based on the SD (variation) of monthly temperature averages (O'Donnell & Ignizio, 2012). Precipitation seasonality accounted for the variation in monthly precipitation across 5 years. This index is the ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation and is expressed as a percentage (O'Donnell & Ignizio, 2012). As a measure of the climatic aridity of each wetland, we used the aridity index at ~1 km^2 resolution, available from the Consortium for Spatial Information's Global Potential Evapotranspiration and Global Aridity Index dataset (Trabucco & Zomer, 2018). As low values of the aridity index indicate arid conditions, we used the inverse in order to assign higher analytical values to wetlands located in more arid areas.

Finally, as a generic measure of the level of human disturbance, we used the 2009 Human Footprint (Venter et al., 2018) at ~1 km^2 resolution, available from the National Aeronautics and Space Administration's (NASA's) Socioeconomic Data and Applications Center. This measure is based on data of eight different human pressures (e.g., built environments, crop and pasture lands, electric infrastructure), which individually have been shown to significantly affect natural systems (e.g., Biasotto & Kindel, 2018; Trombulak & Frissell, 2000). It ranges from 0 to 50, with higher values corresponding to areas with higher anthropogenic impact.

2.5 | Statistical analyses

To test our four hypotheses, we applied Bayesian JSDMs using the *Hmsc* R-package (Tikhonov et al., 2022), jointly estimating the responses of macroinvertebrate families to the environment as a function of their traits and phylogeny, and simultaneously estimating associations between taxa (Ovaskainen & Abrego, 2020; Tikhonov et al., 2020). We modeled the occupancy of 96 families using a "probit" model including family traits, phylogenetic relationships, environmental predictors, and two random effects (i.e., wetland site and region, which account for the two spatial scales considered in our study). Random effects reflected the hierarchical spatial scheme as wetland sites (756) were nested within regions (21). Both hierarchical levels (hereafter referred to as spatial scales) were modeled as categorical random effects.

We first used a nonparametric Spearman rank correlation among the nine continuous environmental variables (area, human footprint, aridity, and six WorldClim variables) to ensure that the selected variables did not contain redundant information. We eliminated three (i.e., minimum temperature of the coldest month, mean annual temperature, and annual precipitation) because they were correlated ($r > \pm .75$) with other variables (see Figure S1; R-package *corrplot*, Wei & Simko, 2021). Then, we ran a series of preliminary models to test different combinations of response variables and random effects. We compared the preliminary models' explanatory and predictive powers based on eightfold cross-validations (measured as both the area under the curve [AUC] and Tjur's R^2). We retained all fixed effects (two categorical and six continuous variables) in the best model (i.e., highest predictive power). The model was run assuming the default prior distributions, and we sampled the posterior distribution with four Markov Chain Monte Carlo (MCMC) chains of 375,000 iterations, out of which the first 125,000 were removed as burn-in and the remaining were thinned by 1000, yielding 1000 posterior samples in total (250 posterior samples per chain).

To detect family-to-family associations across spatial scales (H_1), we explored the omega parameter from the JSDM framework (Figure 1), which measures associations by using the covariance structure of the model's residuals (i.e., after accounting for the effect of the environmental variable in their occurrence; Ovaskainen & Abrego, 2020). We obtained a correlation matrix (family-to-family) showing those associations with at least 95% posterior probability across two hierarchical spatial scales (random levels).

To compare the effects of environmental variables on macroinvertebrate family occurrences and traits (H_2), we calculated the beta and gamma parameters from the fitted JSDM, respectively (Figure 1). The beta parameter reflects how environmental variables influence (positively, negatively, or no response) each family occurrence probability (here with at least 95% posterior probability; Ovaskainen & Abrego, 2020). We displayed trait–environment relationships, extracting the signs of gamma parameters (positive, negative, or no response) with at least 90% posterior probability (a 95% posterior probability would show only a few relationships). We also partitioned the explained variance of the fitted model to get the proportion explained by each environmental variable on families and traits (Ovaskainen & Abrego, 2020).

To test for a potential phylogenetic signal in macroinvertebrate family–environment relationships (H_3), we examined the rho parameter from the fitted JSDM. This parameter measures the phylogenetic signal in family–environmental relationships after accounting for the measured traits and varies from 0 (*no measurable signal*) to 1 (*strong phylogenetic signal*; Ovaskainen & Abrego, 2020).

Finally, we explored the predicted trait values across the six numerical environmental gradients (H_4). We only explored relationships with a gamma posterior support of at least 90% (Figure 1). For selected relationships, we constructed environmental gradients and then predicted trait responses over them. We only kept those predicted responses that exhibited a predicted posterior support >0.8. Meaning that minimum trait values (from 0 to 3) would be lower or higher than the maximum with a probability of at least 80%.

We conducted all analyses using R software version 4.3.1 (R Core Team, 2023). Raw data and R code are available in figshare (https://figshare.com/s/54714da7a776820c31d2).

3 | RESULTS

The fitted JSDM convergence was satisfactory, as indicated by the mean potential scale reduction factors (psrf <1.15; Table S4). The mean explanatory power of the model showed a good fit to the data, with a mean AUC value of .95 and a mean Tjur's R^2 value of .33. The mean predictive power of both models (based on the eightfold cross-validation) was .87 and .22 for AUC and Tjur's R^2, respectively.

3.1 | Family-to-family associations

We found a relatively large number of family residual co-occurrences with a ≥95% posterior probability (27.2% and 18.1% from a total of 4512 possible pairwise co-occurrences, for wetland and regional scales, respectively; Figure 2 and Figure S2), which displayed scale-dependent patterns. At the wetland scale, most detected co-occurrences were positive (95.6%; ≥95% posterior probability), with only Crangonyctidae, Streptocephalidae, and Platyhelminthes displaying negative associations with other macroinvertebrate families (Figure S2). However, we found a lower proportion (68.7%) of positive associations (≥95% posterior probability) among regional spatial-scale associations. At a regional scale, Lumbriculidae, Ceratopogonidae, and Hydrophilidae were frequently positively associated with other macroinvertebrate families, while Stratiomyidae, Veliidae, and Muscidae showed a negative association with most other families.

3.2 | Family–environment relationships

Among fixed effects, the variance partitioning analysis of the JSDM showed that the most important variables were maximum temperature (10.1%), followed by precipitation seasonality and temperature seasonality (8.8%, respectively). Overall, the human footprint and the wetland hydroperiod were the least important predictors (3% and 2.4%, respectively). Of the explained variance, about half was attributed to the scale-structured random effects of region and wetland (41.4% and 11.7%, respectively; Figure S3).

When we analyzed each macroinvertebrate family response to environmental factors (beta parameter; Figure 1), we found that they were mainly related with maximum temperature and precipitation seasonality (47 and 45 families, respectively; ≥95% posterior probability), followed by temperature seasonality (41 families) (Figure 3a and Figure S4). Family responses to maximum temperature were mostly positive (87.5%), but six families were negatively associated with that factor (Gammaridae, Hydridae, Limnephilidae, Lumbricidae, Lumbriculidae, Polycentropodidae, Figure S4). In contrast, only one family (Notonectidae) was positively related with precipitation seasonality (Figure S4).

3.3 | Trait–environment relationships

Interestingly, trait–environment relationship patterns differed from those identified for family–environment relationships (Figure 3b and Figure S4). We found that eight traits were related to temporary wetlands with a posterior probability ≥90%, including positive (e.g., drought-resistant eggs or cysts and atmospheric respiration traits) and negative relationships (e.g., drought avoider and aquatic immature traits). Precipitation seasonality, wetland area, and montane exhibited relations with four traits each, but the sign of the trait–environment relations contrasted with family–environment relations for the same environmental parameters (e.g., precipitation seasonality was negatively related with families and positively with traits).

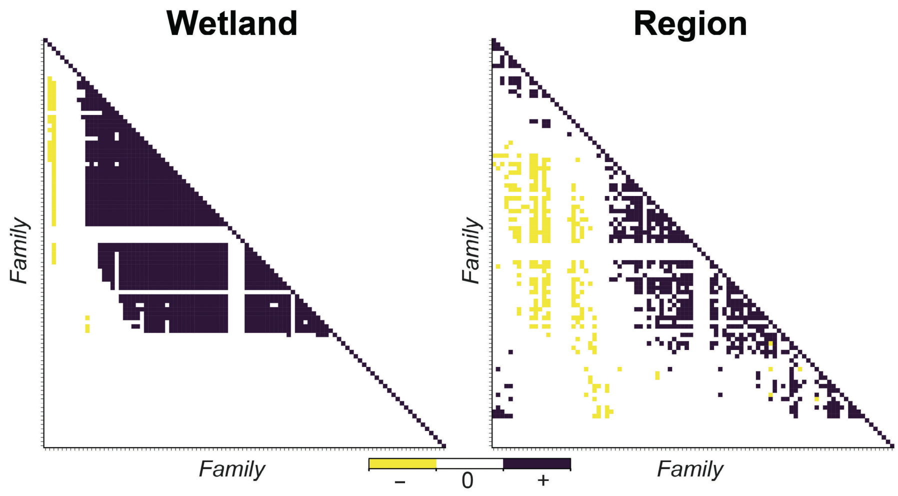
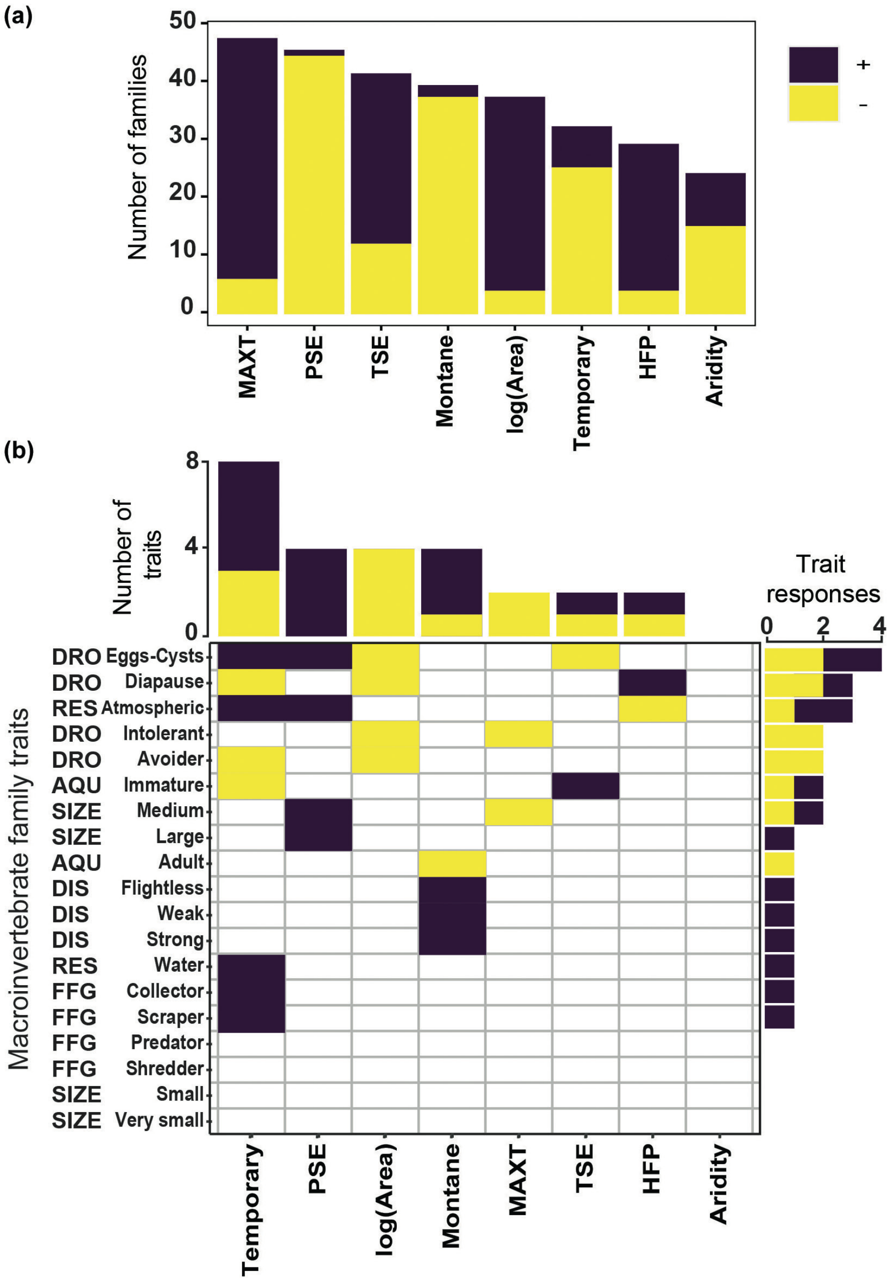


FIGURE 2 Macroinvertebrate family-to-family associations across two hierarchical spatial scales (i.e., wetland and region), after accounting for their environmental constraints. Pairs of families illustrated by violet and yellow show positive and negative associations, respectively, with statistical support of ≥95% posterior probability (see Figure S2 for macroinvertebrate family names). The Left and bottom ticks represent each wetland macroinvertebrate family (96 families in total). Each correlation matrix (left and right) is independently ordered to get correlated families closer together (positively or negatively; corrplot R-package option: AOE, angular order of the eigenvectors).

FIGURE 3 (a) Summary of the number of macroinvertebrate family responses to each predictor with ≥95% posterior probability. The colors indicate the responses that are estimated to be positive (violet) or negative (yellow). Variables in the *x*-axis are decreasingly ordered to express the number of families responding to each one. (b) Macroinvertebrate trait responses to the environmental predictors with a ≥90% posterior probability. The upper and right bars summarize the number of trait–environment relationships and the number of responses per trait, respectively. See that the *x*-axis variables are differently ordered from (a). Environmental variable abbreviations: MAXT, maximum temperature; PSE, precipitation seasonality; TSE, temperature seasonality; HFP, human footprint. Grouping feature abbreviations (see also Table S3): AQU, aquatic stage; DIS, dispersal ability; DRO, drought tolerance; FFG, functional feeding group; RES, respiration; SIZE, body size.



Furthermore, two of the main predictors of family occurrences (i.e., maximum temperature and temperature seasonality) were only associated with two traits each (Figure 3b). The drought resistance grouping feature included the most responsive macroinvertebrate traits to environmental variables, followed by respiration strategy and aquatic stage.

3.4 | Phylogenetic relationships

We found that related families (i.e., within the same order) did not show similar responses to environmental variables (Figure S4), reflected in the posterior mean of the phylogenetic correlation parameter rho (Figure 1) being only 0.09 (where 1 indicates the strongest possible phylogenetic signal).

3.5 | Predicted macroinvertebrate trait–environment relationships

We also found five traits whose predicted responses to environmental gradients were strong (predicted probability ≥80%; Figure 4). Drought-associated traits (see Table 1) were the most responsive ones, including the three environmental predictors. The drought-resistant eggs–cysts trait was the most responsive trait to predicted environmental gradients, being positively related with precipitation

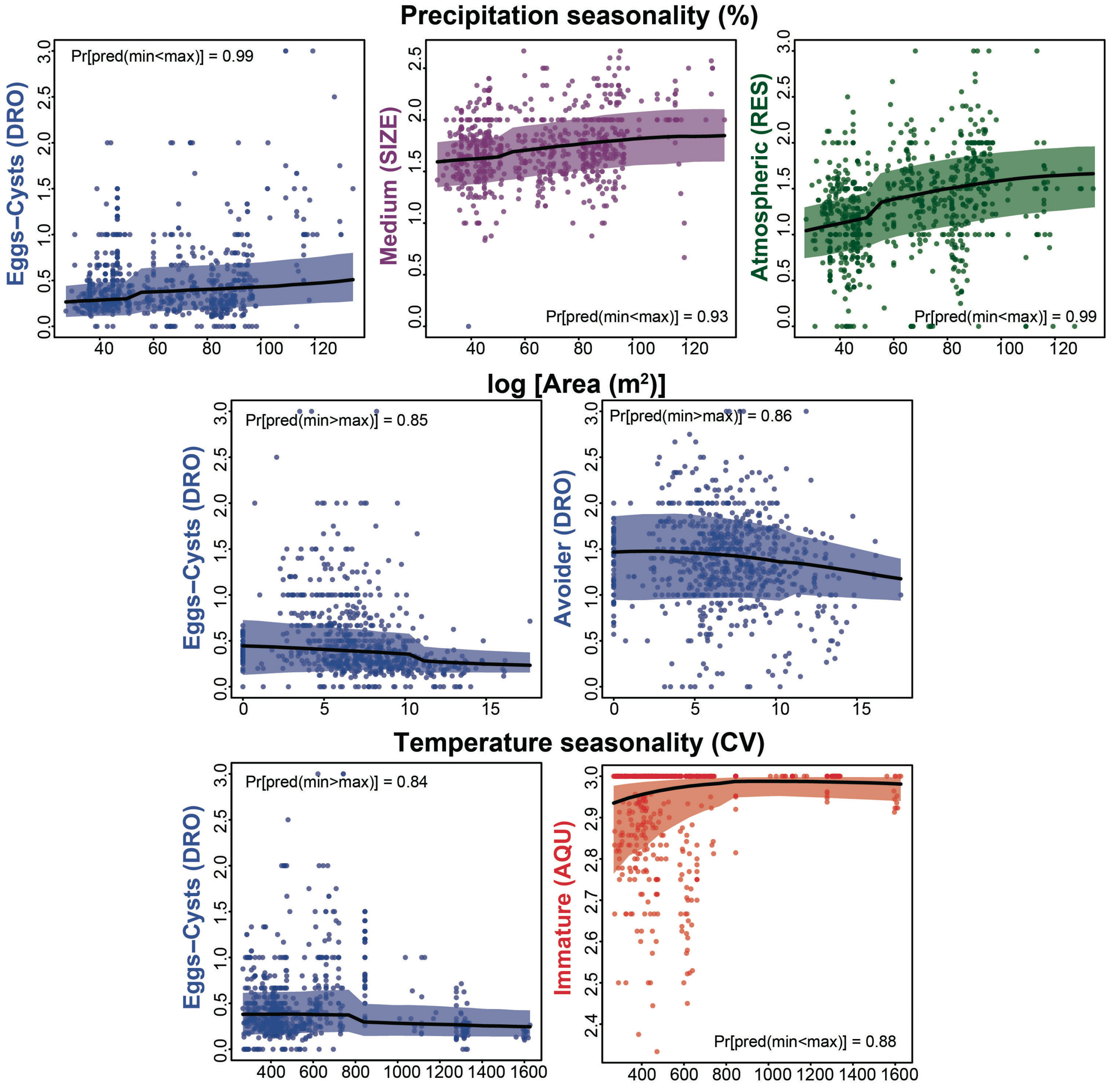


FIGURE 4 Predicted effects of environmental variables on macroinvertebrate traits with a predicted posterior support probability (Pr) >0.80 (minimum different from maximum across the environmental gradient). Inside each sub-figure panel is the posterior support of the predicted change from minimum to maximum across environmental variables. The solid lines show the posterior median, and the shaded areas represent 90% credible intervals. The colors on the shaded areas are used for different grouping features (blue: DRO, drought tolerance; purple: SIZE, body size; green: RES, respiration strategy; red: AQU, aquatic stage). The small dots show individual predicted trait observations.

seasonality and negatively with wetland area and temperature seasonality (Figures 3b and 4). Macroinvertebrates that obtained oxygen from the atmosphere and those with medium sizes were also positively related with precipitation seasonality. The drought avoidance trait was more likely to occur in wetlands with smaller areas. Meanwhile, macroinvertebrates whose immatures are obligate aquatic were more likely to occur in regions with higher temperature seasonality (Figure 4).

4 | DISCUSSION

In line with a previous global-scale study on wetland macroinvertebrates (Epele et al., 2022), our taxonomic assessment suggested that among the modeled environmental variables, maximum temperature and precipitation seasonality are the main influences on wetland macroinvertebrate community occurrence. However, our trait-based assessment suggested that trait-level responses were mainly affected by hydroperiod, precipitation seasonality, and wetland area. Combining taxonomy- and trait-based approaches through JSDM provides complementary insights into environment–macroinvertebrate relationships at a global scale.

In agreement with our first hypothesis, we detected a higher number of family-to-family associations at the local scale than at the regional scale, while controlling for environmental characteristics. This finding echoes a number of other studies that have documented that the spatial signature of biotic interactions should be most evident at small spatial scales and decline when assemblages are analyzed at coarser resolutions (e.g., König et al., 2021; Weigel et al., 2023). This hierarchical scale dependence would suggest a decrease in spatial connectivity, and biotic filtering (i.e., local associations) would lead to a stronger role of broad-scale environmental drivers. Unexpectedly, most family-to-family associations were positive at the wetland scale (i.e., where organisms directly interact), which complicates interpretation. Since only a few biotic interactions among macroinvertebrate taxa would be positive (i.e., mutualism, commensalism, indirect facilitation; Holomuzki et al., 2010), the positive relationships among taxa observed here may involve other unmeasured ecological processes such as shared habitat preferences, productivity–diversity (e.g., Chase & Ryberg, 2004), and diversity–invasibility relationships (Catford et al., 2022; Fridley et al., 2007; Stohlgren et al., 2003). As here, Riley et al. (2023) also found mostly positive associations among macroinvertebrates in a study of nine depressional wetlands (Georgia, USA), concluding that negative biotic interactions (e.g., predation, competition) were weak modulators in their system. This lack of evidence for negative species associations in local wetland communities may also reflect the macroinvertebrate focus of these datasets, as much evidence for negative interactions structuring species assemblages in wetlands is from systems where vertebrate top predators such as centrarchid or percid fishes or paedomorphic salamanders limit species distributions and/or modulate competitive interactions among invertebrate taxa (Wellborn et al., 1996; Wissinger, 1999; Wissinger et al., 2009). Thus, the trophic breadth and body size range of assemblages may be an important determinant of local assemblage composition.

In contrast to local wetlands, at the regional scale, we found a higher proportion of negative macroinvertebrate associations (4.4% vs. 31.3%, respectively). This suggests that, despite sharing similar ecological requirements, those families are co-occurring less frequently than would be expected by chance, which is expected because the natural ranges of a number of families do not overlap (e.g., Belostomatidae occurs in America, China, and South Africa, but not in Europe or New Zealand). Nevertheless, changing climates would lead to shifts in macroinvertebrate associations (e.g., families shifting their current distributions), which could feed back into their family occurrence patterns. Our results showed that many macroinvertebrates follow environmental variation; therefore, the prediction of their potential associations under different scenarios of environmental change could become an important tool to understand the effects of changing climates to wetland biodiversity.

We hypothesized that environmental variables would generate contrasting taxonomic-based and trait-based responses (H_2). Indeed, we found that broad-scale climatic variables drove taxonomy-based responses, while trait-based ones depended on local factors like hydroperiod. Similar taxonomic–environment relationships were anticipated by Epele et al. (2022), who reported that macroinvertebrate alpha and beta diversity in depressional wetlands respond to a continuum of temperature and precipitation seasonality at a global scale. However, many responses to environmental factors are likely taxon specific and that complexity would be obscured using diversity metrics (e.g., taxonomic richness). Here, we were able to disentangle the role of each environmental factor on individual macroinvertebrate families, finding positive and negative responses to environmental variables. For example, since macroinvertebrate metabolism regulation depends on climate temperature (Irlich et al., 2009), higher temperatures would trigger higher metabolism rates, leading to a high proportion of positive temperature–macroinvertebrate relationships, unless they are cold adapted. In fact, we detected six families negatively associated with warmer temperatures that would be interesting to track in future studies, comparing the potential effects of global warming.

We found that hydroperiod was a key environmental filter that operated on macroinvertebrate traits. Wetland hydroperiod may be a weak driver of macroinvertebrate communities across broad scales (Epele et al., 2022; Faustino de Queiroz et al., 2022; Oertli et al., 2002), but it may be a strong control at smaller spatial resolutions, such as among local wetlands that vary in hydroperiod (i.e., Boix et al., 2008; Sim et al., 2013). This may result because local adaptation occurs through behaviors, physiology, and life history parameters that are better captured using trait-based analyses (Green et al., 2022). Certainly, macroinvertebrates inhabiting temporary wetlands should be adapted to the harshness imposed by wetland desiccation (Batzer & Boix, 2016), which here was reflected by four grouping features (eight traits) being related to hydroperiod. Some of those traits reflect adaptations to temporary wetlands (e.g., drought tolerance strategies) that can trade-off with performance in more permanent wetlands, but others, like feeding strategies, have less obvious connections to hydroperiod. Collector and scraper traits were positively related with temporary wetlands, which could be related with the expected lower predation pressure than permanent wetlands (Wellborn et al., 1996), or perhaps the higher benthic primary productivity of shallower wetland basins. Nevertheless, our results indicate that changes in the time of water permanence would filter macroinvertebrate communities through their traits, potentially affecting wetland ecological processes such as litter decomposition (Wissinger et al., 2021) and food web dynamics (e.g., invertebrates serving as food resources for amphibians, fishes, and birds; Batzer & Wissinger, 1996).

Unexpectedly, our results indicated weak phylogenetic responses to environmental variation, and thus we reject our third hypothesis (H_3). The low phylogenetic signal may indicate that non-related families are exhibiting similar traits or adaptations for wetland environments. It is well known that many crustaceans tolerate desiccation and certain insect groups are well adapted for montane environments (e.g., Mani, 2013; Strachan et al., 2015; Williams, 2006), suggesting a phylogenetic signal in macroinvertebrate responses to the environment should exist. However, certain phylogenetically distant families appeared to proliferate under relatively harsh environmental conditions, like high precipitation seasonality (Notonectidae), montane conditions (Gerridae and Phryganeidae), and temporary hydroperiods (e.g., Asellidae, Ceratopogonidae, Hydraenidae, and Lumbriculidae, among others; Figure S4). These findings suggest that harsh wetland conditions (such as unpredictable desiccation periods) could produce strong natural selection that might lead to convergent trait evolution occurring over multiple, distant macroinvertebrate lineages.

Interestingly, trait responses to environmental conditions differed among variables that might be expected to exert similar effects on macroinvertebrate communities. For example, larger wetland areas are commonly associated with longer water permanence and thus should be positively inter-correlated (Wellborn et al., 1996). Indeed, as might be expected, we found that macroinvertebrates that avoid wetland dry periods (i.e., drought-avoiding trait) were less common in both temporary and smaller wetlands (Ebert & Balko, 1987; March & Bass, 1995; Spencer et al., 1999; Williams, 1996). However, highly drought-resistant macroinvertebrates (i.e., those producing resistant eggs or cysts) were more likely to be found in temporary wetlands but less likely to occur in small wetlands. Aridity was weakly related with both macroinvertebrate families and their traits. A plausible explanation would be that wetland macroinvertebrates are well adapted to historical patterns (Batzer et al., 2004) and thus no longer respond to pervasive conditions (i.e., aridity is a regional scale factor ecologically constant long before the Anthropocene). Organisms may be more affected by those variables likely to change across shorter time periods (i.e., variable patterns of precipitation triggering unexpected hydroperiod shifts). Although more investigation is required (i.e., through experimental study designs), we suggest that these unequal trait responses reflect the intrinsic complexity of wetland macroinvertebrate communities already well adapted to unpredictable environmental conditions (Batzer, 2013). But importantly, it appears that wetland macroinvertebrate responses to the environment differ at taxonomic and trait levels, and responses are also variable across environmental gradients. The integration of both taxonomic-based and trait-based approaches is likely a useful potential path to disentangle that complexity.

Our model suggested that responses of macroinvertebrate traits to environmental gradients are associated with precipitation seasonality and temperature seasonality as well as with wetland area, partially supporting our fourth hypothesis (H_4). Evaluating the predicted trait responses across the aforementioned environmental gradients at a global scale allowed us to better understand the potential effects of changing climates on wetland macroinvertebrates. Three traits were strongly and positively associated with precipitation seasonality, a variable that accounts for the predictability of rainfall events (i.e., high values indicate high temporal fluctuation in precipitation). Among those traits, drought-resistance eggs–cyst seemed like a strategy that would favor macroinvertebrates in those regions where water scarcity is expected due to changes in climate (i.e., higher precipitation seasonality). Further, severe droughts would lead to wetland area and hydroperiod reductions (e.g., Boix et al., 2020; Crego et al., 2013), favoring those macroinvertebrate families with drought tolerance strategies.

Climate change is producing more rapid increases in winter temperatures in comparison to those in summer (Osland et al., 2021; Seneviratne et al., 2021). Higher temperature seasonalities are found in regions with large temperature variations between winter and summer. Support for control of temperature seasonality on wetland invertebrates has been minimal (see Osland et al., 2021), perhaps because trait-based approaches are not widely used for wetland studies. However, Stenert et al. (2020) indirectly highlighted the role of temperature seasonality on wetland macroinvertebrates. They concluded that temperate zones (higher temperature seasonality) and sub-tropical climate zones in North and South America, which harbor unique macroinvertebrate assemblages, might become homogenized if temperatures shift to warmer conditions (i.e., reduction in the seasonality of temperature). Thus, the seasonality of temperate zones may decline, possibly triggering macroinvertebrate range shifts that would establish new assemblages at higher latitudes or altitudes (Balik et al., 2023; Epele et al., 2022; Shepard et al., 2021; Stenert et al., 2020).

5 | CONCLUSION

At a global scale, wetland macroinvertebrate families appear to be more influenced by environmental factors that vary across broad spatial scales, such as temperature and precipitation, while macroinvertebrate traits are more influenced by environmental factors that vary across small spatial scales, such as temporary versus permanent hydroperiod habitats. By including multiple metrics, JSDM also helped to improve our understanding of the potential effects of environmental changes on biological communities. We anticipate that changes in both macroinvertebrate assemblages and ecological processes will occur with a changing climate. Severe droughts becoming more common globally might benefit drought-adapted macroinvertebrates (i.e., macroinvertebrates with drought-resistance eggs–cysts) and organisms that can use oxygen from the atmosphere. Current climate warming could also trigger macroinvertebrate range shifts that would lead to new assemblages at higher latitudes or altitudes, altering biotic relations and wetland functioning (Balik et al., 2023; Epele et al., 2022; Shepard et al., 2021; Stenert et al., 2020). Our findings allow us to move forward in understanding wetland functioning at a global scale. Insights from our complementary family- and trait-based study echo many studies warning about the effects that climate change could soon produce in our world.

AUTHOR CONTRIBUTIONS

Luis B. Epele: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Emilio A. Williams-Subiza:** Investigation; visualization; writing – original draft; writing – review and editing. **Matthew S. Bird:** Investigation; writing – review and editing. **Aurelie Boissezon:** Investigation; writing – review and editing. **Dani Boix:** Investigation; writing – review and editing. **Eliane Demierre:** Investigation; writing – review and editing. **Conor G. Fair:** Resources; writing – review and editing. **Patricia E. García:** Investigation; writing – review and editing. **Stephanie Gascón:** Investigation; writing – review and editing. **Marta G. Grech:** Investigation; writing – review and editing. **Hamish S. Greig:** Investigation; writing – review and editing. **Michael Jeffries:** Investigation; writing – review and editing. **Jamie M. Kneitel:** Investigation; writing – review and editing. **Olga Loskutova:** Investigation; writing – review and editing. **Leonardo Maltchik:** Investigation; writing – review and editing. **Luz M. Manzo:** Investigation; writing – review and editing. **Gabriela Mataloni:** Investigation; writing – review and editing. **Kyle McLean:** Investigation; writing – review and editing. **Musa C. Mlambo:** Investigation; writing – review and editing. **Beat Oertli:** Investigation; writing – review and editing. **Mateus Marques Pires:** Investigation; writing – review and editing. **Jordi Sala:** Investigation; writing – review and editing. **Erica E. Scheibler:** Investigation; writing – review and editing. **Cristina Stenert:** Investigation; writing – review and editing. **Haitao Wu:** Investigation; writing – review and editing. **Scott A. Wissinger:** Investigation; methodology. **Darold P. Batzer:** Conceptualization; funding acquisition; investigation; resources; supervision; writing – original draft; writing – review and editing.

AFFILIATIONS

[1]Centro de Investigación Esquel de Montaña y Estepa Patagónica (CONICET-UNPSJB), Esquel, Chubut, Argentina
[2]Department of Zoology, University of Johannesburg, Auckland Park, South Africa
[3]University of Applied Sciences and Arts Western Switzerland, HEPIA, Geneva, Switzerland
[4]GRECO, Institute of Aquatic Ecology, University of Girona, Girona, Spain
[5]Department of Entomology, University of Georgia, Athens, Georgia, USA
[6]Grupo de Ecología de Sistemas Acuáticos a escala de Paisaje (GESAP) INIBIOMA, Universidad Nacional del Comahue, CONICET, San Carlos de Bariloche, Argentina
[7]School of Biology and Ecology, University of Maine, Orono, Maine, USA
[8]Rocky Mountain Biological Laboratory, Gothic, Colorado, USA
[9]Department of Geography and Environmental Sciences, Northumbria University, Newcastle upon Tyne, UK
[10]Department of Biological Sciences, California State University-Sacramento, Sacramento, California, USA
[11]Institute of Biology of Komi Scientific Centre of the Ural Branch of the Russian Academy of Sciences, Syktyvkar, Russia
[12]Programa de Pós-Graduação em Biologia de Ambientes Aquáticos Continentais, Universidade Federal do Rio Grande, FURG, Rio Grande, Brazil
[13]Instituto de Investigación e Ingeniería Ambiental -IIIA, UNSAM, CONICET, Buenos Aires, Argentina
[14]U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA
[15]Department of Freshwater Invertebrates, Albany Museum, Makhanda (Grahamstown), South Africa
[16]Department of Zoology and Entomology, Rhodes University, Makhanda (Grahamstown), South Africa
[17]Programa de Pós-graduação em Ambiente e Desenvolvimento, Universidade do Vale do Taquari (UNIVATES), Lajeado, Brazil
[18]Entomology Laboratory, IADIZA CCT Mendoza CONICET, National University of Cuyo, Mendoza, Argentina
[19]Key Laboratory of Wetland Ecology and Environment, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun, China
[20]Biology Department, Allegheny College, Meadville, Pennsylvania, USA
[21]Environmental Science Department, Allegheny College, Meadville, Pennsylvania, USA

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and the R code that support the findings of this study are openly available in figshare at https://figshare.com/s/54714da7a776820c31d2. U.S. Federally funded data generated during this study are available as a USGS data release at https://doi.org/10.5066/F7BK1B77 (Mushet et al., 2017) and a USGS Scientific Investigations Report at https://doi.org/10.3133/sir20155126 (Mushet et al., 2015, Appendix S5).

ORCID

Luis B. Epele https://orcid.org/0000-0001-9982-1201
Olga Loskutova https://orcid.org/0000-0002-9059-2745
Mateus Marques Pires https://orcid.org/0000-0002-5728-8733
Cristina Stenert https://orcid.org/0000-0002-9095-2018

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