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RESEARCH ARTICLE

A global meta-analysis of ecological functions and regulating ecosystem services of freshwater bivalves

Alexandra Zieritz[1*] **Joshua I. Brian**[2] **Ronaldo Sousa**[3] **David C. Aldridge**[4] **Carla L. Atkinson**[5] **Karel Douda**[6] **Caryn Vaughn**[7] **Yulia Bespalaya**[8] **Tabitha Richmond**,[1] **Adam M. Ćmiel**[9] **Alma Crisp**,[10] **Andreas H. Dobler**[11] **Fabio Ercoli**[10,12] **Eduardo Esteves**,[13] **Noé Ferreira-Rodríquez**[14] **Juergen Geist**[11] **Irene Sánchez González**,[15] **Dariusz Halabowski**[16,17] **Philipp Hoos**[11] **Garrett W. Hopper**[18] **Heini Hyvärinen**[10] **Martina Ilarri**[19] **Iga Lewin**,[20] **Anna M. Lipińska**,[9] **Jon H. Mageroy**,[21] **Daniele Nizzoli**[22] **Isobel Ollard**[4] **Martin Österling**[23] **Nicoletta Riccardi**[24] **Sebastian L. Rock**[23] **Tuomo Sjönberg**[10] **Jouni Taskinen**[10] **Gorazd Urbanič**[25,26,27] **Maria Urbańska**[28] **Qingqing Yu**,[29] **Ana Sofia Vaz**[30,31,32]

[1]School of Geography, University of Nottingham, Nottingham, UK; [2]Department of Geography, King's College London, London, UK; [3]Department of Biology, University of Minho, Campus Gualtar, Braga, Portugal; [4]Department of Zoology, University of Cambridge, Cambridge, UK; [5]Department of Biological Sciences and Center for Freshwater Studies, University of Alabama, Tuscaloosa, Alabama, USA; [6]Department of Zoology and Fisheries, Czech University of Life Sciences, Prague, Czech Republic; [7]Oklahoma Biological Survey and School of Biological Sciences, University of Oklahoma, Norman, Oklahoma, USA; [8]N. Laverov Federal Center for Integrated Arctic Research, Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia; [9]Institute of Nature Conservation, Polish Academy of Sciences, Kraków, Poland; [10]Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland; [11]Aquatic Systems Biology, Technical University of Munich, Freising, Germany; [12]Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia; [13]CCMAR-Centre of Marine Sciences, Universidade do Algarve, Faro, Portugal; [14]Department of Natural Sciences, Ovidius University of Constanta, Constanta, Romania; [15]Odum School of Ecology, University of Georgia, Athens, Georgia, USA; [16]Department of Ecology and Vertebrate Zoology, University of Lodz, Lodz, Poland; [17]Institute of Vertebrate Biology, Czech Academy of Science, Brno, Czech Republic; [18]School of Renewable Natural Resources, Louisiana State University and Agricultural Center, Baton Rouge, Louisiana, USA; [19]Interdisciplinary Centre of Marine and Environmental Research (CIIMAR/CIMAR), University of Porto, Matosinhos, Portugal; [20]Institute of Biology, University of Silesia, Katowice, Poland; [21]Norwegian Institute for Nature Research (NINA), Oslo, Norway; [22]Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parma, Italy; [23]Department of Environmental and Life Sciences, Karlstad University, Karlstad, Sweden; [24]CNR Water Research Institute, National Research Council of Italy, Verbania, Italy; [25]URBANZERO Institute for Holistic Environmental Management, Mirna, Slovenia; [26]Department of Biology, University of Ljubljana, Ljubljana, Slovenia; [27]College of Ptuj, Ptuj, Slovenia; [28]Department of Zoology, Poznań University of Life Sciences, Poznań, Poland; [29]School of Resources and Environmental Engineering, Anhui University, Hefei, China; [30]Natural Business Intelligence, Vila Real, Portugal; [31]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Vairão, Portugal; [32]BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Vairão, Portugal

Abstract

Freshwater bivalves are globally distributed, diverse, and common in benthic communities. Many taxa, particularly in the most species-rich order, Unionida, are declining due to anthropogenic stressors, while a small

*Correspondence: alexandra.zieritz@nottingham.ac.uk

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number of non-native species have become increasingly abundant and widespread, commonly replacing native bivalve assemblages. To understand how these global changes may impact ecosystems and people, we conducted a meta-analysis of existing literature quantifying the ecological functions (= supporting or intermediate ecosystem services) and regulating ecosystem services of freshwater bivalves (hereafter "ecosystem services"). Random effects meta-analysis modeling across 447 case studies revealed a positive effect on human health, safety, or comfort of freshwater bivalve ecosystem services overall and specifically, via effects on native macrofauna, microorganisms, wastes, and pollutants, and the physico-chemical condition or quantity of sediments. Generally, effects of native species and species within the orders Unionida and Venerida were more significant and positive than those of other freshwater bivalves. No significant overall effect was found for ecosystem services related to zooplankton, algae, invasive species, and the physico-chemical condition of ambient water. Moreover, a significant bias toward publication of positive results existed for studies quantifying ecosystem services related to algae. These findings illustrate the global importance of the ecosystem services of freshwater bivalves and highlight the need for large-scale conservation and restoration efforts for their species and populations globally, including those of common species. Our findings also question common assumptions of strong and ubiquitous effects of freshwater bivalves on algae and water condition, cautioning against extrapolating observations across systems.

Biodiversity is declining faster in freshwaters than in terrestrial and marine systems (Reid et al. 2019; WWF 2022). Freshwater bivalves are one of the most threatened animal groups, spanning ~ 1300 extant species from eight orders, with the Unionida representing > 75% of the species diversity (Graf 2013; Graf and Cummings 2021). Freshwater bivalves inhabit freshwaters across the globe and can make up > 90% of the benthic biomass (Okland 1963; Sousa et al. 2008). Due to their sensitivity to environmental change, freshwater bivalve assemblages are changing globally (Schloesser et al. 2006; Zieritz et al. 2016; Lopes-Lima et al. 2018). Many species are declining in range and/or population sizes, and > 45% of unionoid species are either considered globally "threatened" or "Data Deficient" (IUCN 2023) (with > 50% of "Data Deficient" species predicted to be threatened [Borgelt et al. 2022]). At the same time, a small number of freshwater bivalves, such as zebra mussels (*Dreissena polymorpha*), quagga mussels (*Dreissena bugensis*), golden mussels (*Limnoperna fortunei*), Chinese pond mussels (*Sinanodonta* spp.), and Asian clams (*Corbicula fluminea*), are highly successful invaders that thrive in anthropogenically modified habitats, and can contribute to the decline of and commonly alter the composition of native freshwater bivalve assemblages (Lopes-Lima et al. 2025).

The changes in the number, population sizes, and species composition of freshwater bivalve assemblages may have severe consequences for ecosystems and society. Freshwater bivalves fulfill important ecological functions and ecosystem services, including nutrient cycling and provisioning habitat, clean water, food, pearls, and spiritual value (Vaughn and Hakenkamp 2001; Vaughn 2018; Zieritz et al. 2022). However, freshwater bivalves can also disrupt these and other functions and services, with negative effects being more commonly associated with invasive species. For example, non-native species were responsible for 81% of the records of bivalve-caused disruption of regulating ecosystem services globally, and the prevalence of service disruption varied among orders and continents (Zieritz et al. 2022).

While previous work has synthesized the range of ecological functions and ecosystem services that are provided and disrupted by freshwater bivalves, the size and variability of these effects have never been quantified globally. As a consequence, we do not know to what extent freshwater bivalves provide or disrupt ecological functions and ecosystem services, and whether and to what extent these effects are dependent on the taxon and origin, environmental conditions, and design of the study. This knowledge is needed to achieve a better understanding of the global impacts of changing freshwater bivalve assemblages on ecosystems and people, and subsequently inform effective management and restoration strategies.

Materials and Methods

Data collection

We quantified the "ecological functions (= supporting or intermediate ecosystem services; Haines-Young and Potschin 2018) and regulating ecosystem services" (hereafter, "ecosystem services") provided and disrupted by freshwater bivalves by conducting a global meta-analysis of existing literature. Freshwater bivalves are here defined as bivalves that complete their life cycle in freshwater habitats. Ecosystem services here correspond to all the ways in which these species change the ambient environment, thereby indirectly or directly affecting human health, safety, or comfort.

Literature search

The literature search was conducted in ISI Web of Knowledge (http://webofknowledge.com/) and Scopus (https://www.scopus.com) on October 2021, updated in January 2022, with no restriction on language. Selection of keywords was based on a previous global review of freshwater bivalve ecosystem services (Zieritz et al. 2022), and further complemented through the participation of experts from the COST Action CA18239 "CONFREMU—Conservation of freshwater mussels: a pan-European approach." Search terms referring to freshwater bivalves included common terms and names (e.g., "freshwater" AND ["mussel" OR "clam"]), and scientific names of all known bivalve genera as well as species within predominantly marine genera that complete their life cycles in freshwater ecosystems (following Graf and Cummings 2023). Search terms referring to ecosystem services included general terms (e.g., "environment*function*" OR "regulating ecosystem service") as well as terms referring to ecosystem services that are potentially associated with freshwater bivalves (e.g., "heavy metal filtration" OR "biological control"). The full search string is shown in Supporting Information "Search string." The literature search retrieved 5629 unduplicated publications (Supporting Information Fig. S1). Relevant literature published between February 2022 and December 2024 was not included in the meta-analysis but was considered in the discussion of the results if it provided new information.

Inclusion and exclusion criteria

We excluded anonymous publications, as well as publications reporting secondary evidence (e.g., in literature reviews or meta-analyses) to avoid double-counting. We kept publications focusing on: (1) freshwater bivalves, and not marine bivalves or other taxonomic groups that might have been caught by our keywords due to similar nomenclature; and (2) freshwater bivalve activities that can alter the ambient environment—and not vice versa, resulting in 447 publications. Also, we only considered studies that (3) compared the effects of freshwater bivalves on a target ecosystem service against a control situation in which freshwater bivalves were absent (i.e., before-after and control-impact scenarios were both included), resulting in 274 publications; (4) provided the sample size (any integer ≥ 1), that is, the number of samples used in the experiment to measure the target ecosystem service-variable associated with freshwater bivalves as well as to the control; and (5) provided a mean or median value with dispersion measures of the target variable associated with freshwater bivalves as well as to the control. The final number of selected publications was 251 (*see* Supporting Information "Data filtering" for details on inclusion and exclusion criteria).

Data extraction

For each publication, we extracted the relevant numerical data for control and freshwater bivalve datasets, that is, replicate number, mean or median value, and dispersion measure (e.g., standard deviation or variance), the taxonomic order, native vs. non-native status, study area (continent), study design (i.e., type and experiment design) and environmental conditions at the start of the study (e.g., water temperature, chlorophyll *a* and nutrient concentrations). When available, we extracted information on the characteristics of freshwater bivalve populations in the study, including their average mass, number, and spatial density. All quantitative factors were harmonized into the same metrics and units to allow comparisons across different studies.

Data analysis

Dataset processing

From the extracted data, individual datasets were created for each ecosystem service-Group. We used a revised classification of ecosystem service-categories (Table 1) that was informed by the Common International Classification of Ecosystem Services (CICES version 5.1) (Haines-Young and Potschin 2018). We considered an initial list of 16 relevant ecosystem service-Groups associated with freshwater bivalves, grouped into three divisions (Supporting Information "Original classification of ecosystem service-Groups and Divisions"). The revised classification, spanning eight ecosystem service-Groups in three ecosystem service-Divisions (Table 1), was developed through discussions among the expert consortium to allow unambiguous classification of all case studies, that is, discrete pieces of data quantifying the effect of a particular freshwater bivalve species or assemblage on an individual ecosystem service-Group.

Data on variables associated with different ecosystem service-Groups or different freshwater bivalve species provided in the same publication were treated as independent case studies. Data on different variables associated with the same ecosystem service-Group and the same freshwater bivalve species provided in the same publication were treated as pseudo-case studies. Values from all pseudo-case studies of a given case study were aggregated to avoid pseudoreplication (Borenstein et al. 2009) (see Supporting Information "Dealing with pseudoreplication in the dataset" for details). In total, our dataset contained 1636 pseudo-case studies and 447 case studies.

For each case study, we calculated a standardized effect size using Hedges' d (Rosenberg et al. 2000) (*see* Supporting Information "Dealing with pseudoreplication in the dataset" for details). The sign of the effect size reflects the direction of the ultimate ecosystem service effect on humans (i.e., positive or negative) as interpreted and expressed by the author(s) of the respective study. This is in contrast to studies in which the direction of the effect relates to the direct effect on the response variable (e.g., benthic invertebrate species richness, phytoplankton abundance, turbidity) (e.g., Albertson et al. 2021; Reynolds and Aldridge 2021; Soto et al. 2024). Thus, a positive effect size indicates that freshwater bivalves have a higher (i.e., more positive or less negative) contribution to the particular ecosystem service than the control and vice versa. For instance, the effect size would be negative in a case study showing an increased number of invasive species with freshwater bivalve presence compared to a control because invasive species represent a negative contribution to the CICES-ecosystem service "Pest and disease control" (adapted ecosystem service-Group "Invasive species" in our study). Conversely, the effect size would be positive in a case study

Table 1. List of "ecological functions and regulating ecosystem services" (here, "ecosystem services") associated with freshwater bivalves, adapted from the Common International Classification of Ecosystem Services (CICES, version 5.1). Ecosystem services are listed in column "Group" and the broader category "Division." The table provides a simple description of freshwater bivalve effects on each ecosystem service, and examples of ecosystem service-variables that measure these effects extracted from the literature.

Division	Group	Simple descriptor	Examples of ecosystem service-variables
1. Organisms	1.1. Macrofauna	Freshwater bivalves affecting the taxonomic richness, diversity, abundance, density, survival rate, population growth rate, or condition of native macrofauna	Macrobenthos taxon richness, abundance, density, or biomass (Mörtl and Rothhaupt 2003; Howard and Cuffey 2006; Mills et al. 2017) Macrobenthos survival rate (Freeman et al. 2011) Fish gut fullness (Shen et al. 2020) Fish growth rate (Limm and Power 2011)
	1.2. Zooplankton	Freshwater bivalves affecting the taxonomic richness, diversity, abundance, density, survival rate, population growth rate, or condition of native zooplankton	Zooplankton abundance (Whitten et al. 2018) Zooplankton survival rate (Molina et al. 2011) Zooplankton fecundity rate (Feniova et al. 2015)
	1.3. Algae (including cyanobacteria)	Freshwater bivalves affecting the taxonomic richness, diversity, abundance, density, survival rate, population growth rate, or condition of native algae	Chlorophyll *a* concentrations or clearance rates (Cataldo et al. 2012; Zieritz et al. 2019) Phytoplankton biomass (Knoll et al. 2008) Diatom concentrations (Holland 1993) Brown algae, green algae and cyanobacteria concentrations (Feniova et al. 2020)
	1.4. Microorganisms (excluding algae)	Freshwater bivalves affecting the taxonomic richness, diversity, abundance, density, survival rate, population growth rate or condition of native bacteria, viruses, protists, or pathogens	Concentration of harmful bacteria in water (Ismail et al. 2016; Mezzanotte et al. 2016) Number of diarrhea-inducing bacteria in freshwater bivalve tissue (Graczyk et al. 1998) Heterotrophic plate counts of bacteria (Lohner et al. 2007) Concentration of cercariae (trematode fish parasites) (Gopko et al. 2017)
	1.5. Invasive species	Freshwater bivalves affecting the taxonomic richness, diversity, abundance, density, survival rate or condition of non-native, invasive species	Number of chironomid larvae per time eaten by invasive fish (Kobak et al. 2016) Population density of invasive species larvae (MacIsaac et al. 1991)
2. Human inputs	2.1. Wastes and pollutants	Freshwater bivalves affecting the abundance or availability of wastes and pollutants in the environment	Concentration of human-caused pollutants, including heavy metals, nutrients, pharmaceuticals, herbicides, pesticides, or microplastics, in water (Gattás et al. 2016; Guilhermino et al. 2018) Accumulation rate of human inputs, such as heavy metals, in freshwater bivalve tissue (Karadede-Akin and Ünlü 2007) Biodeposition rate of polychlorinated biphenyls and cadmium (Dobson and Mackie 1998)
3. Physico-chemical conditions	3.1. Sediment	Freshwater bivalves affecting quantity or physico-chemical conditions of the sediment	Sediment oxygen content (Zhang et al. 2011) Sediment cohesion (sediment shear strength and compression) (Zimmerman and de Szalay 2007) Sedimentation or biodeposition rate (Thayer et al. 1997; Mörtl and Rothhaupt 2003)
	3.2. Water	Freshwater bivalves affecting physico-chemical conditions of the water	Secchi depth (Holland 1993; Klerks et al. 1996) Dissolved oxygen concentration in water (Caraco et al. 2000) Nutrient concentrations in water (Orlova et al. 2004; Song et al. 2014)

reporting a decrease of concentrations of a pollutant with freshwater bivalve presence compared to a control because the maintenance of water quality has positive effects on humans. It is, therefore, possible for the same ecological effect to have a positive sign in one case study but a negative sign in another case study (e.g., decreased turbidity being perceived as positive to humans in one instance but negative in another instance).

Calculating grand mean effect sizes

To assess the contribution of freshwater bivalves to each ecosystem service-Group, all effect sizes (Hedges' *d*) obtained for each ecosystem service were combined using a random effects meta-analysis (REMA) model to provide a grand mean effect size, where the weight of each case study was the reciprocal of the case study variance (Supporting Information "Further details on statistical analysis"). In a random-effects model, the variance of each study results from the variability within (i.e., sampling error) and among case studies (i.e., the random component). The latter was calculated using the restricted maximum-likelihood estimation (Borenstein et al. 2009; Viechtbauer 2010), using the rma() function implemented in the R package metafor (Viechtbauer 2010). This function also provides the 95% confidence intervals for each grand mean effect size and a two-tailed parametric test checking whether the effect size differs from zero. We additionally ran nonparametric permutation tests using 1000 iterations, considering the non-normal distribution of the residuals of some models, using the permutest() function from package metafor (Viechtbauer 2010). Each moderator was tested in an individual model, as collinearities between moderators could not be assessed due to many studies failing to report moderators (see Supporting Information Table S1).

Testing moderators of freshwater bivalve effects

We computed the heterogeneity across effect sizes of each grand mean effect size using random effects meta-analysis and the QT statistic. The QT statistics represent the sum of squares of the deviations of each effect size from the grand effect size, weighted by the inverse of the effect sizes' variances. To assess whether the observed heterogeneity is greater than expected by chance, QT was tested against a chi-squared distribution with $n - 1$ degrees of freedom ($n =$ number of case studies) (Borenstein et al. 2009), using the rma() function of the metafor R package. Then, we assessed whether the variation of effect sizes could be explained by one or more out of a set of six categorical and 14 quantitative moderators related to the species, design, location, and environmental conditions of the study (Table 2). To do so, we used a random-effects structured meta-analysis, which allows incorporating moderators and returns coefficients and an omnibus test assessing whether the coefficient differs from zero. For continuous (quantitative) moderators, the function also provides the regression slope and its significance. Due to the non-normal distribution of residuals in our dataset, we assessed the significance of the moderators over 1000 iterations with the permutest() function (Viechtbauer 2010).

Publication bias

Meta-analysis results can be affected by publication bias, that is, selective publication of articles reporting positively significant effects over those reporting negative or non-significant effects (and vice versa) (Begg 1994). The publication bias for each ecosystem service was investigated by exploring asymmetry in a funnel plot of effect sizes vs. standard error of effect sizes (see Supporting Information Figs. S2–S12). A symmetric funnel shape may indicate the absence of publication bias, with a larger dispersion of effect sizes for studies with smaller sample size, that is, those with large standard errors of effect size (Borenstein et al. 2009). The funnel asymmetry was analyzed with the Egger's test, using the random mixed-effects version of the test, which performs a structured meta-analysis with the standard error as predictor, and returns its slope and significance (Sterne and Egger 2005). The Egger's test was applied using the regtest() function of the metafor package (Viechtbauer 2010). A significant result of the Egger's test suggests asymmetry in the funnel plot, which may indicate a publication bias due to missing values on one side of the funnel.

When the Egger's test on the meta-analysis without moderators indicated asymmetry, we repeated the test on the meta-analysis with the moderators, which explained more heterogeneity. If this test still reported asymmetry, we assessed the impact of publication bias by removing case studies responsible for funnel asymmetry (Borenstein et al. 2009), and by applying the trim-and-fill method (Duval and Tweedie 2000). This method uses an iterative procedure to remove the most extreme small studies from the asymmetric side of the funnel plot, then adds the original studies back into the analysis, imputes a mirror image for each one, and re-computes the meta-analysis. If the new grand mean effect size retains the same sign and significance, publication bias has a trivial or modest impact; if there is a shift of the sign or significance of the grand mean effect size, the impact of publication bias may unduly influence interpretation (Nakagawa and Santos 2012).

Results and Discussion

Our final dataset spanned 447 case studies distributed across eight ecosystem service-Groups from three ecosystem service-Divisions (Table 1, Fig. 1a). The majority of case studies fell into Groups 1.3 Algae, 2.1 Wastes and pollutants, and 3.2 Water (each > 100 case studies), with only 5–32 case studies in the other five ecosystem service-Groups (Fig. 1a).

Globally significant effects on ecosystem services

Freshwater bivalves significantly positively affected ecosystem services overall as well as four of the eight ecosystem service-Groups individually (Hedges' *d*; see Methods and Supporting Information Table S3 for details), that is, 1.1

Table 2. Information extracted from each individual publication. All quantitative moderators were recorded at the time the ecosystem service effect was measured.

Moderators	Description
Categorical moderators	
Continent	Continent where the study area is located or experiment conducted: North America, South America, Europe, Asia, Africa, Australasia
Study type	Type of experiment or assessment conducted: Field, Laboratory, Mesocosm (i.e., a controlled environment in the field)
Experiment design	Type of experiment conducted based on the control: Independent (at a different location with similar biophysical conditions), Repeated (the same system but different measurements over time before and after freshwater bivalve effects)
Presence of other freshwater bivalves	Indicates presence of other freshwater bivalves in the system (besides the freshwater bivalve taxa under study): Yes, No
Freshwater bivalve Order	Order of the freshwater bivalve taxa: Unionida, Myida, Mytilida, Venerida
Origin	Indicates whether the freshwater bivalve is considered native or non-native in the region of assessment: Native, Non-native
Quantitative moderators	
Freshwater bivalve number	Number of living freshwater bivalve individuals in the experiment
Freshwater bivalve dry weight	Average dry weight or total dry weight of freshwater bivalve (in grams) in the experiment
Freshwater bivalve length	Average or total length of freshwater bivalve shell (in centimeters) in the experiment
Freshwater bivalve density per volume	Number of living freshwater bivalve individuals per volume of water (number of individuals per liter) in the experiment
Freshwater bivalve density per area	Number of living freshwater bivalve individuals per area (number of individuals per square meter) in the experiment
Freshwater bivalve weight per area	Average or total weight of the freshwater bivalve (unspecified parts, in grams) in the experiment
Temperature	Temperature (degrees Celsius) in the water system
Oxygen concentration	Dissolved oxygen concentration (milligrams per liter) in the water system
P concentration	Phosphorous concentration (milligrams per liter) in the water system
N concentration	Nitrogen concentration (milligrams per liter) in the water system
Chl *a* concentration	Chlorophyll *a* concentration (milligrams per liter) in the water system
Water volume	Volume of water in the tank or aquarium (in liters) where experiment was conducted
Water depth	Average or total water depth of the system (in meters) where experiment was conducted
Tank size	Area of the tank or aquarium (in square meters) where experiment was conducted

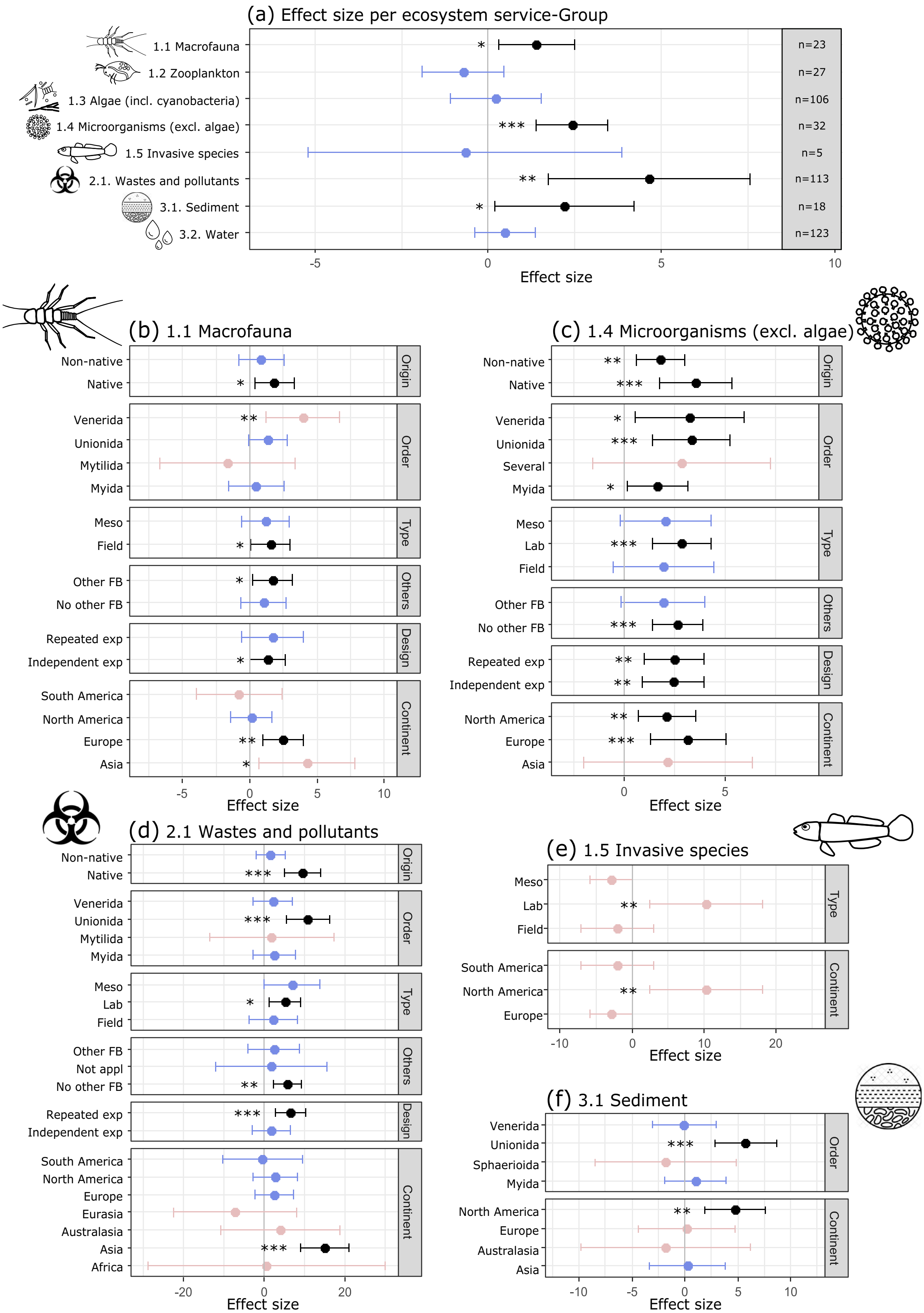
Macrofauna, 1.4 Microorganisms, 2.1 Wastes and pollutants, and 3.1 Sediments (Fig. 1a).

Macrofauna

Effects of freshwater bivalves on native macrofauna are almost always positive, with freshwater bivalve presence leading to a higher diversity, density, and rate of survival, growth, or reproduction of native animal populations, thus contributing to the natural functioning of freshwater ecosystems. Commonly, this positive effect is related to bottom-up impacts of freshwater bivalves on food webs, with freshwater bivalves increasing the availability and quality of food for macrofauna (Spooner and Vaughn 2006; Limm and Power 2011; Shen et al. 2020), and to the increased habitat complexity provided by freshwater bivalves (Spooner and Vaughn 2006; Ilarri et al. 2018). However, in some studies, this effect was absent (Howard and Cuffey 2006; Mills et al. 2017) or even negative; for example, native suspension feeding mayfly larvae (*Hexagenia* spp.) survival was lower in laboratory microcosms with invasive dreissenid freshwater bivalves compared to those without freshwater bivalves (Freeman et al. 2011).

Microorganisms, wastes, and pollutants

Effects of freshwater bivalves on ecosystem services related to microorganisms, and human-made wastes and pollutants are particularly strong and consistent. These effects are usually related to the clearance capacity of freshwater bivalves. Freshwater bivalves can efficiently ingest, accumulate, and in some cases, transform harmful or otherwise undesired microorganisms (e.g., *Escherichia coli*; Ismail et al. 2016), pathogens (e.g., rota- and polio-viruses; Mezzanotte et al. 2016), parasites (Graczyk et al. 1998), wastes (e.g., heavy metals; Karadede-Akin and Ünlü 2007; Ranjbar et al. 2021) and human-made pollutants (e.g., microplastics, pharmaceuticals, biocides; Ismail et al. 2014; Gattás et al. 2016; Moreschi et al. 2020; Xu et al. 2023; Mohammed-Geba et al. 2024). As a result,



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concentrations of these undesired organisms and substances in the water are reduced, providing positive ecosystem services to people who consume or otherwise use this water. However, as freshwater bivalves take up these substances, their concentrations in freshwater bivalve tissue and shells increase, which can present a danger to human health, for example, due to their potential role as a vector for water-borne diseases (Graczyk et al. 1998) or contamination by heavy metals or radioactive elements (Brenner et al. 2007; Guilhermino et al. 2018). In addition, if these substances are not catabolized by freshwater bivalves, they will ultimately be deposited to the sediment, either through biodeposition of (pseudo)feces or freshwater bivalve mortality. These potentially negative effects of freshwater bivalves via their interaction with the benthic environment have been rarely studied but are, for example, illustrated by an up to 10-fold increase in deposition rate of polychlorinated biphenyls and cadmium caused by the presence of the invasive *D. polymorpha* in Lake Erie, Canada (Dobson and Mackie 1998).

Sediment

While freshwater bivalves affect the quantity and physico-chemical conditions of the sediment in diverse ways, their overall effect on 3.1 Sediment was significantly positive. Due to their predominantly benthic, suspension feeding life habit, freshwater bivalves transfer energy, food, and organic material from the water column to the benthic environment and sediment. This commonly has positive effects on other benthic organisms (Mörtl and Rothhaupt 2003) and benthivorous fish (Thayer et al. 1997), supporting the functioning of the ecosystem or humans directly. In some case studies related to non-native freshwater bivalves, their biodeposition and sedimentation is, however, interpreted as a negative ecosystem service effect. For example, *D. polymorpha* invasion dramatically increased sedimentation rates in Lake Erie, which altered the natural functioning of this ecosystem (Klerks et al. 1996). Burial activity of freshwater bivalves and resulting bioturbation can lead to increased oxygenation of sediment, supporting broader ecosystem functioning by positively affecting interstitial and benthic biodiversity (Zhang et al. 2011). The evidence for positive effects of freshwater bivalves on this ecosystem service-Group is particularly strong and significant for the Unionida and North American datasets (Fig. 1f), which includes an artificial stream experiment showing that freshwater bivalves can increase sediment cohesion and stability and ultimately, resistance of the streambed to scouring during flooding events (Zimmerman and de Szalay 2007).

Ecosystem services without a significant overall effect

While none of the ecosystem service categories were significantly negatively affected by freshwater bivalves in our meta-analysis, there was a lack of a significant positive overall effect on 1.2 Zooplankton, 1.3 Algae, 1.5 Invasive species, and 3.2 Water.

Algae and physico-chemical conditions of the ambient water

One of the most commonly mentioned ecosystem services provided by freshwater bivalves is their ability to clear water of phytoplankton, often including nuisance or harmful species, such as certain cyanobacteria, which in turn leads to increased water clarity with benefits to humans (Vaughn 2018). The lack of a significant positive overall effect for ecosystem service-Groups 1.3 Algae and 3.2 Water in our dataset was therefore unexpected. Highly cited studies quantifying the phytoplankton clearance capacity of freshwater bivalves and resulting increases in water clarity span both native (Douda and Čadková 2018) and non-native species (Holland 1993). Furthermore, multiple studies illustrate that due to these capacities, freshwater bivalves can be used in bioremediation and successfully control phytoplankton, for example, in fish aquaculture (Yu et al. 2021) and urban ponds (Waajen et al. 2016). However, as illustrated by our study outcomes, there are also numerous examples of freshwater bivalves negatively affecting these ecosystem service-Groups. Some of these relate to non-native species, such as *L. fortunei* significantly increasing harmful cyanobacteria blooms in mesocosm experiments in a reservoir in Argentina (Cataldo et al. 2012), and *Sinanodonta pacifica* from a eutrophic lake in Malaysia significantly increasing chlorophyll *a* concentrations (a proxy for phytoplankton abundance) in laboratory experiments (Zieritz et al. 2019). An example of a negative ecosystem service effect of native freshwater bivalves via algae is McKenzie and Ozbay (2010), who observed that the addition of *Elliptio complanata* to catfish aquaculture ponds in the USA resulted in an undesired increase in chlorophyll *a* concentrations.

Apart from water clarity, freshwater bivalves affect several other physico-chemical conditions of their ambient water, including nutrient (especially nitrogen and phosphorus) and oxygen concentrations. Multiple studies have quantified the effects of freshwater bivalves on nutrient concentrations in

(Figure legend continued from previous page.)

Fig. 1. Effects (grand mean effect size ± 95% confidence intervals) of freshwater bivalves on ecological functions and regulating ecosystem services (here, “ecosystem services”). Direction of effect relates to the ultimate effect on human health, safety, or comfort. (**a**) Overall effects on each ecosystem service-Group; and (**b–f**) influence of categorical moderators on freshwater bivalve effect sizes for each ecosystem service-Group that was affected by at least one categorical moderator (only data for significant moderators are shown); for full results see Supporting Information Table S2. Point and line color indicates replicate number and statistical significance of effect size: Black, $n \geq 5$ and effect significant; blue, $n \geq 5$ and effect not significant; red, $n < 5$. Statistical significance of effects: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

the water, resulting in both positive (e.g., *C. fluminea* resulting in nitrogen removal in ecological floating-beds in Lake Taihu, China; Song et al. 2014) as well as negative ecosystem service effects (e.g., *D. polymorpha* polluting the eastern Gulf of Finland; Orlova et al. 2004). Freshwater bivalve effects on dissolved oxygen concentrations in the water were predominantly negative, particularly for non-native species, as illustrated by decreasing dissolved oxygen concentrations in the tidal Hudson River after invasion by *D. polymorpha* (Caraco et al. 2000). The diversity of these ecological effects and how they ultimately affect ecosystem services appears to be a major reason for the lack of a significant overall effect of freshwater bivalves on 3.2 Water.

The lack of a consistent overall effect of freshwater bivalves on 1.3 Algae is likely also connected to the wide variation in the environmental conditions, design, and experimental setups of studies included in this category. As discussed below, the effect of freshwater bivalves on 1.3 Algae was significantly affected by freshwater bivalve dry weight and chlorophyll *a* concentrations and water temperature at the start of the experiment. These and other factors, such as parasitic infestation (Brian et al. 2022), can therefore affect the direction, size, and statistical significance of the effect. Studies quantifying phytoplankton clearance rates additionally vary with regard to, for example, the treatment of freshwater bivalves before the experiment (e.g., inclusion and length of starvation period), flow conditions, and type or species of algal food. In addition, the same ecological effect may be interpreted as a positive ecosystem service effect in one situation but negative in another situation. For example, the fact that non-native freshwater bivalves increase water clarity is interpreted as a positive ecosystem service effect in some case studies (e.g., due to increasing amenity value of the water body; Waajen et al. 2016) but a negative effect in others (e.g., due to changing functioning of the natural ecosystem; Klerks et al. 1996). Our approach of focusing on the authors' interpretations of the direction of the ultimate ecosystem service effect on humans (i.e., positive or negative) rather than the direction of the ecological effect itself (see Materials and Methods) also explains discrepancies between our results and those of Reynolds and Aldridge (2021), who observed a significant negative global effect of non-native freshwater bivalves on phytoplankton densities.

Finally, we detected a clear and significant publication bias on 1.3 Algae, which remained even after the trim-and-fill adjustments (Supporting Information Figs. S3, S6). Publication bias is a well-known phenomenon in ecological research and—if untested and undetected—invalidates the quantitative findings of meta-analyses (Jennions and Moeller 2002; Nakagawa et al. 2022). Specifically, our results indicate that studies observing a significant positive effect of freshwater bivalves on ecosystem services related to algae are more likely to be published than studies observing a negative effect. We believe that this may be due to the prevailing opinion in the current research community that freshwater bivalves are generally providing positive algae-related ecosystem services, discouraging submission and publication of work that contradicts this assumption.

Overall, these findings question common assumptions of freshwater bivalves exerting strong and ubiquitous effects on algae and water conditions, and caution against extrapolating observations from one system to another.

Invasive species and zooplankton

For ecosystem service-Groups 1.2 Zooplankton and 1.5 Invasive species, the overall mean effect size was negative, albeit not statistically significant (Fig. 1a). Effects on zooplankton are largely related to freshwater bivalve suspension feeding. Particularly, non-native freshwater bivalves, such as *Dreissena* spp. in North America (Whitten et al. 2018) and Europe (Feniova et al. 2015), and *L. fortunei* in South America (Molina et al. 2011), can reduce native zooplankton abundances and change community composition, thereby altering the natural functioning of the invaded habitats. In some cases, non-native invasive zooplankton species were promoted by non-native freshwater bivalves (Feniova et al. 2015). Examples of positive ecosystem service effects in these categories include *Dreissena* spp. cannibalizing on their own larvae (MacIsaac et al. 1991) and the native New Zealand unionoid *Echyridella menziesii* feeding on non-native cladocerans (Pearson and Duggan 2019). Examples of freshwater bivalves affecting invasive non-zooplankton taxa include the presence of non-native *D. polymorpha* leading to increased feeding rates in invasive Ponto-Caspian goby fish (Kobak et al. 2016) and invasive *D. polymorpha* growing faster on native unionoid freshwater bivalves than on stones (Hörmann and Maier 2006).

What drives differences in ecosystem service effects?

At least one moderator significantly affected the effect of freshwater bivalves on six of the eight ecosystem service-Groups, that is, 1.1 Macrofauna, 1.3 Algae, 1.4 Microorganisms, 1.5 Invasive species, 2.1 Wastes and pollutants, and 3.1 Sediment (Fig. 1b–f, Table 3; for all results see Supporting Information Tables S1 (quantitative moderators) and S2 (categorical moderators)).

Moderators related to characteristics of freshwater bivalves

Significant effects were commonly restricted to and/or more positive in native rather than non-native freshwater bivalves (i.e., for 1.1 Macrofauna, 1.4 Microorganisms and 2.1 Wastes and pollutants datasets), and Unionida and/or Venerida rather than other freshwater bivalve orders (i.e., for 1.1 Macrofauna, 2.1 Wastes and pollutants, and 3.1 Sediment datasets; 1.4 Microorganisms also Myida significant) (Fig. 1b–d, f). This suggests that non-native species do not fulfill ecosystem services to the same extent as native species and highlights the particular importance of unionoid and veneroid freshwater bivalves in providing positive and strong ecosystem services. However, it does not preclude the possibility of some

Table 3. Effect of quantitative moderators on freshwater bivalve effects on ecosystem service categories; black and gray shading indicates significant positive and negative effects, respectively. Values indicate the influence of a one-unit increase in the moderator on the estimated effect of freshwater bivalves for a given category, with replicate numbers given in brackets. Only moderators that significantly affected at least one category are listed; for full results see Supporting Information Table S1.

	Freshwater bivalve number	Freshwater bivalve dry weight	Freshwater bivalve weight per area	Freshwater bivalve density per volume	Freshwater bivalve density per area	Temperature	Oxygen concentration	P-concentration	Chl *a* concentration	Water depth	Tank size
1. Organisms			−0.001 (22)			−0.255 (118)			0.072 (57)		
1.1. Macrofauna	0.029 (16)				−0.001 (12)						−3.827 (8)
1.2. Zooplankton											
1.3. Algae (including cyanobacteria)		1.161 (8)				−0.430 (68)			0.176 (41)		
1.4. Microorganisms (excluding algae)				0.155 (18)				50.543 (4)	0.046 (5)	−0.611 (8)	
1.5. Invasive species											
2. Human inputs = 2.1. Wastes and pollutants							1.848 (30)				0.085 (22)
3. Physico-chemical conditions											
3.1. Sediment				−7.043 (7)				43.216 (3)			
3.2. Water											

non-natives having positive impacts under certain conditions (Albertson et al. 2021; Soto et al. 2024).

Contrary to our expectations, there was no consistent effect of moderators related to freshwater bivalve biomass affecting their ecosystem service effect. While ecosystem service-provisioning by freshwater bivalves significantly increased with freshwater bivalve size, weight, and densities in some instances (e.g., 1.3 Algae—freshwater bivalve dry weight, 1.4 Microorganisms—freshwater bivalve density per volume), the opposite pattern was found for other associations (e.g., 1.1 Macrofauna—freshwater bivalve number) (Table 2). This contradicts studies by Vaughn et al. (2004) and Atkinson and Vaughn (2015), which observed a clear increase in ecosystem services with increasing freshwater bivalve population densities or abundances. These disparities are likely due to the heterogeneity of our dataset, which spans a wide range of freshwater bivalve taxa, study designs, habitat types, environmental conditions, and climatic zones. For example, in rivers, unionids have strong biomass-related effects on ecosystem services during low flow conditions, but not under high flow conditions (Atkinson and Vaughn 2015), and stronger effects in pristine streams than in agriculturally impacted streams with high nutrient loads (Spooner et al. 2013).

Moderators related to experimental design

Significant overall effects were restricted to laboratory studies rather than field or mesocosm studies for ecosystem service—Groups 1.4 Microorganisms, 1.5 Invasive species, and 2.1 Wastes and pollutants (Fig. 1c–e). This is expected, as laboratory experiments are conducted to minimize noise in the dataset by controlling conditions across replicates, including environmental conditions, such as temperature and flow, and biotic interactions with other organisms. However, for 1.1 Macrofauna, a significant overall effect was restricted to field studies rather than mesocosm studies (Fig. 1b), which can be explained by the generally low diversity of macroinvertebrates in mesocosms compared to the natural environment (Allen et al. 2012). Finally, we note that commonly, the aforementioned restrictions of significant effects to laboratory and field studies, respectively, coincided with a similar restriction to studies without and with other freshwater bivalves being present, respectively (Fig. 1b–d). These associations can be explained by field studies focusing on natural freshwater bivalve assemblages that commonly feature more than one species, while laboratory experiments are usually conducted on a single freshwater bivalve species at a time.

Moderators related to environmental conditions

Environmental parameters that significantly influenced effects for at least one ecosystem service-Group included temperature, dissolved oxygen concentrations, and chlorophyll *a* concentrations in the water (Table 3). Effects related to 1.3 Algae were significantly negatively affected by temperature and significantly positively affected by chlorophyll *a* concentrations. Positive effects of freshwater bivalves on algae-related ecosystem services, which most commonly refer to phytoplankton communities in our dataset, thus become stronger and more positive with increasing phytoplankton concentrations at the start of the experiment. This result conforms with observations of unionid clearance rate increasing with increasing algal flux (Byllaardt and Ackerman 2014); although freshwater bivalve clearance capacity does become saturated at high particle flux (Mistry and Ackerman 2018). While effects of freshwater bivalves on algae-related ecosystem services became stronger and more positive with decreasing temperature, this observation is more difficult to explain considering the heterogeneity of our dataset that spans tropical to cold-temperate habitats, which support different algal communities with different physiological optima and growth rates.

Conclusions

This study provides the first quantitative synthesis of global ecosystem services provision by freshwater bivalves. Despite the wide variety of taxa, study designs, and contexts within our dataset, some clear patterns emerged. Freshwater bivalves had a significant positive ecosystem service effect overall and specifically, via effects on macrofauna, microorganisms, wastes and pollutants, and sediments. As such, the widely held assertion for the important roles and services provided by freshwater bivalves is supported by our meta-analysis. However, our analyses also unexpectedly found that freshwater bivalves do not have strong, ubiquitous ecosystem service effects related to algae and water condition. These findings, exacerbated by the observed bias toward publishing positive rather than non-significant or negative results on ecosystem services of freshwater bivalves related to algae, warn against selective extrapolation of high-profile studies to all freshwater bivalve species in all settings.

Our meta-analysis showed that not all freshwater bivalves are equal in their ecosystem service provision, with native species and species from the orders Unionida and Venerida generally providing more significant and positive effects than other freshwater bivalves. This challenges arguments by other authors stating that replacement of native freshwater bivalves (e.g., unionids) with non-native invasive freshwater bivalves (e.g., *D. polymorpha*) retains overall ecosystem services (Pearce 2016). In fact, our findings stress the importance of large-scale conservation efforts for freshwater bivalves globally and particularly of the Unionida, one of the most globally imperiled taxa (Lopes-Lima et al. 2018; IUCN 2023). While conservation efforts are currently commonly focused on the most vulnerable species, the wider ecosystem-level impacts of declines in the commonest species may be the most profound (Aldridge et al. 2023). Apart from targeted efforts toward restoring freshwater bivalve population densities to ecologically functional levels, outreach efforts are urgently needed globally to raise awareness of freshwater bivalves to the public and decision makers.

Our study revealed a considerable bias and context-dependency in our current understanding of how freshwater bivalves affect ecosystem services. (1) There are clear biases in the available dataset, including a low representation from studies in the tropics and the Global South and a dominance of certain taxa (e.g., *D. polymorpha*). A better understanding of the roles of freshwater bivalves in the Global South is needed because the freshwater bivalve fauna in this region is one of the most diverse and endemic globally yet suffers some of the fastest declines (Zieritz et al. 2018; Aldridge et al. 2023). (2) More detailed studies are needed to disentangle how specific factors related to freshwater bivalve species and populations, environmental conditions, and experimental setup and scale (DuBose et al. 2024) affect the direction and size of specific ecosystem service effects. (3) Assessing the spatial and temporal variation in ecosystem service provision of freshwater bivalves will require the development and application of standardized protocols for measuring their ecosystem services, similar to what is already available for trees (Nowak 2023). Availability of such protocols may also encourage the publication of results that show no significant effects and help to address concerns over publication bias.

Author Contributions

Alexandra Zieritz: conceptualization; data curation; investigation; methodology; project administration; validation; writing—original draft preparation; writing–review and editing. Joshua I. Brian: formal analysis; visualization; writing—original draft preparation; writing—review and editing. Ronaldo Sousa, David C. Aldridge: conceptualization; investigation; writing—review and editing. Carla L. Atkinson, Caryn Vaughn, Yulia Bespalaya, Tabitha Richmond, Alma Crisp, Garrett W. Hopper, Adam M. Ćmiel, Andreas H. Dobler, Fabio Ercoli, Eduardo Esteves, Juergen Geist, Irene Sánchez González, Dariusz Halabowski, Philipp Hoos, Heini Hyvärinen, Martina Ilarri, Iga Lewin, Anna M. Lipińska, Jon H. Mageroy, Daniele Nizzoli, Isobel Ollard, Martin Österling, Nicoletta Riccardi, Sebastian L. Rock, Noé Ferreira-Rodríquez, Tuomo Sjönberg, Jouni Taskinen, Gorazd Urbanič, Maria Urbańska, Qingqing Yu: investigation; writing—review and editing. Karel Douda: conceptualization; investigation; validation; writing—review and editing. Ana Sofia Vaz: conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing—original draft preparation; writing—review and editing.

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Conflicts of Interest

None declared.

Data Availability Statement

All data and code supporting the manuscript are available from Zenodo: https://doi.org/10.5281/zenodo.15210266.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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