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TOPICAL REVIEW

Oxygen is a better predictor of macroinvertebrate richness than temperature—a systematic review

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Abstract

Despite ongoing loss of diversity in freshwater ecosystems, and despite mitigation measures to halt this loss, it is still not clear what ecological drivers underlies lotic biodiversity. A complicating factor is that two of the main drivers, oxygen and temperature, are correlated, and hence studies towards drivers of lotic diversity are confounded. Here, we undertook a systematic review, consisting of both qualitative and quantitative analyses, to disentangle these two drivers. We accessed two literature repositories and assessed papers for eligibility using a set of predetermined criteria. For the qualitative part of this systematic review, we used results on patterns of taxonomic richness and multivariate ordination analyses to expose effects of temperature and dissolved oxygen concentration on biodiversity. For the meta-analysis, we could only use raw data of a few papers in generalized linear models. The qualitative analysis did not show strong consistent effects of either dissolved oxygen concentration or temperature on diversity. However, the meta-analysis showed that taxonomic richness is positively related with dissolved oxygen concentration. Inversely a negative correlation with temperature was found, but adding temperature to a model which already included dissolved oxygen content did not significantly improve the model. These results show the strength of a systematic review and meta-analysis over a conventional review without a meta-analysis; we found no pattern with the qualitative analysis, but a strong pattern with the quantitative analysis.

1. Introduction

Understanding the relative importance of temperature and dissolved oxygen for aquatic biodiversity is urgent, because human activities alter the abiotic conditions of aquatic systems worldwide. Many rivers are still threatened by organic pollution in the form of run-off fertilizers and pesticides from intensive agriculture (Foley *et al* 2005, Valle *et al* 2015), discharge from saw mills (Davies and Nelson 1994), paper pulp factories (Karrasch *et al* 2006), potato or cassava starch companies (Arimoro *et al* 2008), and urban sewage (Couceiro *et al* 2007, Wen *et al* 2017). Many developed countries manage to reduce the organic loading of freshwater systems with extensive water treatment facilities and regulations. Furthermore, organic loading is generally low in developing economies. Discharge into rivers is, however, less under control in countries like China, India and Brazil (the so-called newly-industrialized countries) (Wen *et al* 2017). Apart from the loading of rivers with organic material, the flow rates of many rivers are slowed down because of barriers to the water flow in the form of dams and barrages (Nilsson *et al* 2005), which can increase temperature (Kokavec *et al* 2018), decrease oxygen solubility (Verberk *et al* 2011), and further lower river dilution potential of organic pollutants (Wen *et al* 2017). Furthermore, climate change may add severity to these threats (Durance and Ormerod 2007, Allen *et al* 2010). To protect and restore lotic ecosystems (i.e. actively moving fresh water ecosystems) to the best extent, it is important to know how oxygen concentration (which is negatively affected by organic loads) and water temperature (which may increase due to climate change) influence macroinvertebrate biodiversity.

The effect of water temperature and oxygen concentration on macroinvertebrate diversity is worth investigating, because aquatic macroinvertebrates form a large and diverse taxonomic group of organisms with widely differing ecological needs and key roles in food webs (Rosenberg *et al* 1997, Rempel *et al* 2000). Many aquatic invertebrates are directly or indirectly affected by both variables and as such of importance for monitoring the effects of both climate change and of (organic) pollution. Because they are ectothermic organisms, the metabolism of invertebrates is directly affected by temperature (Van der Have and De Jong 1996, Have 2002, De Jong and Van der Have 2009, Verberk *et al* 2011). Also, most lotic macroinvertebrates are directly dependent on dissolved oxygen, as they frequently possess gills or other underwater respiratory systems (Verberk *et al* 2016). Other macroinvertebrates are not directly dependent on this dissolved oxygen for their respiration, because of specialized structures that allow them to breath or store oxygen from the water surface (Lock *et al* 2013). The former group would be expected to be more affected by lower dissolved oxygen concentrations than the latter (Lock *et al* 2013, Leiva *et al* 2019).

Dissolved oxygen concentration and water temperature are two closely related variables. It is well understood that higher water temperatures have a lower capacity for the uptake of dissolved oxygen (Verberk *et al* 2011). Dissolved oxygen concentration is however dependent on a variety of other factors, like: salinity, altitude, water flow, organic pollution and oxygen consumption by aquatic organisms (Verberk *et al* 2011). Furthermore, increased concentrations of raw organic material lead to a high oxygen demand by micro-organisms that break down these organic materials. This, in turn, lowers the oxygen concentration (Foley *et al* 2005).

Water temperature and dissolved oxygen concentration are often measured in studies into the effect of various environmental variables on the biodiversity of lotic macroinvertebrates. However, despite the great wealth of articles, clear consistent patterns between temperature or dissolved oxygen and macroinvertebrate biodiversity remain to be established. Many researches do not find a significant effect of either temperature or dissolved oxygen on biodiversity (e.g. Boon *et al* 2016, Reis *et al* 2017), whereas others find contrasting effects. For example, it was found that increased temperatures could reduce the number of rarer taxa (Durance and Ormerod 2007) and the diversity of specific functional groups such as 'shredders' (Salmah *et al* 2014). However, in another study the number of insect orders and families was found to be positively related to temperature (Jacobsen *et al* 1997). Results were mixed for oxygen concentration, with biodiversity found to be highest at high (e.g. Wittman *et al* 2013), intermediate (e.g. Docile *et al* 2016) and even at low levels of oxygen (e.g. Couceiro *et al* 2010). Also, in most statistical models, measurements of either dissolved oxygen or water temperature are merely treated as random factors, without further addressing their effects (e.g. Xu *et al* 2014, Valle *et al* 2015, Docile *et al* 2016). The only review that looks at the effects of various abiotic variables on lotic macroinvertebrate biodiversity is inconclusive on the effect of temperature, does not mention dissolved oxygen, and is already over 20 years old (Vinson and Hawkins 1998). Another review that specifically looks at the effect of dissolved oxygen on macroinvertebrate richness points to a positive relation between dissolved oxygen concentration and macroinvertebrate richness (Verberk *et al* 2011). However, the four data sets that were used in this review are all from studies performed in high altitudinal ranges in the Americas, which is too limiting a context to show worldwide patterns. Moreover, to date no comprehensive and systematic literature search has been performed.

For these reasons, we chose to perform a systematic review, including a meta-analysis, to examine whether and to what extent water temperature and dissolved oxygen concentration influence macroinvertebrate biodiversity. The quantitative part of a systematic review combines raw data of a multitude of articles, which allows for synthesizing a combined dataset with data on different geographical localities and contexts.

2. Methods

2.1. Protocol

The protocol for this systematic review is based on the PRISMA flow diagram (Moher *et al* 2009). All steps are elucidated below, but a summary of steps is presented in the decision tree (figure 1). First, (1) we chose search terms and inclusion and exclusion criteria. Thereafter, (2) we conducted an article search and vetting of abstracts on inclusion criteria, followed by (3) a further examination of the full-text articles to vet for inclusion of the paper based on the full set of inclusion and exclusion criteria. We judged papers that made it past these first steps as 'eligible, to be included in the qualitative and quantitative analysis of this systematic review'. However, (4) for the qualitative analysis, authors had to report effects of temperature and/or dissolved oxygen concentration on biodiversity using either taxonomic richness or multivariate ordination analyses. Also, (5) we screened these papers for the availability of data necessary for inclusion into the meta-analysis. Thus, certain papers were not useful for the qualitative analysis, but we could include them in our quantitative analysis. These authors did not report relevant information within the published version, but the data on which these were based were available in a way that allowed inclusion into the quantitative meta-analysis.

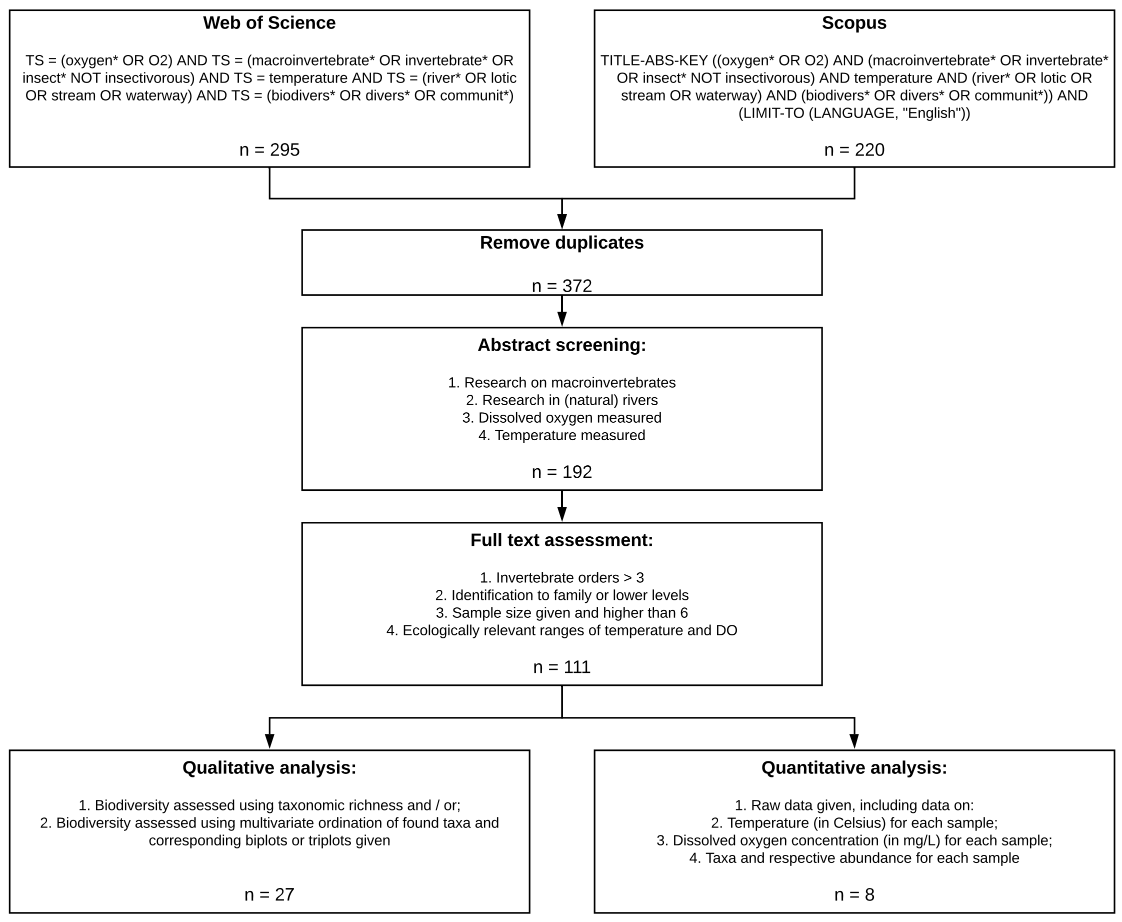

Figure 1. Decision tree of this systematic review and meta-analysis. Above are the two databases with their respective search terms and number of hits. The next step was the abstract screening, which is given with its four criteria. Thereafter, the full text assessment with four criteria that had to be met for both the quantitative and the qualitative analysis. At the bottom, the qualitative and quantitative analyses are given with their respective criteria.

2.2. Electronic search strategy

An iterative process of the selection of search terms preceded the eventual decisive set of search terms. We created search terms to include papers of greatest relevance, whilst retaining both a sufficient and workable number of total articles. We used two databases to garner papers (*viz.*, Web of Science and Scopus) to reduce bias created by selective results from either database. We created five clusters of search terms, which all had to be included in either the title or abstract of the paper. These clusters were: (1) oxygen, (2) temperature, (3) test-organism, (4) ecosystem, (5) biodiversity. Cluster (1) was defined by the following two search terms: 'oxygen*' and 'O2'; cluster (2) simply by the term 'temperature'; cluster (3) by 'macroinvertebrate*', 'invertebrate*' and 'insect*', but excluding 'insectivorous'; cluster (4) by the terms 'river*', 'lotic', 'stream' and 'waterway'; cluster (5) had the terms 'biodivers*', 'divers*' and 'communit*'. For Web of Science and Scopus we chose to search for inclusion of the terms in both title, abstract and keywords. Furthermore, in Scopus we chose to only include 'articles' (excluding reviews) and to only include articles in the English language. The exact search terms can be found in figure 1. We accessed both Web of Science and Scopus through the library service of Wageningen University.

We searched these databases from 31st of July to 2nd of August (Web of Science) and on the 3th of August (Scopus) 2019. This search resulted in a total of 295 articles on Web of Science and 220 articles on Scopus. We chose not to contact any authors to identify additional studies or to ask for supplementary material (available online at stacks.iop.org/ERL/16/023002/mmedia), because of unforeseeable biases as one may assume that not all authors would react to requests. We only judged published, peer-reviewed research articles, regardless of journal impact factors.

2.3. Abstract screening and removal of duplicates

We evaluated the abstracts to make sure the papers mentioned research in which samples of (macro)invertebrates were taken to assess biodiversity in rivers, and that also dissolved oxygen and temperature were measured along with these samples. When these four criteria—invertebrates, river, dissolved oxygen, temperature—were met, the article was included in the full-text screening step (figure 1).

We discarded any duplicate articles and took notice of the number of duplicates (figures 1 and A1).

2.4. Judging of full texts

Our judging of the full texts of research papers mainly hinged on the materials & methods and results sections of the papers. We avoided reading the introduction and discussion sections as much as possible to steer clear of the authors' interpretations of their results. We judged texts for several qualitative and operational criteria, and some information was noted. Firstly, we demanded that sampled invertebrates had to come from at least three different orders or higher taxonomic levels. In that way we ensured that observed patterns of differences in biodiversity could be established on a broad taxonomic scale. We recorded the orders (or higher taxonomic scale, whenever applicable) of the invertebrates reported in the research. Secondly, diversity had to have been assessed at family or lower taxonomic levels. We recorded the taxonomical levels assessed within the research. We made several exceptions on this rule for certain widely accepted groups like nematodes and oligochaetes, as these groups had often not been identified to family or lower taxonomic levels. This was mainly due to either the absence of taxonomic keys or the high expert knowledge necessary for these groups (Couceiro *et al* 2010, Rađa and Puljas 2010, Dohet *et al* 2015, Sabater *et al* 2016). Thirdly, at the minimum, diversity had to have been assessed using taxonomic richness, defined as the number of taxa found within a sample; or multivariate ordination had to be used to assess patterns in invertebrate assemblages and figures given. We judged this latter method as a good method to assess diversity, as it considers both taxonomic richness and abundance of separate taxa (Barrantes and Sandoval 2009). Fourthly, the sample size had to have been given and had to have been higher than six, to ensure adequate replication in each study. If one or more clearly defined treatments or groups had been compared in the published study, then each group should have had a sample size of at least six. We also recorded minimum and maximum temperatures as published in each selected study. Further, we found it essential for each study that we included in our systematic review that information on study location (country/climate/geographic details), research period and a clear description of the statistical methods that had been used to analyse the relation between richness and temperature and/or dissolved oxygen were reported. We used all articles that passed these four criteria for the qualitative analysis of this systematic review. However, in the next step we also judged these articles for their applicability in the quantitative meta-analysis (figure 1).

2.5. Qualitative analysis

We qualitatively assessed the effect of dissolved oxygen and temperature on biodiversity for separate studies in two ways. Firstly, we analysed the relation between richness and dissolved oxygen and temperature in articles that used taxonomic richness as a measure for biodiversity. We assessed if these studies mention correlations between the variables of interest and taxonomic richness and classified them based on their findings: 'positive' ($p < 0.05$), 'neutral' ($p > 0.05$) and 'negative' ($p < 0.05$), or 'not mentioned'.

However, taxonomic richness was regularly not used as a measure for diversity or authors did not elaborate on the effect of temperature or dissolved oxygen on diversity. Therefore, we also included articles in which the authors explained their results using multivariate constrained analyses (CCA and RDA) that combined data on taxa abundance with environmental parameters and presented biplots or triplots to visualise their results. For this purpose, we first drew a line extending the vector of a variable of interest (temperature or dissolved oxygen). Secondly, for CCA's, we drew lines perpendicular to the arrow at distances equal to component scores of 0.3 on the ordination axis, both on the positive and the negative side. Hereafter we classified taxa based on where they fell in relation to the two perpendicular lines: taxa abundant at high (outside the perpendicular lines, on the arrow side), intermediate (inside the perpendicular lines) and low (outside the perpendicular lines, opposite of the arrow side) values of the variable of interest. For RDA's, we drew lines at an angle of 45° on both sides of the line over the vector. Within RDA plots, correlation coefficients can be calculated using the cosine of the angle between these vectors, thus an angle of 45° equals roughly a correlation coefficient of 0.7. Taxa that fell within those lines on either of the side were considered as either positively or negatively correlated to the variable of interest, whereas taxa that fell outside of those lines were considered as having no significant correlation with the variable of interest.

Lastly, the number of species falling in the different categories were counted per study and analysed using chi-square tests. Diversity was considered to be correlated to the variable of interest when the chi-square analysis indicated significantly higher counts of taxa correlated with either high or low values of the variable of interest (for CCA). Diversity was also considered to be correlated to the variable of interest when the chi-square analysis indicated significantly higher counts of taxa correlated either positively or negatively with the variable (for RDA).

2.6. Quantitative meta-analysis

For the quantitative meta-analysis, we chose to only include articles that provided raw data on temperature, dissolved oxygen and taxonomic richness on each site. This data could have been included within the article or added as supplementary material. Taxonomic richness did not have to be given as such but could also be supplied in the form of extensive lists of the taxa found per site, or otherwise; as long as taxonomic richness could be derived from the data. For the meta-analysis, taxonomic richness was considered as the number of invertebrate families found within the research. Whenever data was on lower taxonomic levels, we deduced the family level. Furthermore, we only included articles in the quantitative meta-analysis when the broad group of macroinvertebrates was considered, and there was no preliminary selection on certain groups within the research (e.g. 'insects', 'crustaceans', 'non-insect invertebrates').

We used generalized linear models (GLM) with a Poisson distribution to analyse the data. Taxonomic richness was used as dependent variable; dissolved oxygen (in mg l^{-1}) and temperature (in °C) as quantitative variables; and a factor for 'study' as a categorical variable. We chose to add a variable for the specific study, or whenever applicable per group or treatment within a study, to account for context dependent variability within different studies. Also, we included the squares of both temperature and dissolved oxygen in the analyses, to test if these variables had a quadratic effect on taxonomic richness. Lastly, we investigated the interaction between temperature and oxygen. We tested all possible models using the above-mentioned variables and gathered corrected Akaike Information Criterion (AICc) values to find the best fitting models. We also noted down the p-values of each applicable variable for each model separately.

3. Results

3.1. Article search

We identified a total of 515 articles through database searching, of which 372 were unique articles. After judging the abstracts according to the predetermined criteria, we excluded 180 articles, and judged 192 articles eligible for full-text assessment. From these 192 articles, we excluded 81 articles since they did not meet the criteria. From the 111 remaining articles, 27 were useable for the qualitative analysis as they presented results in a desirable way (either using richness or a multivariate approach for the analyses). Another nine articles were useable for the quantitative analysis, of which six were also used for the qualitative analysis. Thus, from the grand total of 192 articles that we fully assessed, 27 were useful for the qualitative analysis and only eight for the quantitative analysis. This synthesis of eligible articles is also given in figures 1 and A1, the choice for eligibility of each article that was fully judged is given in table A1.

3.2. Geographical range

The geographical range of the 31 articles that were used for both the qualitative and quantitative analyses was as follows: nine in Europe, ten in South-America, six in Asia, two in North-America, one in Oceania and three in Africa (figure 2). From the six studies performed in Asia; one was performed in the Middle-East, one in Tibet and the other four throughout South-East Asia. The most northern study reported on samples taken in Scotland (*viz.*, Boon *et al* 2016), whereas the three most southern studies were sampled close to the border between Chile and Argentina (*viz.*, Brand and Miserendino 2015, Subiza and Brand 2018) and in New-Zealand (*viz.*, James and Suren 2009).

3.3. Qualitative analysis

A total of 15 articles were eligible for the qualitative analysis of the effect of temperature and dissolved oxygen on diversity using multivariate analyses (table 1). Another 14 articles, of which two that we also used for the former analysis, were eligible to assess the effect of temperature and dissolved oxygen on taxonomic richness (table 1). The results show that diversity and dissolved oxygen concentration were positively correlated in one out of 14 eligible articles (only during autumn in Banagar *et al* 2018). All 14 articles did not show a significant correlation between diversity and dissolved oxygen (including the other seasons in Banagar *et al* 2018) (table 1). For temperature, three out of 15 articles showed a negative correlation (including autumn and summer in Banagar *et al* 2018) and 13 articles showed no correlation at all (including spring and winter in Banagar *et al* 2018) (table 1).

Richness showed a similar pattern for both temperature and oxygen; most studies did not show any correlation. For temperature, one of the 14 studies showed a significantly negative correlation between richness and temperature. Two studies showed a significantly positive correlation. Six studies showed no correlation at all, and two studies did not comment on a possible correlation between temperature and richness. Dissolved oxygen was positively correlated with richness in three of the 14 studies and negatively correlated in another three studies. Dissolved oxygen did not show any correlation with richness in six studies. The remaining two studies did not mention having tested the effect of dissolved oxygen on richness (table 1).

3.4. Quantitative analysis

A multitude of articles describe a research set-up that would have suited the quantitative analysis, but most articles did not provide the necessary raw data either within the article or as supplementary material. So, eight articles remained for the quantitative analysis. From these eight articles, we distinguished 12 groups: the data from most articles were considered as one group per article (namely, Collier *et al* 1998, Jacobsen and Marín 2008, Wittman *et al* 2013, Xu *et al* 2014, Reis *et al* 2017), the data from two articles was split

Figure 2. Map with the locations of all studies that were used for either the quantitative or qualitative analyses. Dots show studies that only sampled locally, whereas polygons indicate the sample area of studies that were performed over larger geographic scales. Colours indicate for which part the studies were eventually used in this systematic review: papers used for the quantitative analysis (purple), papers used exclusively for the qualitative analysis (blue). Whenever a paper was used for both the quantitative and qualitative analyses it was included within the purple dots.

into two distinct groups recognised within the article (*viz.*, Docile *et al* 2016, Echelpoel *et al* 2019), and the data of one article was split into three groups (*viz.*, Boon *et al* 2016). Next, we considered these groups as blocks in the generalized linear models (GLM) and used them as qualitative factor, hereafter named 'STUDY'.

Considering the AICc values, the best fitting model was found to be one that solely included (1) dissolved oxygen concentration and 'STUDY' (table 2). However, three other models also scored similarly to this first model (ΔAICc < 6). In all three models the variables of model (1) were incorporated, but with the addition of one to three other variables. In order of lowest AICc value: (2) also incorporated the squared value of dissolved oxygen (DO^2), which on its own was not significant ($P = 0.058$); (3) incorporated temperature (T) and the interaction between dissolved oxygen concentration and temperature (T^*DO), here all variables were significant predictors ($P < 0.007$); lastly (4) incorporated temperature without the interaction between temperature and dissolved oxygen, here temperature was not a significant predictor of variation in taxonomic richness. We would however argue that the most parsimonious model is model (1) as it includes both the lowest number of variables, whilst also having the lowest AICc value.

4. Discussion

Our quantitative meta-analysis showed that macroinvertebrate richness correlates weakly with temperature and strongly with dissolved oxygen. The qualitative analysis, on the other hand, did not show a clear effect of either temperature or dissolved oxygen on richness or biodiversity (table 1). This shows that separate investigations might not be able to distinguish patterns that only become apparent in combined data sets of studies from various geographical contexts. Without the meta-analysis, we would not have been able to distinguish a clear pattern between oxygen concentration and taxonomic richness. This systematic review also exposes the dearth of raw data, as many authors still do not publish these. The field of ecology should become more transparent, so that future authors of systematic reviews will be better able to uncover overarching ecological patterns.

The outcome of our systematic review shows that any model without oxygen had a markedly lower explanatory value. Adding temperature as an extra variable can slightly enhance the explained variation, but temperature on its own is a poor predictor of taxonomic richness. Hence, most of the effect of temperature is likely mediated through the availability of oxygen. This is in accordance with physiological research on aquatic macroinvertebrate heat resistance in differentially oxygenated systems. For example, Verberk *et al* (2016) found that two species of gill-breathing mayflies could withstand higher temperatures when placed in hyperoxic waters, whereas lower temperatures were already lethal in hypoxic waters. Furthermore, a general trend is that air-breathing aquatic invertebrates can withstand higher temperatures than water-breathing invertebrates, which is to be expected if oxygen is the main driver of

Table 1. The effect of temperature and dissolved oxygen on diversity using results from multivariate analyses; and diversity using correlations with richness. A '0' indicates no correlation between the variable of interest (temperature or dissolved oxygen) and diversity was found, a '+' indicates that significantly more species were positively related than negatively correlated (RDA) or significantly more species were related with higher values (CCA) or $p < 0.05$ (correlation with richness), a '−' indicates that significantly more species were negatively correlated than positively correlated (RDA) or significantly more species were related with lower values (CCA) or $p < 0.05$ (correlation with richness), 'N/A' indicates that effect of the variable of interest could not be deduced from the article. '*' indicates that the variable of interest was not included into the triplot after forward selection of explanatory variables. Number of studies with either a positive or negative response for each variable and method of deducing diversity is given at the bottom. For an explanation of the 'correlation regions' and the use of multivariate ordinations, see Materials & Methods—Qualitative analysis.

	Correlation Temperature		**Correlation Dissolved O2**	
Study	*Multivariate*	*Richness*	*Multivariate*	*Richness*
(Subiza and Brand 2018)	N/A	0	N/A	0
(Niba and Sakwe 2018)	0	N/A	0	N/A
(Kokavec *et al* 2018)	0	N/A	0*	N/A
(Banagar *et al* 2018) (winter)	0	N/A	0	N/A
(Banagar *et al* 2018) (Autumn)	−	N/A	+	N/A
(Banagar *et al* 2018) (Summer)	−	N/A	0	N/A
(Banagar *et al* 2018) (spring)	0	N/A	0	N/A
(Fumetti *et al* 2017)	0	0	0*	0
(Krolak *et al* 2017)	N/A	+	N/A	−
(Reis *et al* 2017)	N/A	0	N/A	0
(Sabater *et al* 2016)	N/A	0	N/A	N/A
(Obolewski *et al* 2016)	0*	N/A	0	N/A
(Mwedzi *et al* 2016)	0	N/A	0	N/A
(Lehotský *et al* 2016)	0	N/A	0	N/A
(Docile *et al* 2016)	−	N/A	0*	N/A
(Chase *et al* 2016)	−	N/A	N/A	N/A
(Boon *et al* 2016)	0	N/A	0	+
(Prommi and Payakka 2015)	N/A	0	N/A	−
(Fu *et al* 2015)	0	N/A	0*	N/A
(Brand and Miserendino 2015)	N/A	0	N/A	N/A
(Hrovat *et al* 2014)	0	N/A	0	N/A
(Wittman *et al* 2013)	N/A	N/A	N/A	+
(Rawi *et al* 2013)	0	N/A	0	N/A
(Rocha *et al* 2012)	N/A	0	N/A	0
(Früh *et al* 2012)	0	N/A	0	N/A
(Arimoro *et al* 2011)	0	N/A	0	N/A
(Couceiro *et al* 2010)	N/A	0	N/A	−
(Jacobsen and Marín 2008)	N/A	−	N/A	0
(Jacobsen 2008)	N/A	+	N/A	0
(Couceiro *et al* 2007)	N/A	0	N/A	+
Total positive	**0**	**2**	**1**	**3**
Total negative	**4**	**1**	**0**	**3**
Total response	**18**	**12**	**17**	**12**

survival (Leiva *et al* 2019). A similar pattern was found for altitude and biodiversity (Verberk *et al* 2011). Verberk *et al* (2011) showed that altitudinal patterns in taxonomic richness might also be due directly to differences in oxygen concentration—or more precisely differences in organism oxygen availability—that are indirectly affected by altitudinal differences in oxygen pressure (Prins *et al* 2017). In turn, macroinvertebrate richness might be positively related to dissolved oxygen concentration as these organisms are mainly limited by minimum oxygen concentrations, but not so much by a maximum oxygen concentration that would occur in nature (Lock *et al* 2013).

Given the importance of oxygen for aquatic macroinvertebrate richness, ongoing human impact on aquatic systems—typically leading to reduced oxygen—is worrying. Water pollution, organic loading and water flow impediments could all negatively impact oxygen concentration (Nilsson *et al* 2005, Valle *et al* 2015, Kokavec *et al* 2018), but also increase the concentration of other solubles with negative consequences for biodiversity (Wen *et al* 2017). Avoiding (organic) water pollution through water treatment, reducing organic loading and increasing water flow in rivers might help improve oxygen availability. Furthermore, these types of measures can be undertaken or enforced by more local governmental bodies. Measures that improve water quality could also lead to reduction of other pollutants that might affect biodiversity, like heavy metals, pesticides and industrial effluents. Hence, we infer that rechannelling of

Table 2. The results from Generalized Linear Models of family richness and all possible models with the given variables: temperature ('T'), dissolved oxygen content ('DO'), the interaction between temperature and dissolved oxygen content ('T*DO'), the study and groups within the study ('STUDY') and the squared values of both temperature (T^2) and dissolved oxygen content (DO^2). AICc and ΔAICc values are given for each model, and the models are ranked by their ΔAICc values. Also, P-values are given for each applicable variable for each model, significant values ($P < 0.05$) are given in bold.

Model											AICc	ΔAICc	P (T)	P (DO)	P (T*DO)	P (STUDY)	P (T^2)	P (DO^2)
		DO			+	STUDY					759.354	0.000		**<0.001**		**<0.001**		
		DO			+	STUDY			+	DO^2	761.436	2.082		**0.007**		**<0.001**		0.058
T	+	DO	+	T*DO	+	STUDY					763.021	3.667	**0.007**	**<0.001**	**0.005**	**<0.001**		
T	+	DO			+	STUDY					765.053	5.699	0.703	**<0.001**		**<0.001**		
T	+	DO	+	T*DO	+	STUDY			+	DO^2	765.369	6.015	**0.006**	**<0.001**	**0.005**	**<0.001**		0.068
T	+	DO			+	STUDY			+	DO^2	767.274	7.920	0.934	**0.008**		**<0.001**		0.063
T	+	DO	+	T*DO	+	STUDY	+	T^2			768.789	9.435	**0.037**	**<0.001**	**0.006**	**<0.001**	0.782	
T	+	DO			+	STUDY	+	T^2			770.449	11.095	0.442	**<0.001**		**<0.001**	0.501	
T	+	DO	+	T*DO	+	STUDY	+	T^2	+	DO^2	771.149	11.795	**0.034**	**<0.001**	**0.006**	**<0.001**	0.799	0.068
T	+	DO			+	STUDY	+	T^2	+	DO^2	772.656	13.302	0.510	**0.008**		**<0.001**	0.494	0.062
						STUDY					777.310	17.956				**<0.001**		
T					+	STUDY					781.476	22.122	0.195			**<0.001**		
T					+	STUDY	+	T^2			786.922	27.568	0.272			**<0.001**	0.526	
T	+	DO									861.154	101.800	**<0.001**	**<0.001**				
T	+	DO					+	T^2			865.387	106.033	**0.003**	**<0.001**			0.199	
T	+	DO							+	DO^2	866.179	106.825	**<0.001**	**0.025**				0.370
T	+	DO	+	T*DO							866.998	107.644	0.385	**0.046**	0.987			
T	+	DO					+	T^2	+	DO^2	870.743	111.389	**0.005**	**0.045**			0.253	0.488
T	+	DO	+	T*DO			+	T^2			871.202	111.848	0.153	0.079	0.863		0.195	
T	+	DO	+	T*DO					+	DO^2	872.022	112.668	0.369	0.060	0.977			0.370
T	+	DO	+	T*DO			+	T^2	+	DO^2	876.549	117.195	0.167	0.114	0.845		0.246	0.485
		DO									896.549	137.195		**<0.001**				
		DO							+	DO^2	901.148	141.794		**0.016**				0.271
T							+	T^2			939.920	180.566	**<0.001**				**0.008**	
T											940.845	181.491	**<0.001**					

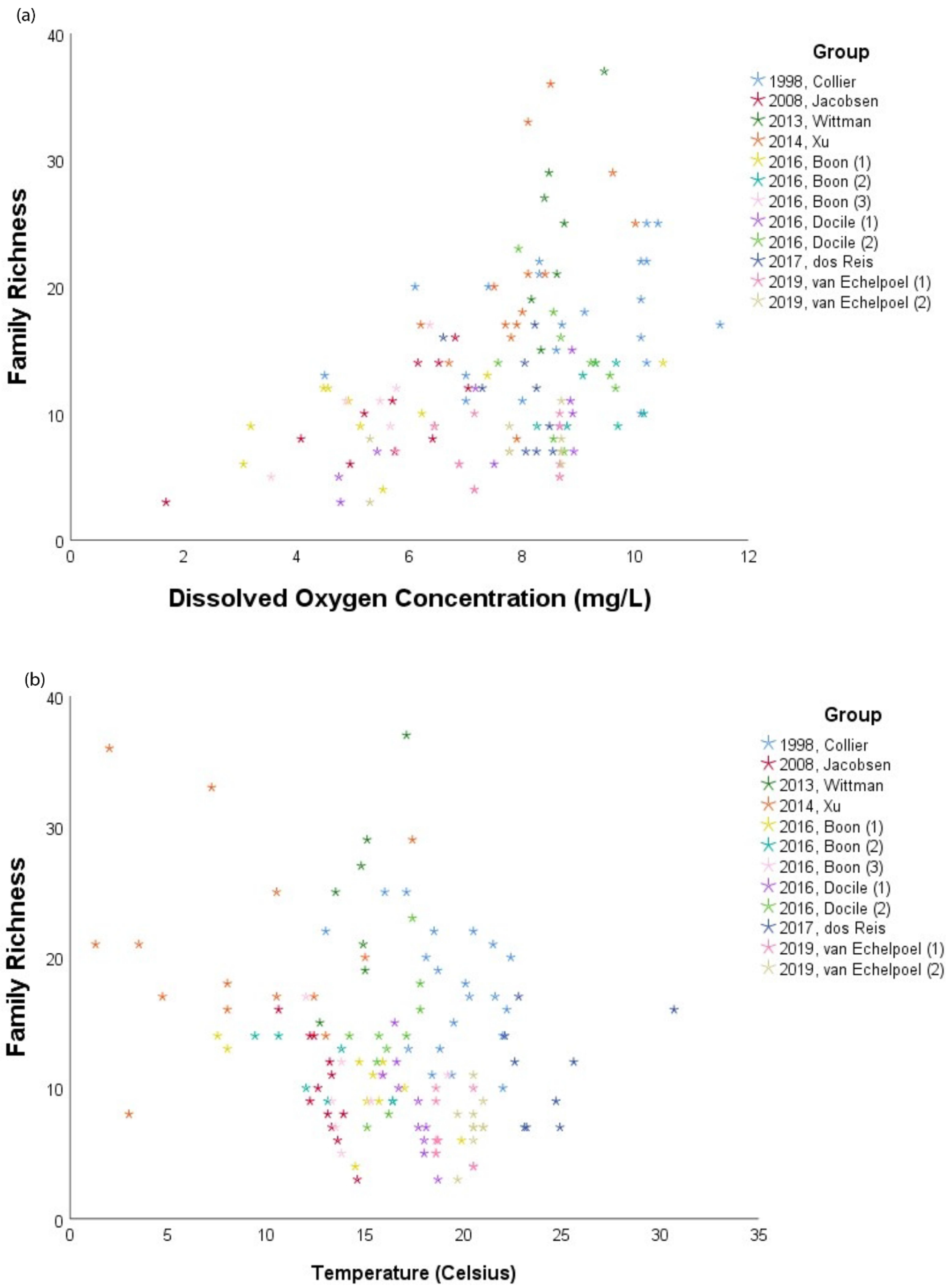

Figure 3. The effect of dissolved oxygen (a) and temperature (b) on family richness. (a) Scatterplot of dissolved oxygen concentration in mg l^{-1} and richness. (b) Scatterplot of temperature in °C and richness. Colours indicate different studies or groups within studies.

rivers with glacial origin into subtropical rivers might be less of a worry, like which is currently happening in Nepal with the tunnelling through the mountains to link the Bheri river with the Babai river; and is being planned for several major rivers on the Tibetan plateau. Perhaps more worrisome is the channelling of water into irrigation systems all over the world. In these irrigation channels there is an increased chance that oxygen concentrations will be lowered because of agricultural practices (Foley *et al* 2005).

We think that the sample sizes of separate articles were generally not sufficient to detect strong associations between macroinvertebrate biodiversity and either temperature or dissolved oxygen. Articles that were both judged eligible and presented results in a desirable way—either using richness or multivariate analyses—were rare. This resulted in a small group of useful articles with an even smaller set of articles that showed some significant correlation. The trend with these articles also seemed to be that there was a positive correlation between biodiversity and dissolved oxygen, but no consistent pattern between temperature and biodiversity seemed to exist. These results show the advantage of the combination of systematic review and meta-analysis, over a conventional review; merely looking at the results of separate studies would not have led to new insights (Vinson and Hawkins 1998), whereas analysing data from separate studies as one dataset did.

The eligible papers that were used for either quantitative or qualitative analyses came from all over the world, with every continent represented by at least one paper. To our opinion the examined studies cover a sufficient geographic scope to account for different altitudinal contexts. Slight biases were apparent for South-America and Europe. Furthermore, from the map (figure 2) it becomes apparent that mainly drier areas—like the Sahara and Sahel, Middle-East, Central Asia, Central Australia, and the Western USA and Mexico—are undersampled. Also, high latitude areas are under-sampled, as we could not identify studies in Canada, Scandinavia or Russia that met our criteria for the systematic review. We would expect that macroinvertebrates in lotic ecosystems in dry areas with high temperatures might still be mainly limited by the markedly lower oxygen concentration in these waters (Verberk *et al* 2016). However, macroinvertebrates inhabiting areas at high latitudes and under extreme colds might actually be limited more by these low temperatures. We do however like to point out that close to zero temperatures do not necessarily have to show reduced macroinvertebrate biodiversity. In their research in the Tibetan plateau, Xu *et al* (2014) found a relatively high taxonomic richness compared to other studies and from their results no apparent effect of temperature becomes apparent, whereas taxonomic richness in this study does seem to follow a positive trend for dissolved oxygen concentration (figure 3).

Authors must have a wealth of data, but most of it appears to be 'sealed away'. We urge authors to make their data more readily available, to increase transparency within the field of ecology and to allow for more analysis of available data. Indeed, in ecological research habitually many variables are measured and a variable that is not of interest for the researcher herself might be of interest for others who desire to carry out a meta-analysis. A generally accessible data depository (as geneticists already do with GenBank and movement ecologists do with MoveBank) would improve the chances of discovering patterns that help to manage the world's resources better. Perhaps uploading data in the Dryad Digital Repository (https://datadryad.org/) or a similar one like DANS (https://dans.knaw.nl/en/about) ought to become compulsory when a manuscript is accepted for publication. Furthermore, efforts could be made to make data available retroactively for papers that have already been published. More readily available data would already open up a wealth of data that can be used in more meta-analyses in the future.

5. Conclusion

We provide evidence that in free-flowing freshwater ecosystems reduced oxygen concentration has a major impact on aquatic biodiversity. In our review we also investigated whether there is a direct effect of temperature on macroinvertebrate richness. We believe that the systematic review that we conducted points more into the direction of a direct effect for oxygen than for temperature, at least for low and middle latitudinal ranges. Our review may indicate that worries about the temperature effects of climate change are perhaps less justified than worries about major land use changes that happen today (Sala *et al* 2000). As such, we call on major funders of large infrastructural works that impede flow rates of rivers or increase organic loads (like the World Bank, the Asian Development Bank, the African Development Bank, and the China Development Bank, etc) to increase their vigilance against negative impacts on biodiversity of the works they finance.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: 10.13140/RG.2.2.33027.66081.

Acknowledgments

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Appendix

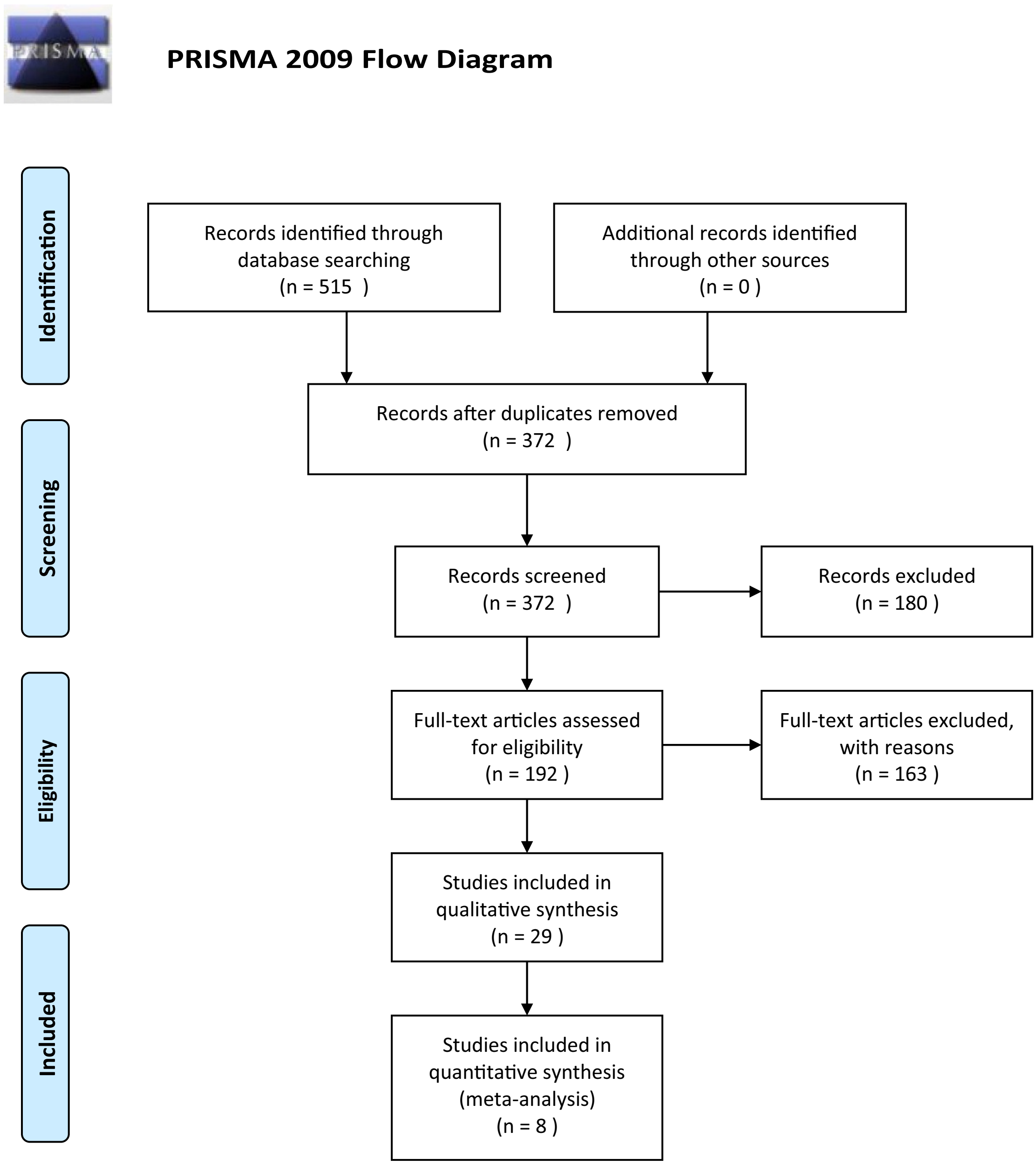

Figure A1. Prisma 2009 flow diagram for this systematic review. Under each step of the flow diagram the number of articles is given. No additional records were identified through other sources, hence the n = 0 underneath. The articles included in the qualitative and quantitative analysis are not mutually exclusive, and studies in the quantitative analysis are not necessarily used in the qualitative analysis. Adapted from Moher *et al* (2009). CC BY 4.0.

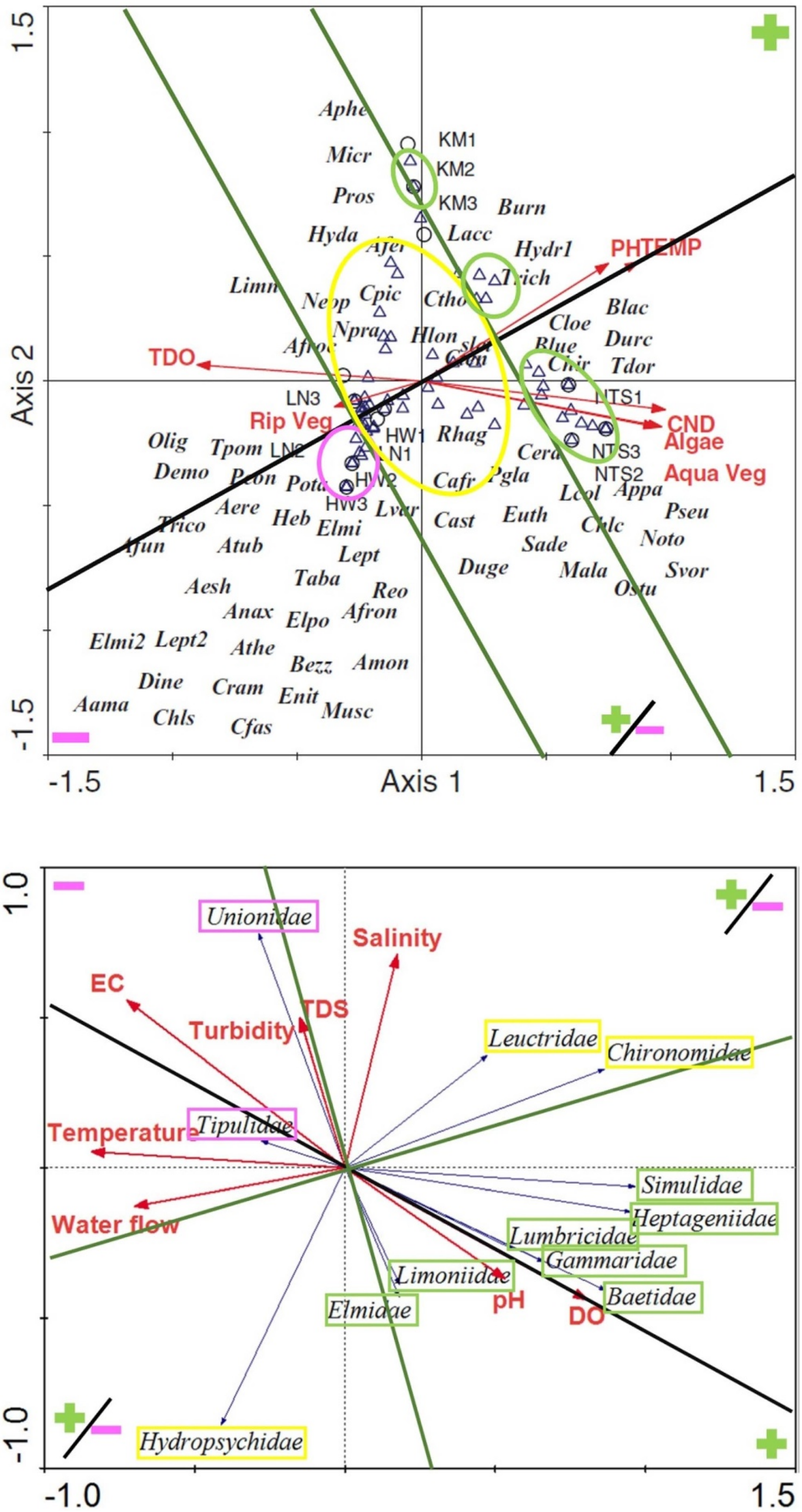

Figure A2. Visual representation of the approach to assess oxygen/temperature vs. diversity relationships using CCA (a) and RDA (b) plots. (a) The black line illustrates the direction of the variable of interest. We grouped the plot in three plot sections, indicated by the green lines perpendicular to the black line. Classification: taxa associated with high (green), intermediate (yellow), and low (pink) values for the environmental variable of interest. Reproduced from Niba *et al* (2018). CC BY 4.0. (b) The black line illustrates the direction of the environmental variable of interest (either temperature or oxygen). The green lines form angles of 45° to the black line. The taxa that fall within these two lines on the black line side have a correlation coefficient of 0.7 or higher with the variable of interest. Classification: positive correlation (green boxes), no correlation (yellow boxes), and negative correlation (pink boxes). In each section we counted the number of taxa. Reprinted by permission from Springer Nature Customer Service Centre GmbH: Springer Nature. Biologia. Monitoring and Assessment of Water Quality in the Haraz River of Iran, Using Benthic Macroinvertebrates Indices. Banagar *et al.* Copyright © 2018, Institute of Zoology, Slovak Academy of Sciences. (2018).

Table A1. A table with all articles of which the full text was screened, whether it was accepted for use in either the qualitative analysis and/or meta-analysis, and the reasoning behind exclusion if this was the case. Whenever 'Data not available' was given as reason for exclusion, the research was performed in an eligible way for the meta-analysis if the data was available. The (*)-sign means that an article could have been useful for the meta-analysis, but data was not supplemented in the desired manner. 'Results not presented in desirable way' was a broad term for articles that did not give results in such a way that they could be used for qualitative analysis, despite that the research would have been eligible.

Article	#	Used for Qualitative Analysis	Used for Meta-Analysis	Reason for exclusion
(Echelpoel *et al* 2019)	1	No	Yes	Results not presented in desirable way.
(Suane *et al* 2019)	2	No	No*	Results not presented in desirable way. Data not available.
(Macneil 2019)	3	No	No	Only two macroinvertebrate orders.
(Li *et al* 2019)	4	No	No*	Results not presented in desirable way. Data not available.
(Karaouzas *et al* 2019)	5	No	No*	Results not presented in desirable way. Data not available.
(Silva Tronco Johann *et al* 2019)	6	No	No*	Results not presented in desirable way. Data not available.
(Jabbar and Grote 2019)	7	No	No*	Results not presented in desirable way. Data not available.
(Ferronato *et al* 2019)	8	No	No*	Results not presented in desirable way. Data not available.
(Tas-Divrik and Kirgiz 2018)	9	No	No*	Results not presented in desirable way. Data not available.
(Subiza and Brand 2018)	10	Yes	No*	Data not available.
(Ridl *et al* 2018)	11	No	No	Only one macroinvertebrate order.
(Niba and Sakwe 2018)	12	Yes	No*	Data not available.
(Mendes *et al* 2018)	13	No	No	Only one macroinvertebrate order.
(Marshalonis and Larson 2018)	14	No	No*	Results not presented in desirable way. Data not available.
(Li *et al* 2018)	15	No	No*	Results not presented in desirable way. Data not available.
(Kokavec *et al* 2018)	16	Yes	No*	Data not available.
(Gunawardhana *et al* 2018)	17	No	No*	Results not presented in desirable way. Data not available.
(Chessman 2018)	18	No	No	Water temperature not measured.
(Banagar *et al* 2018)	19	Yes	No*	Data not available.
(Zagarola *et al* 2017)	20	No	No	Sample size too low.
(Yao *et al* 2017)	21	No	No	Taxonomic accuracy too low.
(Fumetti *et al* 2017)	22	Yes	No*	Data not available.
(Vincent Nakin *et al* 2017)	23	No	No	Dissolved oxygen not measured.
(Vilenica 2017)	24	No	No	Only one macroinvertebrate order.
(Saulino *et al* 2017)	25	No	No	Only one macroinvertebrate order.
(Riis *et al* 2017)	26	No	No	Macroinvertebrate diversity not measured. Sample size unclear.
(Northington and Webster 2017)	27	No	No	Macroinvertebrate diversity not measured.
(Sor *et al* 2017)	28	No	No*	Taxonomic accuracy unclear. Data not available.
(Shafie *et al* 2017)	29	No	No	Sample size too low.
(Martins *et al* 2017)	30	No	No*	Results not presented in desirable way. Data not available.
(Krolak *et al* 2017)	31	Yes	No*	Data not available.
(Kazanci *et al* 2017)	32	No	No	Only one macroinvertebrate order.
(Jia *et al* 2017)	33	No	No	Only one macroinvertebrate order.
(García-García *et al* 2017)	34	No	No	Only one macroinvertebrate order.
(Reis *et al* 2017)	35	Yes	Yes	
(Abbaspour *et al* 2017)	36	No	No*	Results not presented in desirable way. Data not available.
(Schuwirth *et al* 2016)	37	No	No	Sample size unclear.
(Sabater *et al* 2016)	38	Yes	No*	Data not available.
(Ríos-Pulgarín *et al* 2016)	39	No	No*	Results not presented in desirable way. Data not available.
(Pardo and García 2016)	40	No	No	Sample size unclear.
(Pakulnicka *et al* 2016)	41	No	No	Only one macroinvertebrate order.

Table A1. (Continued)

Article	#	Used for Qualitative Analysis	Used for Meta-Analysis	Reason for exclusion
(Obolewski *et al* 2016)	42	Yes	No*	Data not available.
(Mwedzi *et al* 2016)	43	Yes	No*	Data not available.
(Lehotský *et al* 2016)	44	Yes	No*	Data not available.
(Kelly *et al* 2016)	45	No	No*	Results not presented in desirable way. Data not available.
(Fu *et al* 2016)	46	No	No*	Results not presented in desirable way. Data not available.
(Edia *et al* 2016)	47	No	No*	Results not presented in desirable way. Data not available.
(Docile *et al* 2016)	48	Yes	Yes	
(Crespo-Pérez *et al* 2016)	49	No	No	Only one macroinvertebrate order.
(Chase *et al* 2016)	50	Yes	No*	Data not available.
(Boon *et al* 2016)	51	Yes	Yes	
(Barros *et al* 2016)	52	No	No	Sample size too low.
(Valle *et al* 2015)	53	Yes	No*	Data not available.
(Serna *et al* 2015)	54	No	No	Only one macroinvertebrate order.
(Prommi and Payakka 2015)	55	Yes	No*	Data not available.
(Fu *et al* 2015)	56	Yes	No*	Data not available.
(Dohet *et al* 2015)	57	No	No*	Results not presented in desirable way. Data not available.
(Dida *et al* 2015)	58	No	No	Results not presented in desirable way. Not 'all' macroinvertebrates measured
(Chessman 2015)	59	No	No*	Results not presented in desirable way. Data not available.
(Brand and Miserendino 2015)	60	Yes	No*	Data not available.
(Barman and Gupta 2015)	61	No	No	Sample size unclear.
(Aazami *et al* 2015)	62	No	No*	Results not presented in desirable way. Data not available.
(Xu *et al* 2014)	63	No	Yes	Results not presented in desirable way.
(Szlauer-Lukaszewska 2014)	64	No	No	Only one macroinvertebrate order.
(Salvarrey *et al* 2014)	65	No	No	Water temperature not measured. Taxonomic accuracy unclear. Sample size unclear.
(Salmah *et al* 2014)	66	No	No	Results not presented in desirable way. Data on DO and T not given per sample
(Sakelarieva and Varadinova 2014)	67	No	No	Taxonomic accuracy unclear.
(Rosa *et al* 2014)	68	No	No	Only two macroinvertebrate orders.
(Rezende *et al* 2014)	69	No	No	Taxonomic accuracy unclear.
(Rada and Santic 2014)	70	No	No*	Results not presented in desirable way. Data not available.
(Pinto *et al* 2014)	71	No	No	Taxonomic accuracy unclear.
(Loayza-Muro *et al* 2014)	72	No	No	Only one macroinvertebrate order. Sample size too low. Macroinvertebrate diversity not measured.
(Knee and Encalada 2014)	73	No	No*	Results not presented in desirable way. Data not available.
(Kilonzo *et al* 2014)	74	No	No	Water temperature not measured.
(Hrovat *et al* 2014)	75	Yes	No	Not 'all' macroinvertebrates measured
(Djiriéoulou *et al* 2014)	76	No	No	Only one macroinvertebrate order.
(Cunha *et al* 2014)	77	No	No	Taxonomic accuracy too low.
(Coffey *et al* 2014)	78	No	No	Sample size unclear.
(Wittman *et al* 2013)	79	Yes	Yes	
(Wahl *et al* 2013)	80	No	No	Taxonomic accuracy too low.
(Villamarín *et al* 2013)	81	No	No*	Results not presented in desirable way. Data not available.
(Takhelmayum *et al* 2013)	82	No	No	Sample size unclear.
(Sternecker *et al* 2013)	83	No	No	Sample size unclear.
(Rawi *et al* 2013)	84	Yes	No*	Data not available.
(Lujan *et al* 2013)	85	No	No	Taxonomic accuracy unclear.
(Linares *et al* 2013)	86	No	No*	Results not presented in desirable way. Data not available.

Table A1. (Continued)

Article	#	Used for Qualitative Analysis	Used for Meta-Analysis	Reason for exclusion
(Capderrey et al 2013)	87	No	No*	Results not presented in desirable way. Data not available.
(Bowles et al 2013)	88	No	No	Sample size too low.
(Alvarez-mieles et al 2013)	89	No	No	Sample size too low.
(Rocha et al 2012)	90	Yes	No*	Data not available.
(Pokorny et al 2012)	91	No	No	Taxonomic accuracy unclear.
(Murakami et al 2012)	92	No	No	Taxonomic accuracy too low.
(Mori et al 2012)	93	No	No	Results not presented in desirable way. Not 'all' macroinvertebrates measured.
(Miserendino et al 2012)	94	No	No	Sample size unclear.
(Khoza et al 2012)	95	No	No	Sample size too low.
(Früh et al 2012)	96	Yes	No	Not 'all' macroinvertebrates measured
(Arco et al 2012)	97	No	No	Sample size too low.
(Wesener et al 2011)	98	No	No*	Results not presented in desirable way. Data not available.
(Simanonok et al 2011)	99	No	No	Sample size too low. Taxonomic accuracy too low.
(Shin et al 2011)	100	No	No	Sample size too low.
(Shilla and Shilla 2011)	101	No	No	Sample size too low. Taxonomic accuracy too low.
(Poquet and Mesquita-joanes 2011)	102	No	No	Only one macroinvertebrate order.
(Patrick and Swan 2011)	103	No	No*	Results not presented in desirable way. Data not available.
(Davies-colley et al 2011)	104	No	No	Taxonomic accuracy unclear.
(Collier and Clements 2011)	105	No	No	Taxonomic accuracy too low.
(Bio et al 2011)	106	No	No*	Results not presented in desirable way. Data not available.
(Arimoro et al 2011)	107	Yes	No*	Data not available.
(Wiseman et al 2010)	108	No	No	Taxonomic accuracy unclear.
(Rađa and Puljas 2010)	109	No	No*	Results not presented in desirable way. Data not available.
(Orzetti et al 2010)	110	No	No	Sample size unclear. Taxonomic accuracy too low.
(Miliša et al 2010)	111	No	No*	Results not presented in desirable way. Data not available.
(Mesa 2010)	112	No	No*	Results not presented in desirable way. Data not available.
(Lefcort et al 2010)	113	No	No	Taxonomic accuracy unclear.
(Couceiro et al 2010)	114	Yes	No*	Data not available.
(Comte et al 2010)	115	No	No*	Results not presented in desirable way. Data not available.
(Al-Shami et al 2010)	116	No	No	Only one macroinvertebrate order.
(Schmidt et al 2009)	117	No	No	Taxonomic accuracy too low.
(Katano et al 2009)	118	No	No*	Results not presented in desirable way. Data not available.
(Jonker et al 2009)	119	No	No*	Results not presented in desirable way. Data not available.
(James and Suren 2009)	120	No	No*	Results not presented in desirable way. Data not available.
(Ellison et al 2009)	121	No	No	Sample size unclear. Taxonomic accuracy too low.
(Durance and Ormerod 2009)	122	No	No*	Results not presented in desirable way. Data not available.
(Carter et al 2009)	123	No	No*	Results not presented in desirable way. Data not available.
(Camara et al 2009)	124	No	No	Only one macroinvertebrate order.
(Bae and Park 2009)	125	No	No*	Results not presented in desirable way. Data not available.
(Jacobsen and Marín 2008)	126	Yes	Yes	
(Jacobsen 2008)	127	Yes	No*	Data not available.

Table A1. (Continued)

Article	#	Used for Qualitative Analysis	Used for Meta-Analysis	Reason for exclusion
(Zampella *et al* 2008)	128	No	No*	Results not presented in desirable way. Data not available.
(Zaikowski *et al* 2008)	129	No	No*	Results not presented in desirable way. Data not available.
(Hall and Lombardozzi 2008)	130	No	No	Taxonomic accuracy too low.
(Brisbois *et al* 2008)	131	No	No	Taxonomic accuracy unclear.
(Couceiro *et al* 2007)	132	Yes	No*	Data not available.
(Hall *et al* 2007)	133	No	No*	Results not presented in desirable way. Data not available.
(Dewson *et al* 2007b)	134	No	No*	Results not presented in desirable way. Data not available.
(Dewson *et al* 2007a)	135	No	No*	Results not presented in desirable way. Data not available.
(Daufresne *et al* 2007)	136	No	No*	Results not presented in desirable way. Data not available.
(Cooksey and Hyland 2007)	137	No	No*	Results not presented in desirable way. Data not available.
(Collins *et al* 2007)	138	No	No*	Results not presented in desirable way. Data not available.
(Carlisle *et al* 2007)	139	No	No*	Results not presented in desirable way. Data not available.
(Bond *et al* 2007)	140	No	No*	Results not presented in desirable way. Data not available.
(Kaller and Kelso 2006)	141	No	No	Sample size too low.
(Camur-Elipek *et al* 2006)	142	No	No	Taxonomic accuracy too low. Sample size too low.
(Sylvestre and Bailey 2005)	143	No	No*	Results not presented in desirable way. Data not available.
(Overmyer *et al* 2005)	144	No	No	Sample size too low.
(Mccreadie *et al* 2005)	145	No	No	Only one macroinvertebrate order.
(Baillie *et al* 2005)	146	No	No	Sample size too low.
(Ndaruga *et al* 2004)	147	No	No	Taxonomic accuracy too low.
(Morais *et al* 2004)	148	No	No	Sample size too low.
(Colon-Gaud *et al* 2004)	149	No	No	Taxonomic accuracy unclear. Sample size too low.
(Wymer and Cook 2003)	150	No	No	Taxonomic accuracy unclear. Sample size too low.
(Olsen and Townsend 2003)	151	No	No	Sample size too low.
(Jacobsen *et al* 2003)	152	No	No	Opinion paper.
(Grandjean *et al* 2003)	153	No	No	Sample size too low.
(Davis *et al* 2003)	154	No	No	Sample size too low.
(Collier and Smith 2003)	155	No	No	Sample size too low. Taxonomic accuracy unclear.
(Chessman 2003)	156	No	No*	Results not presented in desirable way. Data not available.
(Ferreira *et al* 2002)	157	No	No*	Results not presented in desirable way. Data not available.
(Schleiter *et al* 2001)	158	No	No*	Results not presented in desirable way. Data not available.
(Fowler and Death 2001)	159	No	No	Taxonomic accuracy unclear
(Angradi *et al* 2001)	160	No	No*	Results not presented in desirable way. Data not available.
(Shieh and Yang 2000)	161	No	No	Sample size too low.
(Phiri 2000)	162	No	No*	Results not presented in desirable way. Data not available.
(Crespin de Billy *et al* 2000)	163	No	No	Sample size too low.
(Schleiter *et al* 1999)	164	No	No	Sample size unclear. Taxonomic accuracy unclear.
(Bachmann and Usseglio-Polatera 1999)	165	No	No	Sample size unclear. Taxonomic accuracy unclear.

Table A1. (Continued)

Article	#	Used for Qualitative Analysis	Used for Meta-Analysis	Reason for exclusion
(Selong and Helfrich 1998)	166	No	No	Taxonomic accuracy too low.
(Kefford 1998)	167	No	No*	Results not presented in desirable way. Data not available.
(Collier et al 1998)	168	No	Yes	Results not presented in desirable way. Data available.
(Camargo and Voelz 1998)	169	No	No	Sample size too low.
(Storey and Cowley 1997)	170	No	No	Sample size too low.
(Pozo et al 1997)	171	No	No*	Results not presented in desirable way. Data not available.
(Battegazzore and Renoldi 1995)	172	No	No	Sample size too low.
(Camargo 1994)	173	No	No	Sample size too low.
(Camargo 1992)	174	No	No	Sample size too low.
(Boulton and Lake 1992)	175	No	No	Sample size too low.
(Storey et al 1991)	176	No	No	Sample size too low.
(Camargo and de Jalon 1990)	177	No	No*	Results not presented in desirable way. Data not available.
(Boulton and Lake 1990)	178	No	No	Sample size too low.
(Tuch and Gasith 1989)	179	No	No	Sample size too low. Taxonomic accuracy too low.
(Bunn et al 1986)	180	No	No*	Results not presented in desirable way. Data not available.
(Harrel 1985)	181	No	No	Sample size too low. Taxonomic accuracy unclear.
(Mayack and Waterhouse 1983)	182	No	No	Water temperature not measured at each site
(Rooke and Mackie 1982)	183	No	No	Sample size too low. Taxonomic accuracy unclear.
(Siegried et al 1980)	184	No	No*	Results not presented in desirable way. Data not available.
(Cook 1976)	185	No	No*	Results not presented in desirable way. Data not available.
(Wayne Minshall 1968)	186	No	No*	Results not presented in desirable way. Data not available.

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