What explains the variation in dam impacts on riverine macroinvertebrates? A global quantitative synthesis

Jun Wang1,2, Chengzhi Ding1,2, Jani Heino3, Xiaoming Jiang4, Juan Tao1,2, Liuyong Ding1,2, Wan Su1,2, Minrui Huang1,2 and Daming He1,2

1 Yunnan Key Laboratory of International Rivers and Transboundary Eco-security, Yunnan University, Kunming 650091, People’s Republic of China
2 Institute of International Rivers and Eco-security, Yunnan University, Kunming 650091, People’s Republic of China
3 Freshwater Centre, Finnish Environment Institute, Oulu, Finland
4 State Key Laboratory of Eco-hydraulic in Northwest Arid Region of China, Xi’an University of Technology, Xi’an 710048, People’s Republic of China

E-mail: chzhding@ynu.edu.cn and dmhe@ynu.edu.cn

Keywords: benthic invertebrates, hydropower, biodiversity, climatic zones, dam size, substrate composition

Abstract

Dams have fragmented rivers and threatened aquatic biodiversity globally. However, the findings regarding dam impacts on riverine macroinvertebrates vary across regions and taxa. We conducted a global meta-analysis to quantify the effects of dams on macroinvertebrate assemblages (i.e. species richness and abundance) based on 3849 data points extracted from 54 publications. Responses of macroinvertebrates to dams varied among climatic zones, dam altitudes, dam sizes (i.e. height), downstream distances from the dams, and taxonomic groups. The overall effect size of dams on macroinvertebrate richness was negative, while that of dams on abundance was positive but varied among different dam types. Richness reductions were most pronounced in cold regions and high-altitude regions and were least pronounced in tropical regions and low-altitude regions, while abundance increases were more obvious in tropical regions and low-altitude regions. Macroinvertebrate richness reduction and abundance increase were coupled (i.e. when the richness slightly decreased, the increase in abundance was more significant, and vice versa) under the influence of dams across different climatic zones, altitudes, dam heights, and downstream distances from the dams. Furthermore, different taxonomic groups responded variably to dams, with stoneflies (Plecoptera), caddisflies (Trichoptera) and true bugs (Hemiptera) being the most sensitive groups (i.e. significant reduction in richness) among the taxa examined. Macroinvertebrate richness reductions were primarily attributed to changes in downstream substrate composition (i.e. from coarse to fine substrates), while abundance increases were potentially caused by replacements among taxa at downstream sites. Collectively, our results contribute to improving the prediction of the effects of dams on riverine macroinvertebrate assemblages and are valuable for guiding assessment and monitoring of river ecosystems, as well as sustainable dam development, planning and restoration.

1. Introduction

Dams have fragmented rivers across nearly every continent excluding Antarctica (Nilsson et al 2005, Poff and Matthews 2013, Zarfl et al 2015, Couto and Olden 2018, Grill et al 2019). Although dams often deliver economic services such as hydropower, flood risk alleviation, water supply, recreation and more, there are concerns that dams have impaired the key functions of rivers in providing diverse habitats and maintaining ecosystem integrity (Baxter 1977, Bunn and Arthington 2002, Carlisle et al 2011, Ellis and Jones 2013, Tonkin et al 2018a, Reid et al 2019). Numerous of aquatic organisms living in rivers are widely acknowledged to be vulnerable to dam-induced thermal and flow alterations, reduced river...
connectivity and altered hydrochemistry (Bunn and Arthurton 2002, Reid et al 2019, Mellado-Díaz et al 2019). Biodiversity loss, e.g. species diversity decline, has pervasively occurred in both large dammed rivers (Cheng et al 2015, Castello and Macedo 2016, Wine-miller et al 2016, Zhang et al 2018, 2019), as well as small dammed rivers and streams (Lessard and Hayes 2003, Couto and Olden 2018, Ding et al 2019). In addition, many terrestrial organisms, such as plants, birds, and mammals, that dwell within riparian zones and wider catchments are threatened by dam-induced environmental changes (Wu et al 2003, Meijaard 2019, Tang et al 2019). Therefore, dams pose a major threat to global biodiversity (Dudgeon et al 2006, Reid et al 2019).

The prospects for freshwater biodiversity around dams (Rolls et al 2018, Turgeon et al 2019), require a more organized assessment for the prediction, restoration and management of the resulting changes in river ecosystems. Macroinvertebrates, which act as key organisms in aquatic food webs, are ideal candidates for studying how aquatic biota and the whole food webs respond to dam construction (Allan and Castillo 2007, Mbaka and Mwaniki 2015, Mor et al 2018), although also other taxonomic groups are considered to show relevant capacity in the detection of anthropogenic stresses (Hering et al 2006). First, because macroinvertebrates are important linkages in the food web, their responses are influenced by changes in primary productivity (e.g. the productivity of algae and macrophytes, and the input of terrestrial organic matters) and further affect the composition, abundance and dynamics of higher-level consumers (e.g. fishes; Malmqvist and Englund 1996, Wallace and Webster 1996, Mcneely and Power 2007). Second, owing to their relatively small lifetime movement in a river segment, macroinvertebrates are better in portraying local environmental changes than other active consumers (e.g. fishes and waterbirds; Rosenberg and Resh 1993, Ormerod and Tyler 1993, Morse et al 2007). Third, many studies assessing river condition have shown that macroinvertebrates are sensitive ecological indicators for reflecting and monitoring multiple anthropogenic disturbances, including flow alteration, pollution, eutrophication, climate change and biological invasions (Bonada et al 2006, Fornaroli et al 2018, Mellado-Díaz et al 2019, Engels et al 2019, Guareschi and Wood 2019). In addition, macroinvertebrates are a taxonomically and functionally diverse group (Hauer and Resh 2007), constituting a large proportion of global freshwater biodiversity (Balian et al 2008).

Responses of macroinvertebrates to dams occur at multiple organization levels from individuals to communities (Brittain and Saltveit 1989, Krajenbrink et al 2019, Wang et al 2019). For example, thermal and flow alterations can change macroinvertebrate life histories (Brittain and Saltveit 1989), drift and dispersal processes (Kennedy et al 2014, Holt et al 2015, Brooks et al 2018), and interspecific relationships (Mor et al 2018), thus further altering their community structure (Lessard and Hayes 2003, Phillips et al 2015, Mor et al 2018) and ecosystem functions (Martinez et al 2013, White et al 2016). Although numerous studies have evaluated the effects of dams on macroinvertebrates (Mbaka and Mwaniki 2015, Wang et al 2019), the conclusions of single case studies diverge and even contradict one another across different regions and taxonomic groups. These discrepancies could be attributed to differences in climate (Turgeon et al 2019, Carr et al 2019), dam size (Poff and Hart 2002, Mor et al 2018), downstream distance from the dam (Ward and Stanford 1983, Ruhi et al 2018), life-history traits (Brittain and Saltveit 1989, Petts et al 1993, Petrin et al 2013), and phylogenetic position of the macroinvertebrate group under investigation (Campbell and Novelo-Gutiérrez 2007). Moreover, a recent study has shown that the influence of dams on macroinvertebrates is scale dependent, suggesting that understanding of river impoundment effects on downstream biota should be extended from individual rivers to larger regions (Krajenbrink et al 2019).

Accurate predictions and effective management strategies addressing the negative effects of dams on aquatic organisms and riverine ecosystems rely on the synthesis and quantification of the general response patterns of key taxa (e.g. linkage organisms, such as macroinvertebrates; higher-level consumers, such as fishes; Turgeon et al 2019) across different geographical and environmental settings. Therefore, we conducted a global meta-analysis to examine the various responses of macroinvertebrate assemblages to multiple factors to increase our understanding of dam impacts on macroinvertebrates in a general context. Rather than focussing on single case studies one-by-one, we provided generalizations across studies, which is the main aim of the meta-analytical approach (Gurevitch et al 2018). We aimed to answer the following questions: 1) What are the overall effects of dam construction on macroinvertebrate assemblages (i.e. species richness and abundance)? 2) Do the responses of macroinvertebrate assemblages differ according to the climate conditions (i.e. climatic zones, dam altitudes), main characteristics of the dam (i.e. dam height and downstream distance from the dam), and taxonomic groups? 3) What are the major environmental factors (or local habitat features) that affect macroinvertebrate richness and abundance at regulated sites?

2. Materials and methods

2.1. Literature search strategy
We conducted an extensive literature search for primary research papers that tested the effects of dams on riverine macroinvertebrates. The literature search was conducted between October 2018 and
April 2019. Relevant studies published from 1900 to 2019 were obtained from two databases (i.e. Web of Science and Scopus) using the following search term combinations: (dam OR dams OR weir OR weirs OR ‘bypass tunnel’ OR dike OR dikes OR dyke OR dykes OR hydropower’ OR hydropoeaking OR ‘hydroelectric project’ OR ‘hydroelectric plant’ OR ‘hydroelectric power’) AND (macroinvertebrate* OR invertebrate* OR zoobenthos OR macrozooobenthos OR macrofauna OR ‘EPT’ OR ‘aquatic insect’* OR Ephemeroptera OR Plecoptera OR Trichoptera OR mayfly OR stonefly OR caddisfly OR Chironomidae* OR Oligochaeta OR Limnodiuridus OR Mollus* OR Bivalvia OR Gastropods OR Snails OR ‘functional feeding group’ OR (Crustacea NOT (zooplankton OR Cladocera OR Copepoda))). These terms (e.g. dam, weir and dyke) were chosen due to these physical structures might affect the environmental conditions and the connectivity of a river network, thereby having further effects on the aquatic biota. We refined the retrieved publications strictly followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (appendix figure S2.1 (available online at stacks.iop.org/ERL/15/124028/mmedia); Moher et al 2009).

2.2. Inclusion and exclusion criteria
We further refined publications based on the following criteria by scanning the title, abstract and full text: 1) field studies evaluating the effects of dams on macroinvertebrates; 2) studies including comparisons of upstream reference (i.e. upstream sites are assumed to represent unregulated conditions) sites and downstream impaired (which are regulated) sites of dams; 3) studies reporting data for species richness or abundance (or both) of macroinvertebrates; 4) sampling sites located at the same river order as the dam, since rivers of different orders inherently may have completely different species compositions (Vannote et al 1980) and are not directly comparable; and 5) studies reporting extreme hydrological events (e.g. large flow release, flooding) were excluded.

2.3. Data extraction
Most data were extracted from tables in the main text or from datasets available in appendices and supplementary materials associated with the research papers. When data were presented in figures, they were extracted using ImageJ software (version 1.57, Schneider et al 2012). Since the direct comparison of pre-damming and post-damming macroinvertebrate communities is often not possible (due to the absence of pre-impoundment baseline monitoring data), most studies have compared communities at regulated sites with those at reference sites. Thus, we adopted this common approach in this meta-analytical study. We extracted the mean richness/abundance, sample size and standard deviation (SD) of macroinvertebrates or specific taxonomic groups for both reference sites and regulated sites, since species richness and abundance are the most widely-used metrics to portray the ecological effects of dams (Martínez et al 2013). For publications including two or more regulated sites/reference sites, we extracted the above data for all possible comparisons, i.e. each regulated site was compared to one or more reference sites. Thus, one publication may contain one or more data points depending on the number of sampling sites and specific taxonomic groups involved.

We recorded data concerning study characteristics as explanatory factors, including the following: 1) geographic location of the dam (i.e. climatic zones, according to the Köppen-Geiger climate classification system: tropical, arid, temperate, cold and polar; Köppen 1936, Beck et al 2018); 2) altitude of the dam location (m); 3) dam types; 4) dam height (m); 5) downstream distance from the dam (km); 6) taxonomic groups; 7) downstream flow discharge (m$^3$ s$^{-1}$); and 8) changes in downstream environmental factors (the values at the downstream sites minus those at the upstream sites) with high occurrence rates (i.e. water temperature (WT, °C), current velocity (m s$^{-1}$), conductivity (µs cm$^{-1}$), total nitrogen (TN, mg l$^{-1}$), total phosphorus (TP, mg l$^{-1}$), dissolved oxygen (DO, mg l$^{-1}$), pH and substrate types: boulder (>256 mm), cobble (64–256 mm), pebble (16–64 mm), gravel (2–16 mm), and silt (<2 mm)) were used to characterize changes of habitat features (appendix figure S2.2). Although the effects of dams on macroinvertebrates were also dependent on operation (water release) type, for example, surface or deep-water release, only 6 out of 54 publications clearly stated the water release type (5 were deep release, and one was surface release). Therefore, this study could not evaluate the contributions of different dam operation types to changes in macroinvertebrate richness and abundance. When the above data on study characteristics were not available in the paper, we searched for relevant information in other publications and website resources in the Internet (i.e. The Australian National Committee on Large Dams Incorporated, 2010, www.fao.org/nr/water/aquastat/dams/, http://ndpdp.stanford.edu/data_access/international_dams_list.php, http://damnet.or.jp/Daminran/binra n/TopIndex_en.html). Dam coordinates and impoundment areas were obtained from Google Earth. The downstream discharge data were estimated according to the methods of Wanders et al (2019), if not available in the original literature (appendix table S1.1).

2.4. Quantification of effect sizes
Differences in the overall effect size (e.g. if the mean of any metrics differed between the regulated sites and the reference sites) were assessed via Hedges’ $d$ metric.
(which is one of the expressions of the standardized mean difference; Hedges and Olkin 1985). Hedges’ \( d \) is often used for ecological meta-analytical studies because it adjusts for differences among studies in terms of sampling effort, corrects for small sample sizes, and can handle zero values for control or treatment groups (Rosenberg et al 2013). Hedges’ \( d \) was calculated as

\[
d = \frac{\bar{X}_{\text{downstream}} - \bar{X}_{\text{upstream}}}{S}
\]

where \( S \) is the pooled SD and was calculated as

\[
S = \sqrt{\left(\frac{(N_{\text{downstream}} - 1)s_{\text{downstream}}^2 - (N_{\text{upstream}} - 1)s_{\text{upstream}}^2}{N_{\text{downstream}} + N_{\text{upstream}} - 2}\right)}.
\]

\( J \) is a weighting factor based on the number of replicates (\( N \)) per data, and was calculated as

\[
J = 1 - \frac{3}{4(N_{\text{downstream}} - N_{\text{upstream}} - 2)}.
\]

The variance of Hedges’ \( d \) was calculated as

\[
\nu_d = \frac{N_{\text{downstream}} + N_{\text{upstream}}}{N_{\text{downstream}}N_{\text{upstream}}} \times \frac{d^2}{2(N_{\text{downstream}} + N_{\text{upstream}})}.
\]

Hedges’ \( d \) for any given metric is negative (<0) if the estimates (e.g. species richness, abundance) are lower for downstream sites than for upstream sites because of a dam and positive (>0) if the estimates are higher. Hedges’ \( d \) values that are close to zero (≈0) indicate little or no effects of a dam.

In all the subsequent meta-analyses and meta-regressions, the observed effect sizes (Hedges’ \( d \)) were weighted by the inverse of the sampling variances (i.e. the SD). For studies that do not report estimates of the SD, we used Bracken (1992) approach to impute the SD using the coefficient of variation from all complete cases (Bracken 1992). These analyses were performed using the package ‘metafor’ in R (Lajeunesse 2016, R Core Team 2016).

2.5. Data analysis

To control for non-independence within the dataset owing to multiple effect sizes per study (Nakagawa and Santos 2012), we performed multilevel mixed-effects meta-analyses with restricted maximum likelihood via the R package ‘metafor’ (version 1.9–8, function rma.mv, Viechtbauer 2010, R Core Team 2016). All analyses were performed separately for the richness and abundance data. We treated study identity and taxon identity as random effects in our models. Random effects were retained or discarded based on the models’ Bayesian information criterion, which is more restrictive than Akaike’s information corrected criterion (Burnham and Anderson 2003). The final retained random-effects structure was (1|Study + 1|Taxon) for both richness and abundance (appendix table S1.2).

Multilevel random-effects meta-analyses were conducted and single mixed-effects meta-regression models were constructed according to different objectives. We assessed the overall reductions in the richness and abundance of macroinvertebrates in the reference vs. dam-impacted sites via multilevel random-effects meta-analysis. Formal Cochran’s Q tests (Q) were used to test the residual heterogeneity of effect sizes, i.e. whether the variability in the observed effect sizes was larger than would be expected based on sampling variability alone. We introduced a number of moderators (appendix table S1.3) to explain the variability in effect sizes if their residual heterogeneity was significant.

We constructed single mixed-effects meta-regression models to assess the relationships between Hedges’ \( d \) and climatic zones, altitude of the dam location, dam height, downstream distance from the dam, and taxonomic groups (appendix table S1.1). Single mixed-effects meta-regression models were also used to estimate Hedges’ \( d \) of the interactions of pairs of variables, i.e. taxonomic groups × climatic zones, taxonomic groups × dam height/altitude/downstream distance from the dam, and climate × dam height/altitude/downstream distance from the dam. Continuous variables were log-transformed and fitted as quadratic polynomials to account for non-linear relationships. Models with categorical factors were also constructed without an intercept to obtain the mean effect size of each level. The heterogeneity captured by the moderators in each independent meta-regression was assessed with omnibus tests (Q statistics, QM; appendix table S1.3). We also used generalized linear models to determine the relationships between Hedges’ \( d \) and changes in habitat features, ultimately aiming to explore how environmental factors may affect macroinvertebrate richness and abundance.

2.6. Publication bias

Publication bias, i.e. if only studies detecting significant effects were published, was assessed using funnel plots by including precision (1/standard error (SE)) as
a covariate with the \texttt{rma.mv} function in the R package \texttt{metafor} and using meta-analytic residuals. Rosenberg's fail-safe numbers were also calculated to assess the robustness of our results against publication bias (Rosenberg 2005). Asymmetric funnel plots and fail-safe numbers less than \(5n + 10\) indicate publication bias, which means that macroinvertebrate richness or abundance significantly affected by dams is easier to publish than that less significantly affected.

3. Results

3.1. Description of the data

In total, 54 publications with publication dates ranging from 1970 to 2019 met our criteria, and 3849 data points (394 for richness and 3455 for abundance) were extracted. Differences in the numbers of data points between richness and abundance were due to the fact that some studies did not report richness data, but only focused on abundance data. This meta-analysis involved 84 dams spanning 22 countries across five major climatic zones (figure 1). Most studies were from temperate (25) and cold regions (22), whereas studies from arid (5), tropical (4) and polar (1) regions were scarce. The altitude of the dam location ranged from 50 to 3120 m above sea level, and the dam height ranged from 0.35 to 219 m. The downstream distance of regulated sites from dams ranged from 0 to 206 km. This study classified the identified taxa into 14 main taxonomic groups: eight aquatic insect orders (Ephemeroptera, Odonata, Plecoptera, Hemiptera, Diptera, Trichoptera, Coleoptera, and Megaloptera) and six aquatic non-insect groups (Platyhelminthes, Nematomorpha, Oligochaeta, Hirudinea, Crustacea, and Mollusca; appendix table S1.1, appendix Data S3).

3.2. Overall effect sizes

The presence of dams resulted in distinct effects on macroinvertebrate richness and abundance along longitudinal river gradients. The overall effect size of dams on macroinvertebrate richness was negative (effect size: \(-1.46, P = 0.015\), figure 2(a)), while that of dams on abundance was positive (effect size: \(2.15, P = 0.006\), figure 2(b)). There was significant residual heterogeneity in the random-effects meta-analysis for the richness dataset (\(Q = 23350.46, P < 0.001\)) and for the abundance dataset (\(Q = 202323.60, P < 0.001\)).

3.3. Effect sizes in different climatic zones and along with dam characteristics

The response of macroinvertebrate assemblages to dam revealed obvious and consistent zonation across different climatic zones and altitudinal regions (figure 3). However, the responses of macroinvertebrate richness and abundance were distinctly different. Specifically, below-dam reductions in richness were most pronounced in the cold region (mean effect size: \(-3.02, P < 0.001\)) and high-altitude regions and were least pronounced in the tropical region (\(-1.44, P < 0.001\)) and low-altitude regions (figures 3(a) and (c)). In contrast to the pattern of richness reduction, downstream abundance was much higher than upstream abundance in all climatic regions, except the polar region, with downstream abundance increases being noticeably higher in the tropical (\(7.49, P = 0.008\)) and arid regions (6.26, \(P < 0.001\)) than in the temperate (0.72, \(P = 0.018\)) and cold regions (2.28, \(P = 0.025\); figure 3(b)). Meanwhile, abundance increases were most pronounced in low-altitude regions, and they were less pronounced in high-altitude regions (figure 3(d)). However, compared with dams in other regions, significant relationship could not be found in polar regions (richness: \(0.319, P = 0.890\); abundance: \(-1.543, P = 0.842\)), due to the low number of studies in this climatic zone. In addition, the dams in the tropical regions had different effects on macroinvertebrate assemblages, with the reduction of richness likely decreases and addition of abundance increases along with the altitude of the dam location (appendix figures S2.3(a) and (d)).

Different dam types had distinct influences on macroinvertebrate assemblages (table 1). Macroinvertebrate richness reduction was significant for hydropower and multiple usage dams. While the increase of macroinvertebrate abundance was shown in most cases, it significantly increased especially at sites downstream of water supply dams. In terms of dam size (height as a proxy), the reduction in downstream richness intensified with increasing dam height, while the abundance increase was more pronounced in the sites downstream of small dams than that of large dams (figures 4(a) and (b)). Besides, dams in tropical regions showed different patterns of impact on macroinvertebrate richness, with the effect on richness decreasing with increasing dam height (appendix figure S2.3(b)). Along with the increase of downstream distance from the dam, the richness reduction decreased while the abundance addition increased (figures 4(c) and (d)). Additionally, the abundance increases along the distance were more significant in the tropical regions than in other regions (appendix figure S2.3(f)). Furthermore, the richness reduction and abundance increase of macroinvertebrates under dams were coupled across climatic zones, dam altitudes, dam sizes, and downstream distances from the dams (figures 3(a) vs. (b); figures 3(c) vs. (d); figures 4(a) vs. (b); figures 4(c) vs. (d)), i.e. when the richness slightly decreased, the increase in abundance was more significant (or vice versa).

3.4. Effect sizes of taxonomic groups

The effects of dams on macroinvertebrate diversity varied among taxonomic groups (figures 5(a) and (b)). Among aquatic insects, Plecoptera (richness, \(-7.68, P < 0.001\); abundance, \(-3.48, P < 0.001\),
Figure 1. Geographical locations of the 54 studies included in the meta-analysis. The black dots indicate studies and may represent multiple effect sizes. The climatic zones are identified according to the Köppen-Geiger climate classification.

Figure 2. Plots of 394 and 3455 effect size estimates for macroinvertebrate (a) richness and (b) abundance, respectively. Effect size (Hedges’ $d$), black dots with the 95% CI as grey lines. Overall weighted mean effect size estimate with red dashed lines and black diamonds.

Trichoptera ($-6.04$, $P < 0.001$; $-0.79$, $P = 0.271$) and Hemiptera ($-4.35$, $P < 0.05$; $6.06$, $P < 0.01$) were most sensitive to dam construction, followed by Diptera ($-1.25$, $P = 0.476$; $1.41$, $P < 0.01$), while Ephemeroptera ($0.39$, $P = 0.803$; $0.82$, $P = 0.287$), Odonata ($2.60$, $P = 0.141$; $2.78$, $P = 0.110$) and Coleoptera ($-1.23$, $P = 0.484$; $-0.61$, $P = 0.530$) did not appear to be as sensitive. No richness data were available for non-insect groups in this study (due to their absence in the literature). In terms of abundance for non-insects (figure 5(b)), the increases were significant for Platyhelminthes ($4.61$, $P < 0.05$), Hirudinea ($0.91$, $P < 0.001$), Crustacea ($15.86$, $P < 0.001$) and Mollusca ($11.15$, $P < 0.001$), but not for Nematomorpha ($0.91$, $P = 0.698$) and Oligochaeta ($1.41$, $P = 0.270$). The richness
and abundance of the different taxonomic groups also varied in response to dams in different climatic zones, dam altitude, dam height, and downstream distance from the dam (appendix figures S2.4–S2.6).

3.5. Variability of effect sizes explained by changing habitat features

The responses of habitat features to dams varied among climatic zones, dam locations, dam sizes and downstream distances from the dams (appendix figures S2.7–2.12). Overall, fine substrates (gravel and silt), WT, DO, and TN increased at sites downstream of dams, while coarse substrates (boulders and pebbles), pH, conductivity, velocity, and TP decreased (appendix figure S2.7). Data for changes in the downstream discharge were not available, but the discharge was relatively low in tropical and polar regions and in high-altitude regions (appendix figure S2.8).

Downstream WT and TN additions were higher in tropical regions than in other regions, while velocity reduction was low (appendix figure S2.9). The reductions in coarse substrates, pH and velocity, accompanied by the addition of fine substrates, DO, and TN, all intensified along with altitude (appendix
Figure 4. Changes in macroinvertebrate richness and abundance with dam height and downstream distance. For richness (a), (c) and abundance (b), (d), (a) and (b) indicate dam height, and (c) and (d) indicate downstream distance from the dam; effect size (Hedges’ $d$) = 0, dashed line; predicted mean effect size (black lines, with the 95% CI in pink). The size of the data points (in blue) is proportional to the sampling variance. The results were obtained with single meta-regressions.

Figure 5. Changes in macroinvertebrate (a) richness and (b) abundance for different taxonomic groups. Effect size (Hedges’ $d$) = 0, dashed line. The results were obtained with single meta-regressions. The solid circles indicate a significant effect, and the open circles indicate a non-significant effect.

The reductions in coarse substrates, pH, conductivity and TP, accompanied by the addition of fine substrates, WT and TN, were more significant at sites downstream of large dams than at downstream of small dams (appendix figure S2.11). In addition, the additions of WT, DO, and TN and the reduction in velocity were high at sites in closer proximity to the dams, while pH and TP reductions were high at
sites farther downstream (appendix figure S2.12). The variation in downstream richness reduction could be primarily explained by the decrease in the amount of coarse substrate (boulder: 22.4% variability; cobble: 10.8%) and the increase in the amount of fine substrate (silt: 27.9%), pH (17.2%) and conductivity (12.8%). Other factors, such as WT and velocity, were significantly correlated with richness reduction, but they explained very low percentages of the variability (figure 6(a)). The increase in downstream abundance was significantly correlated with WT, DO, pH, TN and TP, but all of these factors also explained a very low percentage of the variability (figure 6(b)).

3.6. Publication bias

The funnel plots revealed no obvious publication bias (appendix figure S2.13). Rosenberg's fail-safe numbers were large enough for both richness ($N = 362,047$, $P < 0.001$) and abundance ($N = 802,400$, $P < 0.001$) to be confident about the reliability of the estimates, which were larger than $5n + 10$ (richness: 1980; abundance: 17,305), implying that publication bias can be ignored in our study.

4. Discussion

This global meta-analysis revealed the heterogeneity of dam impacts on macroinvertebrate assemblages (i.e. species richness and abundance) among climatic zone, dam altitude, dam height, downstream distance from the dam, and taxonomic groups. Overall, while dams had negative effects on macroinvertebrate richness, they had positive effects on macroinvertebrate abundance. The reduction in richness and the increase in abundance varied consistently across climatic zones and altitude levels. Macroinvertebrate richness reduction was greater in cold and high-altitude regions, while the increase in abundance exhibited the opposite response pattern to dams, i.e. the increase in abundance was greater in tropical and low-altitude regions. The degree of macroinvertebrate abundance increase was generally coupled with the degree of richness reduction, and vice versa. In terms of taxonomic groups, the response of aquatic insect richness and abundance to dams varied, with Plecoptera, Trichoptera, and Hemiptera being the most sensitive groups, but for aquatic non-insects, the overall abundance increased at dam-impacted sites. Richness reductions were likely to be explained primarily by changes in downstream substrate composition, while abundance increases can barely be attributed to changes in any of the considered environmental factors characterizing habitat features.

4.1. Effects of changing habitat features on macroinvertebrate richness and abundance

The reduction in downstream macroinvertebrate richness detected in this meta-analysis study can be attributed to changes in substrate composition (figure 6(a)), which is consistent with the findings of other studies (Ward and Stanford 1979, Cortes et al 2002, Extence et al 2011). The decrease in coarse substrates and increase in fine substrates were generally concurrent at the sites downstream of dams (Petts 1984). Coarse substrates can provide a wide range of refuges and a high environmental heterogeneity, and thus can support diverse sets of macroinvertebrate taxa (Beisel et al 1998, Mathers and Wood 2016). In contrast, fine substrates can homogenize benthic habitats and decrease the available space among coarse substrates for macroinvertebrates (Harrison et al 2007, Extence et al 2011, Buendia et al 2013). Moreover, fine sediments can particularly damage the gills of macroinvertebrates and thus are detrimental to taxa with a high oxygen demand, e.g. some mayfly species (Jones et al 2012, Descloux et al 2013). Secondarily, changes in physicochemical factors, such as pH, conductivity and velocity, may also reduce richness by affecting life-history processes, food sources and species interactions (Hart and Finelli 1999, Wellnitz et al 2001, Lancaster and Downes 2010). However, we found that these factors explained less variation in richness reduction than did the changes in benthic substrates. Therefore, the richness reduction was very likely driven by loss of taxa and the replacement of coarse substrates by fine substrates.

We found that the macroinvertebrate abundance downstream of dams generally increased (figure 2(b)) and, interestingly, this increase was associated with reduction of richness (figures 3, 4 and 6). However, on the basis of the data and results, it is difficult to infer whether there is a causal relationship between the patterns shown by the response metrics. The first likely explanation for abundance increase would be replacement of taxa, reflecting by the recolonization by taxa with high reproductive output ones, such as chironomids and Oligochaeta (appendix Data S3.1; Cortes et al 2002, Katano et al 2009). These taxa might benefit from the released large amounts of planktonic and sestonic production which were accumulated for a long time in the reservoir, finally resulting in the increase of their density (Lessard and Hayes 2003, Tao et al 2020). Second, the increase in abundance could also be explained by competitive release. Once a few species are lost because of a disturbance, the remaining taxa are able to obtain more resources for growth and reproduction, resulting in increased population densities (Kareiva 1982). Third, the increased WT, DO, and nutrient conditions and the reduced flow and velocity may also
have contributed to the increase in macroinvertebrate abundance through providing macroinvertebrates with more energy and food sources (Matthaei et al 2010) and causing macroinvertebrate individuals to concentrate into a smaller area of the benthic habitat (Dewson et al 2007). However, due to the very low amount of variation explained by these factors (figure 6(b)), the data and results of this study do not provide adequate support for this explanation.

4.2. Effects of climatic zone, dam altitude, dam height and downstream distance from dam on macroinvertebrates

The results of our study demonstrated that the effects of dams on macroinvertebrate richness showed clear and consistent variation across climatic zones and altitudes. The influencing mechanisms associated with climatic zones and altitudes could be the same and may be related to biodiversity dynamics (e.g. stability, resistance and resilience) and the magnitude

Figure 6. Relationship between effect size (Hedges’ $d$) for macroinvertebrate (a) richness and (b) abundance with changes in environmental factors. WT: water temperature, DO: dissolved oxygen, TN: total nitrogen, TP: total phosphorous. Boulder, Cobble, Pebble, Gravel and Silt are substrate types. Regression lines are shown in black (with the 95% CI in pink). The black dashed line indicates no effect.
of environmental change. First, from the perspective of processes, disturbance outcomes may be initially determined by the resistance of ecosystems, which is largely dependent on biodiversity dynamics. It has been demonstrated that high biodiversity can increase ecosystem resistance to disturbances (Naæem and Li 1997, Isbell et al 2015). Generally, broad-scale variation in biodiversity is strongly correlated with climate and available energy (Currie et al 2004). In tropical and low-altitude regions, high primary productivity and habitat heterogeneity can support diverse aquatic biota and complex community structures (Dudgeon 2008), thus forming a stable network structure and potentially increasing the resistance of river ecosystems to dam disturbance. In contrast, in high-altitude and high-latitude waterbodies, low primary productivity generally restricts the survival, development, and reproduction of macroinvertebrates, resulting in lower diversity and resistance (Maïolini and Bruno 2007, Scott et al 2011, Culp et al 2019). Second, the outcomes of disturbances are determined by the resilience of ecosystems. High-diversity regions naturally have a large regional species pool, which is an important source for macroinvertebrate recolonization at regulated sites (Sundermann et al 2011, Tonkin et al 2014). In such regions, the diminished richness due to dam disturbance could be supplemented from adjacent river sections, especially by aquatic insects with a strong dispersal ability. Third, the degree of environmental changes under dam disturbance varies from region to region (e.g. Carlisle et al 2011), which could lead to among-region differences in richness reductions. Environmental conditions in cold and high-altitude regions are often challenging (e.g. Heino et al 2020), and the disturbances caused by dams could thus lead to greater changes in the river environment in these regions (Baxter 1977). For example, the negative WT increase in cold regions (appendix figure S2.9) and greater fine sediment addition at high altitudes (appendix figure S2.10) caused a severe reduction in downstream macroinvertebrate richness compared with that in other regions. Moreover, flow regulation has resulted in seasonal interruptions in high-altitude rivers (Gabbud and Lane 2016, Bruno et al 2019), and many studies have shown that interruptions (e.g. flow intermittence) have a significant effect on macroinvertebrate community structure and composition (Mcintosh et al 2002, Belmar et al 2019).

The overall effect of dams on macroinvertebrate richness reduction was found to increase with dam size and decrease with downstream distance, which is in line with previous studies (Mellado-Díaz et al 2019) and conforms to the logic of disturbance intensity and recovery processes. Large dams can cause more substantial environmental changes (e.g. those related to WT, flow regime, sediment dynamics and nutrients; Poff and Hart 2002, Mbaka and Mwaniki 2015), whereas small dams tend to pass peak flows and are therefore less likely to substantially change the WT and nutrient conditions (Poff and Hart 2002). The influence of large dams on macroinvertebrate assemblages in the present study was also partly indicated by a greater reduction in nutrient levels (e.g. TP) at downstream sites (appendix figure S2.11). In addition, the effects of dams were shown to be more drastic in the areas just downstream of the dam than in areas farther downstream (Ellis and Jones 2013). Generally, water release has the greatest effects in the areas immediately below the dam through scouring and flow regime alterations (Mellado-Díaz et al 2019). However, it has been suggested that this influence can be attenuated during the environmental recovery process along longitudinal gradients (Song et al 2019). Notably, tributaries of downstream rivers can also contribute to community recovery in disturbed river sections by providing new colonists and by creating transitional habitats (Jones and Schmidt 2018, Milner et al 2019).

4.3. Responses of different taxonomic groups

Different taxonomic groups respond differently to dam construction, which could be caused by the differences in assemblage diversity (i.e. taxonomic and functional diversity), life-history characteristics, and niche breadth (e.g. environmental tolerance) among taxonomic groups. For instance, Ephemeroptera comprises numerous species (Barber-James et al 2007) that are affected by different mechanisms and are widely adapted to a range of aquatic environments (Brittain and Saltveit 1989, Malmqvist and Englund 1996). In addition, the various responses of macroinvertebrates to dams may also be related to differences in dispersal capability (Heino et al 2015, Tonkin et al 2018b) because the reduced connectivity caused by dams hinders organisms’ dispersal in the river network (Ward and Stanford 1983, Dynesius and Nilsson 1994). The distinct dispersal abilities of aquatic insects (with overland flight capability) and non-insects (passive overland dispersal at best) could lead to differences in their recolonization abilities after dam construction and subsequent continuing disturbance. In addition, macroinvertebrate taxa have different life-history characteristics (i.e. distinct differences in the voltinism of mayflies and stoneflies) in regulated lotic ecosystems, which reflects their resilience to environmental changes and their different responses to dam disturbance (Petrin et al 2013). Lastly, macroinvertebrate taxa with different tolerances to natural and anthropogenically-altered environmental conditions (e.g. sensitive taxa, such as EPT, and tolerant taxa, such as Oligochaeta) also respond distinctly to dams because of changes in the downstream environment.
Generally, EPT are considered to be sensitive taxonomic groups that respond quickly to dam-induced environmental changes (Stanford and Ward 1979, Mihalicz et al. 2019, Krajenbrink et al. 2019). However, the results of our meta-analytical study demonstrated that Ephemeroptera, as a whole, are not significantly affected by dams (figure 5). This may be related to species turnover within Ephemeroptera in relation to environmental change; for example, sensitive species could have been replaced by tolerant species (Brittain and Salveit 1989, Buendia et al. 2013). This kind of a turnover could also be attributed to changes in species with different life-history characteristics (Petren et al. 2013). However, because EPT taxa are commonly used as indicators of water quality and anthropogenic disturbance (Carlson et al. 2018, Krajenbrink et al. 2019, Mihalicz et al. 2019), the importance of Ephemeroptera in further dam impact assessments and monitoring should be given due attention.

The richness of Hemiptera notably decreased under dam disturbance, while their abundance significantly increased. This finding contrasts with decreases in richness being dependent on sensitive taxa, but is consistent with increases in abundance relying on tolerant taxa (Camargo et al. 2005). Aquatic Hemiptera are abundant and occur on most continents (Polhemus and Polhemus 2008), with various species displaying different tolerances to environmental change (Jansson 1977). Hemiptera have a strong dispersal capability and are early colonizers if newly-flooded habitats (Turic et al. 2015). Dam-induced flow alterations can cause fluctuation events in the habitats of Hemiptera species, which could result in a rapid decline in richness, at least to some extent. However, some tolerant species can also recolonize and show increases in population abundance. Owing to the diverse responses of Hemiptera species to heterogeneous environmental conditions (e.g. Jansson 1977, Skern et al. 2010) and the substantial decrease in the richness of Hemiptera in response to dam disturbance, our study suggests the use of this taxonomic group (via its richness) as a potential indicator of dam disturbance in river ecosystems.

4.4. Limitations, predictions and restoration implications

Notably, most data points of macroinvertebrate richness and abundance in this study were from sites downstream of hydropower plant-related and multiple-used dam. However, our results showed that the responses of richness and abundance of macroinvertebrate are similar in most cases among dam types (table 1). This finding indicates a general response pattern of macroinvertebrate assemblages to dams, although different type of dams may have distinct operation modes that could result in varied response patterns shown by organisms downstream from dams. Meanwhile, the alterations of downstream macroinvertebrate richness linked to environmental conditions (e.g. thermal regime and seston availability) are suggested to be affected by the type of water release of dams (e.g. where, how and when; Ward and Short 1978, Stanford and Ward 1979, Haxton and Findlay 2008, Olden and Naiman 2010). Unfortunately, owing to limitations of the literature data, we were unable to examine the effects of dam release type on macroinvertebrate richness and abundance. In addition, dams with different age (i.e. the interval time from dam construction to sampling) may have distinct influence on downstream biota. However, the heterogeneity of effect sizes caused by the interval time were smaller than those of other parameters, even for richness, the Q statistics (QM) were not significant (appendix table S1.3), suggesting a slight effect of interval time on the heterogeneity of effect sizes for macroinvertebrate richness in the present dataset. Thus, we did not detect the effect of interval time on macroinvertebrate, but which should be highlighted in future case studies and global syntheses. Furthermore, although taxonomic resolution often varies among different regions, it would have little effect on the main results because previous studies have suggested that the responses of richness or composition of biotic communities to ecological gradients may not necessarily be strongly affected by taxonomic resolution (e.g., Jones 2008, Vijapure and Sukumaran 2019).

By untangling the roles of different factors in dam impacts on macroinvertebrates, our study provides evidence-based knowledge to help aquatic environmental managers to make defensible decisions. These include predicting dam effects on riverine biota, assessing and monitoring of river ecosystems, as well as guiding sustainable dam development, planning and restoration. First, for example, the finding showing the coupled relationship between reduced richness and increased abundance increases the ability to predict macroinvertebrate responses to dam construction. The clear variation in macroinvertebrate responses across climatic zones and altitudes highlights the vulnerability of river ecosystems to dam disturbance specifically in cold regions. Additionally, further studies in polar regions are recommended to be conducted due to the paucity of data to predict the effects of dam construction in the present study ($n = 4$ for richness and abundance, respectively). Second, the different sensitivities of different taxonomic groups in their response to dams could be informative for the further use of macroinvertebrates in the evaluation and monitoring of the ecological effects of dams. Particular attention should be paid to the traditionally-used sensitive taxa (e.g. EPT) and overlooked taxa (e.g. Hemiptera) identified in this study. Additionally, due to the large variation
in the responses among taxonomic groups, trait-based analyses would aid the understanding of the ecological responses of macroinvertebrates to dam disturbance (Martínez et al 2013, Alahuhta et al 2019, Wang et al 2019). Third, findings concerning climatic zones and dam characteristics (i.e. the altitude of the dam location and dam height) also have implications for future dam development, including site selection and the scale of new dams. Lastly, considering the strong influence of substrate composition on macroinvertebrate assemblages, future restoration and management programs should devote more attention to this aspect of the river environment (Cortes et al 2002).

5. Conclusions

Collectively, this study quantitatively synthesized general response patterns of macroinvertebrates (i.e. richness and abundance) to dams across different environmental settings based on data derived from case studies covering a wide range of geographical areas. Factors contributing to the variation in dam impacts on macroinvertebrates were comprehensively considered. The ecological consequences of dams on macroinvertebrates depend largely on the ecological context. Changes in downstream substrate composition likely play a vital role in driving richness reduction, replacement of taxa, and abundance increase of macroinvertebrates in response to dams. According to this global quantitative synthesis, it is obvious that dams negatively affect macroinvertebrates to various degrees, but the responses of macroinvertebrate assemblages become more predictable when abiotic factors related to dam-caused changes can be quantified. In addition, the findings of our study also have broad implications for the assessment and monitoring of dam impacts, providing constructive suggestions for future dam development in rivers over the world.

Acknowledgments

We appreciated Professor Jessica Gurevitch and Dr Shuang Zhang for their suggestions in data processing. This study was financially supported by the National Natural Science Foundation of China (No. 41907400, 41867072, 41807402), the Biodiversity Survey and Assessment Project of the Ministry of Ecology and Environment, China (No. 2019HJ2096001006), China Postdoctoral Science Foundation (No. 2019M663583), the Yunnan Applied Basic Research Projects (No. 2019FB131, 202001BB050053) and Yunnan University ‘Double First-Class’ Construction Project (Nos. C176210215, C176240208002). JW was partly supported by the project ‘Regoverning the existing hydropower system: integrating ecological, economic and societal aspects of sustainability’ funded by the Academy of Finland.

Statement of authorship

C D, J T, D H and J W conceived and designed the research, J W and W S extracted the data; J W, L D and M H analyzed the data and made the figures. J W wrote the manuscript; C D, J H, J T, X, J and D H contributed to the discussion and, subsequently, various versions of the manuscript; all authors reviewed the manuscript before submission.

Data availability statement

All data that support the findings of this study are included within the article (and any supplementary information files).

ORCID iD

Jun Wang  @ https://orcid.org/0000-0003-2481-1409

References

Alahuhta J, Erös T, Kärnä O M, Soininen J, Wang J J and Heino J 2019 Understanding environmental change through the lens of trait-based functional and phylogenetic biodiversity in freshwater ecosystems Environ. Rev. 27 263–73

Allan J D and Castillo M M 2007 Stream Ecology: Structure and Function of Running Waters 2nd edn (Berlin: Springer)

Balian E V , Leveque C, Segers H and Martens K 2008 Freshwater Animal Diversity Assessment (Berlin: Springer)

Barber-James H M, Gattollatti J L, Sartori M and Hubbard M D 2007 Global diversity of mayflies (Ephemeroptera, Insecta) in freshwater Hydrobiologia 595 339–50

Baxter T M 1977 Environmental effects of dams and impoundments Am. Rev. Ecol. Syst. 8 255–183

Beck H E, Zimmermann N E, Mecvaric T R, Vergopolan N, Berg A and Wood E F 2018 Present and future Koppen-Geiger climate classification maps at 1-km resolution Sci. Data 5 180214

Beisel J N, Ussligio-Ploatera P, Thomas S and Moreteau J C 1998 Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics Hydrobiologia 389 73–86

Belmar O et al 2019 Functional responses of aquatic macroinvertebrates to flow regulation are shaped by natural flow intermittence in Mediterranean streams Freshwater Biol. 264 1064–77

Bonada N, Prat N, Resh V H and Stattzner B 2006 Developments in aquatic insect biomonitoring: a comparative analysis of recent approaches Annu. Rev. Entomol. 51 495–525

Bracken M B 1992 Effective Care of the Newborn Infant, eds J C Sinclair and M B Bracken (Oxford: Oxford University Press) pp 13–20

Brittain J E and Saltveit S J 1989 A review of the effect of river regulation on Mayflies (Ephemeroptera) Regul. Rivers-Res. Manage 3 191–204

Brooks A J, Woldenben D, Downes B J and Lancaster J 2018 Barriers to dispersal: the effect of a weir on stream insect drift River Res. Appl. 34 1244–53

Bruno D, Belmar O, Maire A, Morel A, Dumont B and Datry T 2019 Structural and functional responses of invertebrate communities to climate change and flow regulation in alpine catchments Glob. Change Biol. 25 1612–28
Buendia G, Gibbins C N, Vericat D, Batalla R J and Douglas A 2013 Detecting the structural and functional impacts of fine sediment on stream invertebrate Ecol. Indic. 25 184–96
Bunn S E and Arthington A H 2002 Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity Environ. Manage. 30 492–507
Burnham K P and Anderson D R 2003 Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (New York: Springer)
Camargo J A, Alonso K and de la Puente M 2005 Eutrophication downstream from small reservoirs in mountain rivers of Central Spain Water. Res. 39 3376–84
Campbell W B and Novelo-Gutiérrez R 2007 Reduction in odonate phylogeographic diversity associated with dam impoundment is revealed using taxonomic distinctness Fund. Appl. Limnol. 168 81–92
Carlisle D M, Wolock D M and Meador M R 2011 Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment Front. Ecol. Environ. 9 264–70
Carlson P E, Donadi S and Sandin L 2018 Responses of macroinvertebrate communities to small dam removals: implications for bioassessment and restoration J. Appl. Ecol. 55 1896–907
Carr M, Li L, Sadeghian A, Phillips I D and Lindenschmidt K-E 2019 Modelling the possible impacts of climate change on the thermal regime and macroinvertebrate species of a regulated prairie river Ecolhydrology 12 e2102
Castello I. and Macedo M N 2016 Large-scale degradation of Amazonian freshwater ecosystems Glob. Change Biol. 22 990–1007
Cheng F, Li W, Castello L and Xie S G 2015 Potential effects of dam cascade on fish: lessons from the Yangtze River Res. Fish Biol. Fish. 25 569–85
Cortes R M V, Ferreria M T, Oliveira S V and Oliveira D 2002 Macroinvertebrate community structure in a regulated river segment with different flow conditions River Res. Appl. 18 367–82
Couto T B A and Olden J D 2018 Global proliferation of small hydropower plants – science and policy Front. Ecol. Environ. 16 91–100
Culp J M, Lento J, Curry R A, Luiker E and Halliwell D 2019 Arctic biodiversity of stream macroinvertebrates declines in response to latitudinal change in the abiotic template Freshwater Sci. 38 465–79
Currie D J et al 2004 Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness Ecol. Lett. 7 1121–34
Descloux S, Dattery T and Marmonier P 2013 Benthic and hyporheic invertebrate assemblages along a gradient of increasing streambed colmation by fine sediment Aquat. Sci. 75 493–507
Dewson Z S, James A B W and Death R G 2007 A review of the longitudinal patterns of benthic invertebrate communities along a regulated river Ecol. Lett. 10 136–48
Dudgeon D et al 2006 Freshwater biodiversity: importance threats status and conservation challenges Biol. Rev. Camb. Philos. Soc. 81 163–82
Dudgeon D 2008 Tropical Stream Ecology (New York: Academic)
Dynesius M and Nilsson C 1994 Fragmentation and flow regulation of river systems in the northern third of the world Science 266 753–62
Ellis I. E and Jones N. E. 2013 Longitudinal trends in regulated rivers: a review and synthesis within the context of the serial discontinuity concept Environ. Rev. 21 136–48
Engels S et al 2019 Temperature change as a driver of spatial patterns and long-term trends in chironomid (Insecta: Diptera) diversity Glob. Change Biol. 26 1159–66
Extence C A, Chadd R P, England J, Dunbar M J and Taylor E D 2011 The assessment of fine sediment accumulation in rivers using macro-invertebrate community response River Res. Appl. 29 17–55
Fornaroli R, Ippolito A, Tolkkinen M J, Mykra H, Muotka T, Balistrieri L S and Schmidt T S 2018 Disentangling the effects of low pH and metal mixture toxicity on macroinvertebrate diversity Environ. Pollut. 235 889–98
Gabbud C and Lane S N 2016 Ecosystem impacts of Alpine water intakes for hydropower: the challenge of sediment management Water. Res. 3 41–61
Grill G et al 2019 Mapping the world's free-flowing rivers Nature 569 215–21
Guarachi S and Wood P J 2019 Taxonomic changes and non-native species: an overview of constraints and new challenges for macroinvertebrate-based indices calculation in river ecosystems Sci. Total Environ. 660 40–46
Gurevitch J, Koricheva J, Nakagawa S and Stewart G 2018 Meta-analysis and the science of research synthesis Nature 555 175–82
Harrison E T, Norris R H and Wilkinson S N 2007 The impact of fine sediment accumulation on benthic macroinvertebrates: implications for river management Proc. of the 5th Australian Stream Management Conf. pp 139–44
Hart D D and Finelli C M 1999 Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms Annu. Rev. Ecol. Evol. S 30 363–95
Hauer F R and Resh V H 2007 Macroinvertebrate Methods in Stream Ecology 2nd edn F R Hauer and G A Lamberti pp 435–8 (Amsterdam: Elsevier)
Haxton T J and Findlay C S 2008 Meta-analysis of the impacts of water management on aquatic communities Can. J. Fish Aquat. Sci. 65 437–47
Hedges L V and Olkin I 1985 Statistical Methods for Meta-analysis (New York: Academic)
Heino J, Culm J M, Eriksson J, Goedkoop W, Lento J, Rühland K M and Smol J P 2020 Abruptly and irreversibly changing arctic freshwaters urgently require standardized monitoring J. Appl. Ecol. 57 1192–8
Heino J, Melo A S, Siqueira T, Soininen J, Valanko S and Bini L M 2015 Metacommunity organisation spatial extent and dispersal in aquatic systems: patterns processes and prospects Freshwater Biol. 60 845–69
Hering D et al 2006 Assessment of European streams with diatoms macrophytes macroinvertebrates and fish: a comparative metric-based analysis of organism response to stress Freshwater Biol. 51 1757–85
Holt C R, Pfister D, Scarley C, Caldwell B A and Batzer D P 2015 Macroinvertebrate community responses to annual flow variation from river regulation: an 11-year study River Res. Appl. 31 798–807
Ibella F et al 2015 Biodiversity increases the resistance of ecosystem productivity to climate extremes Nature 526 574–7
Jansson A 1977 Micronectae (Heteroptera, Corixidae) as indicators of water quality in two lakes in southern Finland Annu. Zool. Fenn. 14 118–24
Jones C F 2008 Taxonomic sufficiency: the influence of taxonomic resolution on freshwater bioassessments using benthic macroinvertebrates Environ. Rev. 16 45–69
Jones J L, Murphy J F, Collins A L, Seur D A, Naden P S and Armitage P D 2012 The impact of fine sediment on macro-invertebrates River Res. Appl. 28 1055–71
Jones N E and Schmidt B J 2018 Influence of tributaries on the longitudinal patterns of benthic invertebrate communities River Res. Appl. 34 165–73
Kareiva P 1982 Exclusion experiments and the competitive release in insects feeding on collards Ecology 63 696–704
Katano I, Noguchi N, Minagawa T, Doi H, Kawaguchi Y and Yachi K 2009 Longitudinal macroinvertebrate organization over contrasting discontinuities: effects of a dam and a tributary J. N. Am. Benthol. Soc. 28 331–51
Kennedy T A, Yackulic C B, Cross W F, Grams P E, Yard M D and Copp A J 2014 The relation between invertebrate drift and two primary controls discharge and benthic densities in a large regulated river Freshwater Biol. 59 557–72
Sundermann A, Stoll S and Haase P 2011 River restoration success depends on the species pool of the immediate surroundings *Ecol. Appl.* 21 1962–71
Tang W W, Wang X Y, Yan M, Zeng G M and Liang J 2019 China's dams threaten green peafowl *Science* 364 943–943
Tao J, Kennard M J, Roberts D T, Fry B, Kainz M J, Chen Y F and Bunn S E 2020 Quality and contribution of food sources to Australian lungfish evaluated using fatty acids and stable isotopes *Aquat. Sci.* 82 8
Tonkin J D et al 2018b The role of dispersal in river network metacommunities: patterns processes and pathways *Freshwater Biol.* 63 141–63
Tonkin J D, Merritt D M, Olden J D, Reynolds L V and Lytle D A 2018a Flow regime alteration degrades ecological networks in riparian ecosystems *Nat. Ecol. Evol.* 2 86–93
Tonkin J D, Stoll S, Sundermann A and Haase P 2014 Dispersal distance and the pool of taxa but not barriers determine the colonisation of restored river reaches by benthic invertebrates *Freshwater Biol.* 59 1843–55
Turgeon K, Turpin C and Gregory-Eaves I 2019 Dams have varying impacts on fish communities across latitudes: a quantitative synthesis *Ecol. Lett.* 22 1501–16
Turic N et al 2015 Flood pulses drive the temporal dynamics of assemblages of aquatic insects (Heteroptera and Coleoptera) in a temperate floodplain *Freshwater Biol.* 60 2051–65
Vannote R L, Minshall G W, Cummins K W, Sedell J R and Cushing C E 1980 The river continuum concept *Can. J. Fish Aquat. Sci.* 37 130–7
Viechtbauer W 2010 Conducting meta-analyses in R with the metafor package *J. Stat. Softw.* 36 1–48
Vijapure T and Sukumaran S 2019 Optimization of the taxonomic resolution of an indicator taxon for cost-effective ecological monitoring: perspectives from a heterogeneous tropical coastline *J. Environ. Manage.* 247 474–83
Wallace J B and Webster J R 1996 The role of macroinvertebrates in stream ecosystem function *Annu. Rev. Entomol.* 41 115–39
Wanders N, Van Vliet M T H, Wada Y, Bierkens M F P and Van Beek L P H 2019 High-resolution global water temperature modeling *Water Res. Res.* 4 2760–78
Wang J, Ding L, Tao J, Ding C and He D 2019 The effects of dams on macroinvertebrates: global trends and insights *River Res. Appl.* 35 702–13
Ward J V and Short R A 1978 Macroinvertebrate community structure of four special lotic habitats in Colorado U S A *Int. Ver. Theor. Angew. Limnol. Verb.* 20 1382–7
Ward J V and Stanford J A 1979 Ecological factors controlling stream zoobenthos *The Ecology of Regulated Streams*, eds J V Ward and J A Stanford (New York: Plenum) pp 35–56
Ward J V and Stanford J A 1983 The serial discontinuity concept of lotic ecosystems *Dynamics of lotic ecosystems*, eds T D Fontaine and S M Bartell (Michigan: Ann Arbor Science Publishers) pp 29–42
Wellnitz T A, Poff N L, Cosyleon G and Steury B 2001 Current velocity and spatial scale as determinants of the distribution and abundance of two rheophilic herbivorous insects *Landscape Ecol.* 16 111–20
White J C, Hannah D M, House A, Beatson S J V, Martin A and Wood P J 2016 Macroinvertebrate responses to flow and stream temperature variability across regulated and non-regulated rivers *Ecohydrology* 10 e1773
Winemiller K O et al 2016 Balancing hydropower and biodiversity in the Amazon Congo and Mekong *Science* 351 128–9
Wu J, Huang J, Han X, Xie Z and Gao X 2003 Three-gorge dam-experiment in habitat fragmentation *Science* 300 1239–40
Zarfl C, Lumsdon A E, Berlekamp J, Tydecks L and Tockner K 2015 A global boom in hydropower dam construction *Aquat. Sci.* 77 161–70
Zhang C, Ding C Z, Ding L Y, Chen L Q, Hu J M, Tao J and Jiang X 2019 Large-scale cascaded dam constructions drive taxonomic and phylogenetic differentiation of fish fauna in the Lancang River China *Rev. Fish Biol. Fish.* 25 895–916
Zhang C, Ding L, Ding C, Chen L, Sun J and Jiang X 2018 Responses of species and phylogenetic diversity of fish communities in the Lancang River to hydropower development and exotic invasions *Ecol. Indic.* 90 261–79