

# Understanding environmental change through the lens of trait-based, functional, and phylogenetic biodiversity in freshwater ecosystems

Janne Alahuhta, Tibor Erős, Olli-Matti Kärnä, Janne Soininen, Jianjun Wang, and Jani Heino

**Abstract:** In the era of the Anthropocene, environmental change is accelerating biodiversity loss across ecosystems on Earth, among which freshwaters are likely the most threatened. Different biodiversity facets in the freshwater realm suffer from various environmental changes that jeopardize the ecosystem functions and services important for humankind. In this work we examine how environmental changes (e.g., climate change, eutrophication, or invasive species) affect trait-based, functional, and phylogenetic diversity of biological communities. We first developed a simple conceptual model of the possible relationships between environmental change and these three diversity facets in freshwaters and, secondly, systematically reviewed articles where these relationships had been investigated in different freshwater ecosystems. Finally, we highlighted research gaps from the perspectives of organisms, ecosystems, stressors, and geographical locations. Our conceptual model suggested that both natural factors and global change operating at various spatial scales influence freshwater community structure and ecosystem functioning. The relationships between biodiversity and environmental change depend on geographical region, organism group, spatial scale, and environmental change gradient length. The systematic review revealed that environmental change impacts biodiversity patterns in freshwaters, but there is no single type of biodiversity response to the observed global changes. Natural stressors had different, even contradictory, effects (i.e., multiple, negative, and positive) on biodiversity compared with anthropogenic stressors. Anthropogenic stressors more often decreased biodiversity, although eutrophication and climate change affected freshwater ecosystems in a complex, more multi-dimensional way. The research gaps we identified were related, for example, to the low number of community-based biodiversity studies, the lack of information on true phylogenies for all freshwater organism groups, the missing evaluations whether species traits are phylogenetically conserved, and the geographical biases in research (i.e., absence of studies from Africa, Southern Asia, and Russia). We hope that our review will stimulate more research on the less well-known facets and topics of biodiversity loss in highly vulnerable freshwater ecosystems.

**Key words:** community ecology, diversity index, functional diversity, global change, lakes, phylogenetic diversity, rivers, species traits, streams.

**Résumé :** À l'ère anthropocène, le changement environnemental cause l'accélération de la perte de biodiversité des écosystèmes sur la Terre, les eaux douces étant probablement les plus menacées. Les différentes facettes de la biodiversité dans la sphère des eaux douces subissent divers changements environnementaux qui compromettent les fonctions écosystémiques et les services importants pour l'humanité. Dans cette étude, nous examinons comment les changements environnementaux (p. ex., le changement climatique, l'eutrophisation ou les espèces envahissantes) influent sur la diversité caractéristique, fonctionnelle et phylogénétique de communautés biologiques. Nous avons d'abord élaboré un modèle conceptuel simple des relations possibles entre le changement environnemental et ces trois facettes de la diversité dans les eaux douces, et ensuite, nous avons systématiquement examiné les articles où ces relations avaient été étudiées au niveau de différents écosystèmes d'eau douce. Enfin, nous avons soulevé les lacunes en matière de recherche du point de vue des organismes, des écosystèmes, des facteurs agressifs du milieu et des emplacements géographiques. Notre modèle conceptuel indique que les facteurs naturels et le changement à l'échelle planétaire opérant à diverses échelles spatiales influent sur la structure des communautés d'eau douce et la dynamique de l'écosystème. Les relations entre la biodiversité et le changement environnemental dépendent de la région géographique, du groupe d'organismes, de l'échelle spatiale et de la longueur de gradient environnemental. La revue systématique a révélé que le changement environnemental a un impact sur les distributions de la biodiversité dans les eaux douces, mais qu'il n'y a pas un type unique de réponse de la biodiversité aux changements observés à l'échelle planétaire. Les facteurs de stress naturels avaient des effets différents, même contradictoires (c.-à-d., multiples, négatifs et positifs) sur la biodiversité comparés aux facteurs de stress anthropiques. Les facteurs de stress anthropiques causaient plus souvent une diminution de la biodiversité, bien que

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L'eutrophisation et le changement climatique aient une incidence sur les écosystèmes d'eau douce de manière complexe, plus multidimensionnelle. Les lacunes en matière de recherche que nous avons identifiées étaient liées, p. ex., au faible nombre d'études de biodiversité selon la communauté, au manque d'informations sur les vraies phylogénies pour tous les groupes d'organismes d'eau douce, aux évaluations manquantes à savoir si les caractères d'espèce sont conservés relativement à la phylogénétique, et aux tendances géographiques au niveau de la recherche (c.-à-d., l'absence d'études de l'Afrique, de l'Asie du Sud et de la Russie). Nous espérons que notre étude stimulera plus de recherche sur les facettes moins connues et les sujets de perte de biodiversité dans les écosystèmes très vulnérables d'eau douce. [Traduit par la Rédaction]

*Mots-clés* : écologie de communauté, indice de diversité, diversité fonctionnelle, changement à l'échelle planétaire, lacs, diversité phylogénétique, rivières, caractères des espèces, cours d'eau.

## Introduction

Environmental change affects biodiversity, but its influence varies in time and space, including within and across ecosystems (Hooper et al. 2012; Dornelas et al. 2014). In the era of the Anthropocene, the general understanding is that biodiversity loss is accelerating, for example, due to increased atmospheric greenhouse gases, land use alteration, environmental pollution including eutrophication, overexploitation of species, and invasion of exotic species (McGill et al. 2015; Maxwell et al. 2016). Such undesirable progress affecting biodiversity is also jeopardizing ecosystem functions and services vital to human well-being (Cardinale et al. 2012). In this sense, perhaps the most threatened ecosystems exposed to environmental changes are freshwaters (Dudgeon et al. 2006; Vörösmarty et al. 2010; Wiens 2016; Vilmi et al. 2017). This is because many freshwater species have limited ability to disperse in the face of changing environmental conditions (Heino et al. 2009) and they are subject to multiple anthropogenic pressures acting simultaneously (Woodward et al. 2010). In addition, freshwaters are not often part of the biodiversity conservation programs.

Although freshwaters account for only ca. 1% of the Earth's total surface area, they are especially important ecosystems, because they (i) host a relatively larger proportion of biodiversity compared with terrestrial systems and (ii) constitute a source for many of the essential but threatened ecosystem services such as drinking water supplies, aquaculture, and climate change mitigation (Dudgeon et al. 2006; Cardinale et al. 2012). In addition, freshwater and terrestrial ecosystems are fundamentally interrelated through the movement of energy, nutrients, and other materials (Soinin et al. 2015). For example, organic matter within a catchment area and terrestrial organisms enter lentic and lotic systems, whereas aquatic insects emerge and fly to surrounding riparian zones, where they are eaten by terrestrial predators. Thus, freshwater ecosystems depend on multiple environmental characteristics operating at various spatial scales (Fig. 1). These issues not only highlight the importance to maintain and protect the taxonomic diversity of ecological communities, but also other facets of biodiversity in the freshwater realm at various spatial scales.

Community ecologists have measured various aspects of biodiversity concurrently within species assemblages, including trait-based, functional, and phylogenetic diversity. In general, a species trait is any single feature or quantifiable feature of an organism that affects its performance or fitness in relation to abiotic and biotic factors (McGill et al. 2006). A set of species traits is related to a site where a species can actually live, how species interact with each other, the strength of competition or consumption efficiency of a predator, and the contribution of species to ecosystem functioning (McGill et al. 2006; Cadotte et al. 2011). Functional diversity is traditionally defined as the diversity of species traits in ecosystems and measures how an ecosystem operates or functions without necessarily considering organisms' evolutionary history (Petchey and Gaston 2006; Schleuter et al. 2010). Phylogenetic diversity, on the other hand, comprises the differences in evolutionary history of species in a community and can possibly be used as a proxy for functional diversity if the species traits consid-

ered are phylogenetically conserved (Winter et al. 2013). Phylogenetic diversity captures various species traits, but is not informative for identifying what they might be (Flynn et al. 2011). These alternative approaches may provide better generality in understanding and predicting the assembly of ecological communities and ecosystem functions than more traditional approaches based on species taxonomic identity (Devictor et al. 2010; Schleuter et al. 2010; Gagic et al. 2015). Although more research is being devoted to understanding and measuring these aspects of biodiversity, our knowledge of their response to environmental change is still limited in freshwater ecosystems (Vaughn 2010; Woodward et al. 2010).

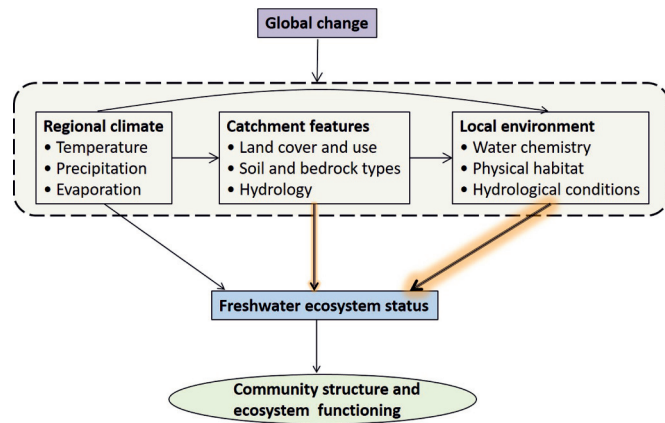
To better understand how environmental change affects trait-based, functional, and phylogenetic diversity of freshwater assemblages, we (i) developed a conceptual model of the possible relationships between environmental change and these three diversity facets in freshwaters and (ii) systematically reviewed articles where these relationships have been studied in different freshwater ecosystems. Our study focused exclusively on the investigations of diversity of biological communities where a trait-based, functional, or phylogenetic index was used to indicate how environmental change has altered freshwater ecosystems. For the systematic review, we specifically investigated which (i) biodiversity facets and (ii) organism groups have been under investigation and (iii) which environmental stressors (i.e., natural vs. anthropogenic) have impacted freshwater biodiversity. In addition, to provide a general picture of what kind of changes in freshwater biodiversity have already been studied, we highlighted research gaps from the perspectives of organisms, ecosystems, stressors, and geographical locations.

## Local communities, biodiversity patterns, and ecosystem functioning

In a freshwater community, species functional traits are likely to be more important than species richness in maintaining ecosystem functioning (Mouillot et al. 2012). Papers investigating the relationships between species traits, ecosystem functioning, and the environment in freshwaters consider various ecosystems and biological groups (Jones et al. 2002; Vaughn et al. 2007; Bruder et al. 2015). For example, increasing and more frequent drying of river channels is expected due to the climate change (Datry et al. 2017; Mustonen et al. 2018), and Bruder et al. (2011) found that drying influenced both fungal decomposers and the decomposition rate of broad-leaved tree litter. However, most studies on the relationship between freshwater biodiversity and ecosystem functioning have been done using a single species trait or functional groups until recent years, possibly resulting in underestimation of species' roles in ecosystem functions (Vaughn 2010).

A local freshwater community not only consists of different taxonomic assemblages but also comprises species with various traits. The foundations of a local community come from the global and regional species pools, from which species with suitable traits are filtered by the biotic and abiotic environment to determine species that can successfully colonize and co-exist at a local site (e.g., Poff et al. 1997). In addition, for a given regional

**Fig. 1.** Conceptual illustration of the relationships between environmental change and freshwater community structure and ecosystem functioning. Freshwater (abiotic) ecosystem status is influenced by different environmental variables, ranging in an increasing order of importance from regional climate and catchment features to local environmental features. Ecological status of surface waters per se comprises of many water quality variables such as nutrient status and oxygen levels.



species pool, species may respond to environmental gradients in different ways, affecting the distribution of different biodiversity measures over different spatial and temporal scales and generating spatial mismatch among taxonomic, functional, and phylogenetic diversities (Devictor et al. 2010).

Dispersal is an essential natural process influencing local freshwater communities, as well as regional species pools and ecosystem functioning (Fig. 2). Dispersal may mask the importance of environmental conditions affecting local communities, because very high or low dispersal rates may restrict species sorting, dissociating the otherwise strong relationship between local communities and local environmental characteristics (Leibold et al. 2004; Winegardner et al. 2012). In addition to dispersal, speciation-extinction rate is a major relatively long-term driver of local communities that should be acknowledged to understand the evolutionary processes driving diversity patterns (Mittelbach and Schemske 2015). Biotic interactions among species, especially competitive interactions, are also important drivers of local community structure that are, at least partly, mediated by species functional traits (Edwards et al. 2011). Ecosystem disturbance often enhances mortality rates and decreases reproduction rates for the species present, causing density-dependent competition to have a weaker effect on taxonomic community structure than on functional community structure (Mouillot et al. 2012). Moreover, global change effects can exclude species with certain traits or strongly decrease their abundance in a community. As a result, trait differences between species can mediate interspecific differences in relation to global change, thus influencing ecosystem functioning in freshwaters (Haddad et al. 2008).

Global change has also other impacts on local community structure and ecosystem functioning (Fig. 2). Climate change affects not only taxonomically defined communities, but also causes shifts in functional space occupation by driving species with traits poorly fitted to the new environment to extinction (Mouillot et al. 2012). In freshwaters, this would affect especially species having traits suitable for coping with cold climates, where species may be severely affected by climate warming (Heino et al. 2009). Climate change also allows colonization of species with better-fitting traits to remove cold-tolerant species from high-latitude and high-elevation freshwaters (Angeler et al. 2013; Boersma et al. 2016; Garcia-Raventos et al. 2017), showing a negative trend between biodiversity and climate change (Fig. 3). In addition, non-native

species can change the functional structure of a given community through altering functional space occupied by native species, for example, through competition (Olden et al. 2006; Mouillot et al. 2012). Although native and non-native species may possess similar functional traits, a competitive advantage may allow non-native species to establish and finally even outcompete native species. Finally, non-native species can function as consumers to diminish native species abundances until they are threatened with extinction (Mouillot et al. 2012).

Eutrophication is a major problem in many freshwater ecosystems across the world. In addition, climate change likely boosts the harmful effects of eutrophication, because warming temperatures and enhanced carbon dioxide concentrations increase eutrophication symptoms (Moss et al. 2011). As a result, trait-based, functional, and phylogenetic diversity are likely to be reduced (Fig. 3), because the combined effects of global change filter out species located in different parts of the functional space or even act additively, leading to rapid extinctions when their effects intersect in functional space (Statzner and Beche 2010; Mouillot et al. 2012). However, the influence of eutrophication likely varies according to the original background ecosystem status (Fig. 3). In mainly oligotrophic systems, the relationship between biodiversity and nutrient enrichment can even be positive (Erős et al. 2009; Leira et al. 2009), whereas mesotrophic freshwaters may show a unimodal response to eutrophication (Nevalainen and Luoto 2017), and a negative relationship is found especially in high-nutrient ecosystems due to competitive exclusion (Peru and Doledec, 2010; Fernandez et al. 2014). In some cases, biodiversity measures may not respond to the measured and anticipated disturbance, leading to a nonsignificant relationship. This kind of pattern has especially been found for taxonomic distinctness (e.g., Heino et al. 2007; Vilmi et al. 2017), which has been used as a proxy for evolutionary relationships among species when no true phylogeny is available (Clarke and Warwick 2001).

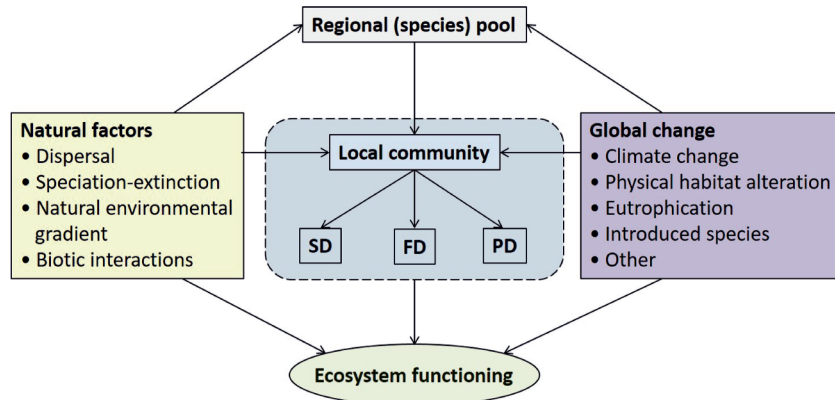
Physical habitat alterations in freshwaters are typically related to damming of rivers, leading to loss or change of hydrological connections, channelization, water level regulation in lakes and rivers, degradation of the riparian zone by land use along both lakes and rivers, and drought events. As hydrological conditions fundamentally govern the establishment, growth, reproduction, dispersal, and extinction of many, if not most, freshwater organisms (Poff et al. 1997), changes in physical habitat have profound effects on biodiversity patterns in freshwaters. Species with poor dispersal abilities and (or) intolerant traits against rapid short-term habitat changes are in a jeopardy to be removed from a given freshwater ecosystem suffering from water level fluctuations and temporally dynamic flood and drought events (Silver et al. 2012; Abgrall et al. 2017). In addition, long-lasting changes in physical habitats due to dam construction or channel modification and destruction of the riparian zone force species to evolve new traits as adaptations to new environmental conditions unless they go to extinct or disperse to new habitats (Bhat and Magurran 2006; Espanol et al. 2015).

## Systematic literature review

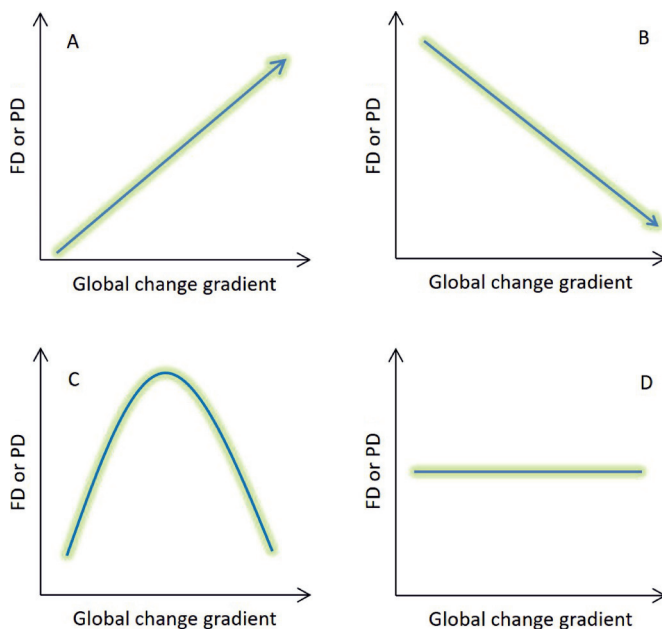
### Selection criteria of systematic review

We performed the literature search in the Web of Science (WoS; <http://apps.webofknowledge.com>) using appropriate keywords related to our study topics. We used four kinds of keywords simultaneously: (i) words that describe the trait-based, functional, and phylogenetic diversity (funct\* OR trait\* OR phylogen\* OR "taxonomic distinctness"); (ii) words related to freshwater habitats (freshwater\* OR lentic\* OR lotic\* OR lake\* OR pond\* OR stream\* OR river\* OR wetland\* OR spring\*); (iii) words that are related to diversity (divers\* OR biodiv\*); and (iv) words that indicate environmental change (environment\* OR "climate change" OR eutrophication OR acidification OR "habitat loss" OR "nutrient enrichment" OR

**Fig. 2.** The relationships between a local community and its environment in relation to ecosystem functioning. Local communities consist of a subset of species with suitable traits from the regional (species) pool that have passed through environmental filters (i.e., natural factors and global changes). Both natural factors and global change affect regional (species) pool, local communities, and ecosystem functioning. SD, species diversity; FD, functional diversity; PD, phylogenetic diversity.



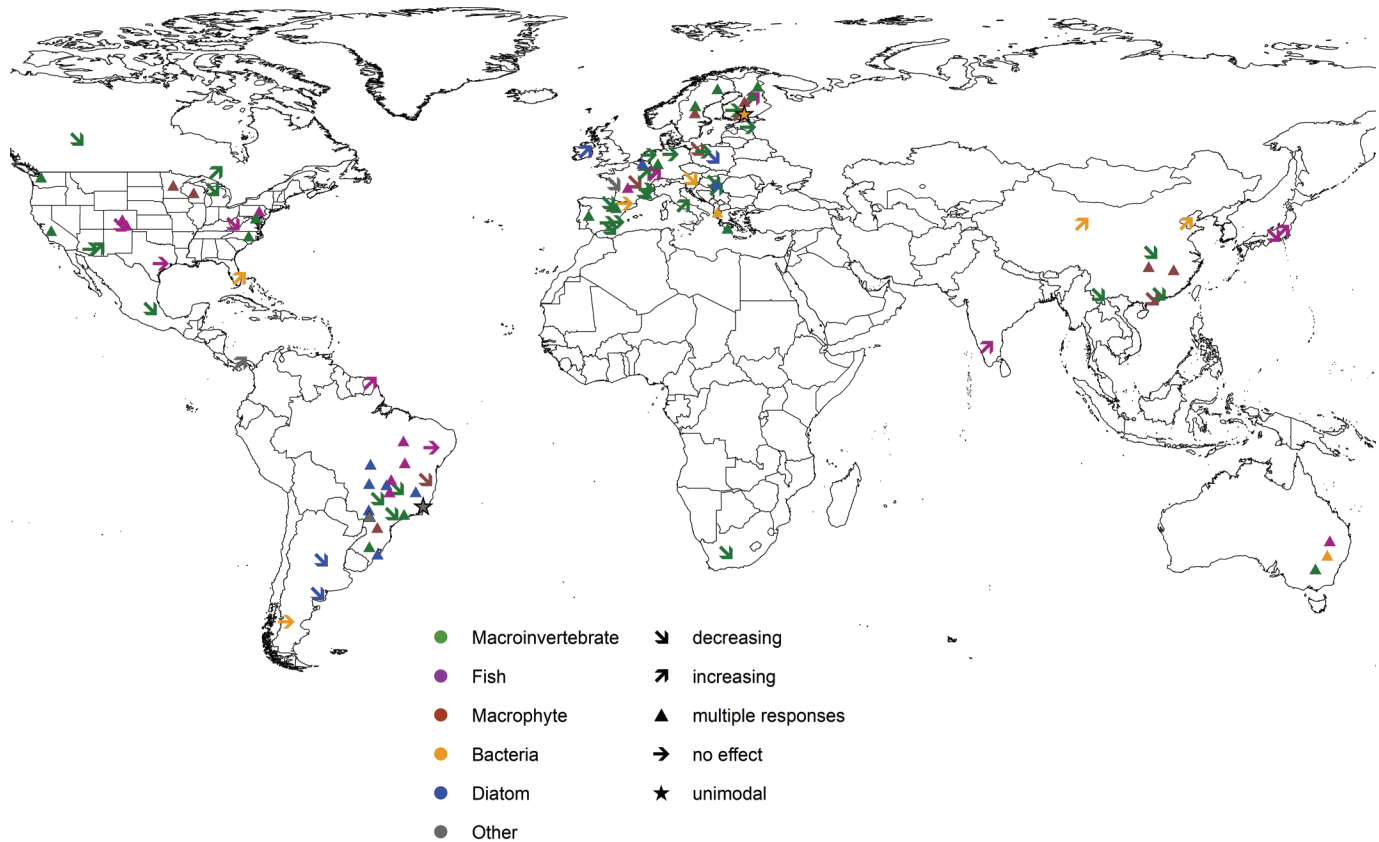
**Fig. 3.** Hypothesised relationships between functional diversity (FD) or phylogenetic diversity (PD) and an environmental change gradient. Depending on the length of the gradient and geographical location of study region, these relationships could be different. Environmental change may enhance diversity in less-disturbed regions situated, for example, in high latitudes (A), where increased nutrient inputs to freshwaters or higher temperatures can boost functional and phylogenetic diversity. On the other hand, the relation between diversity and environmental change is often negative in more human-impacted regions (B), where eutrophication, invasive species, or increased temperatures may strongly affect local (native) communities by decreasing functional and phylogenetic diversity. When the focus is on a full environmental change gradient, such as at global scale, the relationship is expected to be unimodal (C). Functional diversity is first enhanced by increased environmental change effects, but the relationship becomes negative when the environmental change pressures increases. In some cases, environmental changes may not have any detectable influence on functional and phylogenetic diversity (for example in the case of short environmental gradients or when species are functionally redundant), resulting in a nonsignificant relationship (D).



“global change” OR “climate warming” OR invasive\* OR exotic\* OR alien\* OR urbanization OR pollution OR drought OR channelization). TITLE was selected for the row describing trait-based, functional, and phylogenetic diversity words, whereas TOPIC was selected for all other rows. Trait-based diversity and functional diversity do not mean the same thing, as the former term is more inclusive than the latter, and the latter should only include traits that really affect ecosystems functions. In practice, both terms have been extensively used in the literature, often also interchangeably. The use of TITLE in other rows would have strongly narrowed the number of potential articles in our search exercises that may have resulted to exclusion of some matching papers. We did not have any temporal limitation in our search but all the possible articles matching our criteria were selected. The main search for suitable articles was executed on 13 April 2017, followed by complementary searches done on 13 February 2018 and 21 September 2018 to account for all published articles in 2017 and to include channelization as an additional environmental change keyword, respectively. This extensive search protocol resulted in a total of 1475 results found. After the main WoS literature search, all authors were given an equal number of articles to go through and select suitable articles matching our study scope. The first author selected suitable articles from the complementary search effort of 2017. The first and the last author together double-checked all the selected articles to ensure uniformity and objectivity in the selection process. We included articles that reported results for freshwater ecosystems and covered the effects of environmental change on trait-based, functional, and phylogenetic diversity of community-based data through different indices. Instead, we excluded articles that used a space-for-time substitution to illustrate, for example, the effects of global warming, articles that tested ecological theories only, articles that did not have any clear stressors, purely predictive articles, review articles, or conference abstracts. These types of articles were common among the initial WoS search results, but they were removed from the final selection. We stress that articles dealing with biological compositions distinguished to functional groups or assemblages did not meet our criteria, because we focussed purely on different indices used to characterize trait-based, functional, and phylogenetic diversity of freshwater organisms. Thus, articles dealing with grouping of species based on their traits or functional properties (e.g., functional feeding groups of macroinvertebrates or growth forms of macrophytes) and based often on ordination methods only did not pass our selection criteria. Articles lacking clear statements of results were not included in the final set of articles. All authors collected information from articles that were likely suitable for

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**Fig. 4.** A map illustrating the biological groups used to study the relationship between trait-based, functional, and phylogenetic diversity and the direction of effect caused by environmental change effects based on our systematic review in the freshwater realm ( $n = 100$ ).



comparative purposes (Table S1<sup>1</sup>). The first author rechecked all the collected information to guarantee data quality, and we formed a number of categories from the different variables. These included, for example, five groups of organisms (i.e., macroinvertebrates, fish, macrophytes, bacteria, diatoms, and other taxa; see Fig. 4), four main stressors (i.e., eutrophication, physical habitat alteration, non-native species, and climate change, and their joint effects; see Fig. 5), and direction of stressor effect (i.e., no effect, increasing, decreasing, and multiple responses). Finally, the first author compiled a consistent data set including main information and variables from the final set of 100 selected articles matching our strict inclusion criteria (Table S2<sup>1</sup>).

### Main findings from the systematic review

Our systematic review on the trait-based, functional, and phylogenetic diversity measures of freshwater communities revealed that the first papers (beyond single ones) were published in 2003 (Fig. 6). Although a clear increase in the absolute numbers of papers was detected after 2011, there was no increasing pattern in the proportion of papers in relation to similar studies executed in terrestrial and marine systems (based on the similar WoS search but freshwater habitats as TOPIC were excluded from the search). This suggests that findings on these community-based diversity measures published in journals with general ecological foci have reached freshwater and terrestrial/marine ecologists only relatively recently. Modern well-recognized papers on community-based functional ecology were published in the mid-2000s (e.g., McGill et al. 2006; Petchey and Gaston 2006; Villegger et al. 2008),

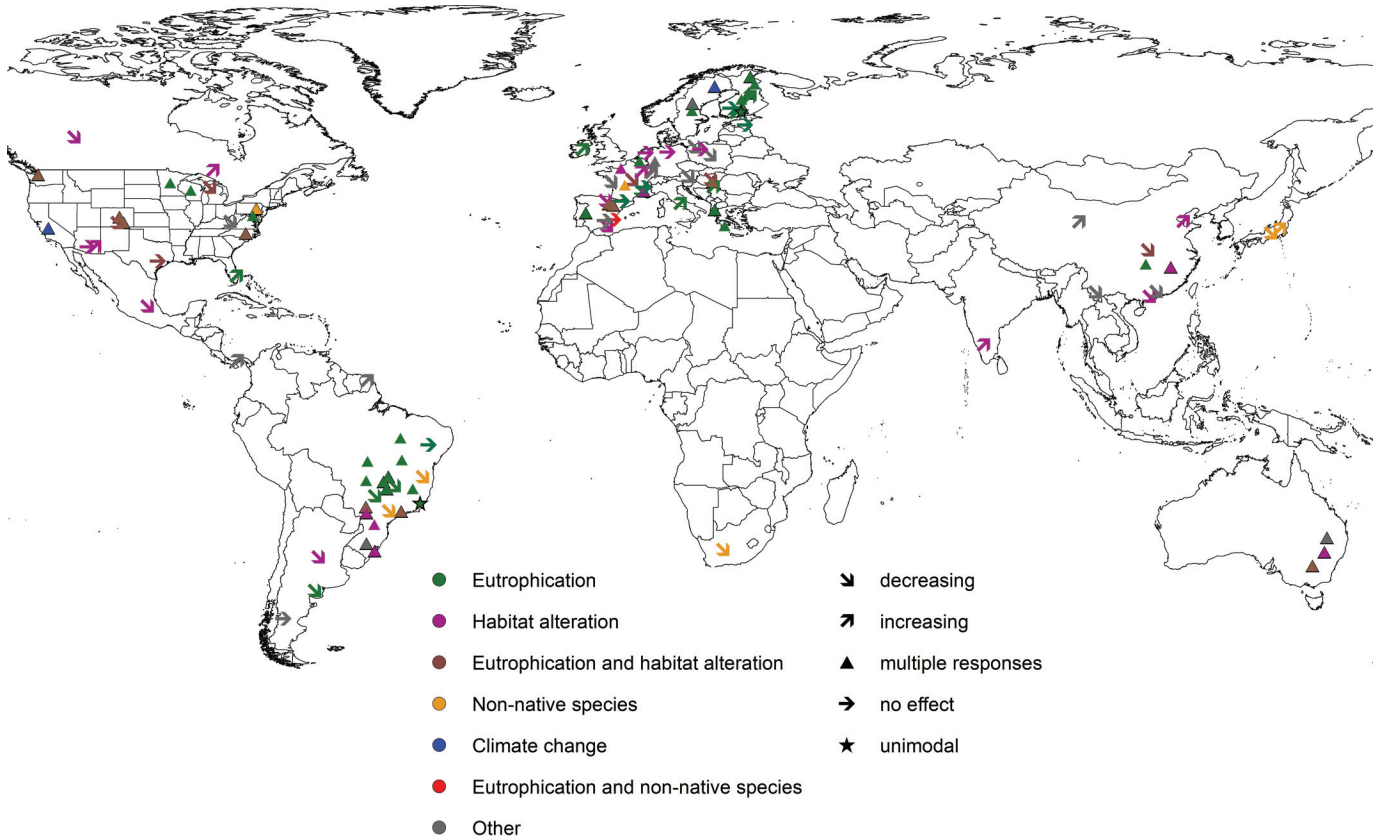
and freshwater ecologists have found these measures relatively well.

The systematic review revealed that various different measures of trait-based, functional, and phylogenetic diversity have been used in the freshwater research over the years. The most common measures were functional richness, functional evenness, functional divergence, and taxonomic distinctness. Beside these indices, various other approaches were used including the following: trait diversity or number of trait combinations (e.g., through community-weighted mean), phylogenetic diversity, Rao's quadratic entropy, and functional beta diversity. The majority of the rarely used measures were used only in a single study.

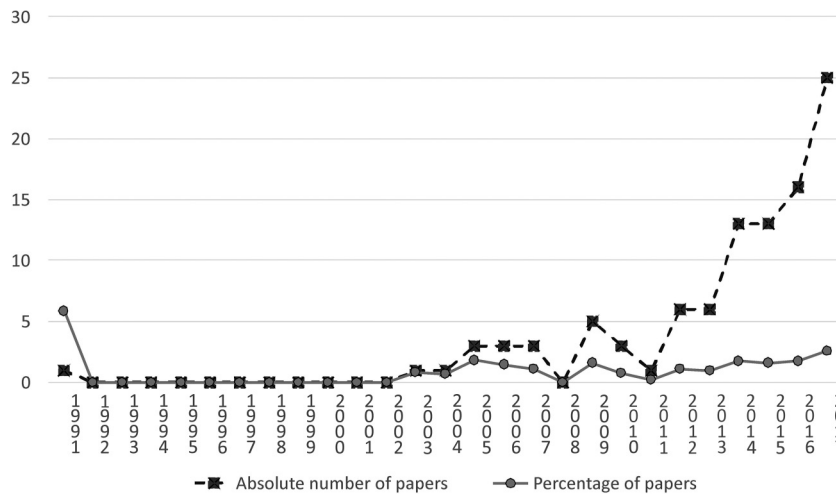
Considering different organism groups, macroinvertebrates were the most studied group utilised in half of the selected papers when investigating the relationship between functional, trait-based, or phylogenetic diversity and the environment (Fig. 4; Fig. S1<sup>1</sup>). Functional diversity was the most widely used approach for macroinvertebrates (in 34 papers out of 47 macroinvertebrate papers), followed by phylogenetic diversity studied in nine papers (Fig. S2<sup>1</sup>). After the introduction of taxonomic distinctness index as a proxy of phylogeny (Clarke and Warwick 2001), there were several papers published where taxonomic distinctness of macroinvertebrates was correlated with environmental variables (e.g., Abellan et al. 2006; Heino et al. 2007; Alahuhta et al. 2017a). Macroinvertebrate studies were mostly done in lotic systems (33 out of 47) and were relatively equally distributed among different years and continents where they had been investigated. Fish were the second most studied organism group (20 out of 100) with 85% of

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/er-2018-0071>.

**Fig. 5.** A map illustrating the relationship between specific environmental change stressor and the direction of effect found in the different articles ( $n = 100$ ) selected in the systematic review.



**Fig. 6.** Absolute and percentage (absolute number of selected papers in relation to all papers dealing with environmental change and functional, trait-based, and phylogenetic diversity in terrestrial and marine systems) changes in the number of articles published that focus on the relationship between environmental change and functional, trait-based, and phylogenetic diversity in freshwaters over the years based on our selection criteria (see Selection criteria of systematic review).



the papers focussed on rivers and streams. Similar to macroinvertebrates, functional diversity was the most studied index (16 out of 20), and fish studies were found from different years and studied continents (e.g., Pool and Olden 2012; Matsuzaki et al. 2016; Sagouis et al. 2017). Bacteria, diatoms, and macrophytes were each investigated in ca. 10% of selected papers. For macrophytes and diatoms, functional diversity was the most studied measure (six out of 10 and nine out of 13, respectively), whereas both functional and phylogenetic diversity were solely used for bacteria. Com-

pared with the other freshwater assemblages, phylogenetic diversity studies on bacteria have been based on true phylogeny instead of proxy measures (e.g., Barberan and Casamayor 2014). Bacteria, diatoms, and macrophytes were mostly investigated in lakes and ponds (6 out of 9, 11 out of 13, and 8 out of 10, respectively), but also some river and stream studies have appeared. All of the three organism groups were researched mostly in North America, South America, Europe, and China during the 2010s. Temporal aspects were considered in ca. 30% of all selected pa-

pers, ranging from phylogenetic diversity of stream macroinvertebrates in relation to damming (Campbell and Novelo-Gutierrez 2007) and measuring the effects of climate change on functional resilience of multiple taxa in subarctic lakes (Angeler et al. 2013) to temporal changes in nutrient enrichment on macroinvertebrate functional diversity in boreal lakes (Nevalainen and Luoto 2017).

Biodiversity measures of different organism groups responded differently to environmental stressors (Fig. S1<sup>1</sup>). For macroinvertebrates (20 out of 47 studies), fish (11 out of 20), diatoms (9 out of 13) and macrophytes (5 out of 10), “multiple effects” were the most common relationship between the biodiversity measure and the stressor(s). On the other hand, all stressor types were equally common in studies of bacterial biodiversity. Considering biodiversity measures across organism groups, the typical relationship was that functional diversity showed multiple relationships with eutrophication and physical habitat alteration (Fig. 5). These two stressor types were also the most studied both separately and jointly. Instead, climate change and non-native species were studied only in less than 6% of the papers. This is a rather alarming finding considering the multiple and additive impacts climate change has been predicted to have on freshwater systems (Heino et al. 2009; Moss et al. 2011). Climate change (2 out of 3), physical habitat alteration (22 out of 42), and eutrophication (31 out of 52) most commonly showed multiple effects on biodiversity measures, whereas only non-native species showed mainly negative influences on the biodiversity (4 out of 7). Physical habitat alteration quite often also decreased trait-based, functional, and phylogenetic diversity in the freshwater realm (11 out of 42). The effects of degradation of habitat conditions and non-native species are often straightforward and direct in freshwater ecosystems, which is why the responses of biodiversity measures to these two environmental changes were negative more often compared with other environmental change stressors (Campbell and Novelo-Gutierrez 2007; Liu et al. 2013; Matsuzaki et al. 2016). On the contrary, the influence of eutrophication and climate change on ecosystem functioning is typically more multi-dimensional, having contradictory and often cumulative effects on different organism groups and food chain levels (Leira et al. 2009; Angeler et al. 2013; Boersma et al. 2016; Vilmi et al. 2017). In addition, functional diversity often consists of several indices (e.g., functional richness, evenness, and divergence) that show variable responses to the environment (Petchey and Gaston 2006; Mouillot et al. 2012), resulting in the multiple effects detected between biodiversity and environmental change. Interestingly, however, human-induced stressors more often decreased biodiversity (18 out of 42), whereas natural stressors had frequently various effects (i.e., multiple, increasing, or no effect) on the studied biodiversity indices. In the examples of decreased biodiversity due to global change, functional diversity was typically lower in impacted sites than in reference water bodies or reduced over time (Liu et al. 2013; Matsuzaki et al. 2016).

### Environmental change drives biodiversity patterns in freshwaters, but there is no single type of biodiversity response to the change

Environmental change, including both natural and human-induced environmental aspects, is driving trait-based, functional, and phylogenetic diversity in global freshwater ecosystems. However, it seems that it is more difficult to find clear relationships between the biodiversity measures and the environment when strong natural gradients are involved in a study. We found that biodiversity indices often had multiple relationships with the environment, especially in cases when both natural and anthropogenic characteristics were investigated in the same study or only natural environmental change was under examination. For example, functional dispersion and functional evenness of fish assemblages were driven by multiple environmental factors related to

both natural and anthropogenic gradients in Australian river basins (Sternberg et al. 2014). Similarly, two measures of taxonomic distinctness of diatoms, macrophytes, and macroinvertebrates showed opposite responses to total phosphorus and nitrogen gradients in a large boreal lake (Vilmi et al. 2017). Previous exercises regarding taxonomic distinctness have evidenced this situation for different freshwater organism groups in various regions. For example, Bhat and Magurran (2006) first reported that the indices of phylogenetic relatedness may be masked by influences of habitat variability on fish species compositions in India. Subsequently, other studies have found that natural environmental characteristics may overshadow the influences of anthropogenic pressures on taxonomic distinctness (Heino et al. 2007; Alahuhta et al. 2017a). In addition, the performance and ability to detect human-induced stress of taxonomic distinctness may depend on the phylogenetic structure of surveyed taxa within a study region, as well as their evolutionary and ecological history (Abellan et al. 2006). These findings are important because taxonomic distinctness measures should be independent of natural environmental gradients and sampling effort (Clarke and Warwick 2001). Our systematic review emphasises that biodiversity measures should be interpreted with caution in the situations where the purpose is to quantify natural environmental changes (separately or together with anthropogenic perturbations) in freshwater ecosystems.

Although the natural environmental characteristics create complexity to the freshwater ecosystems and challenge ecologists in how to portray ecosystem functioning, we also found promising examples of studies where diversity measures responded to anthropogenic disturbance in a predicted way (i.e., negatively; Arthaud et al. 2012; Liu et al. 2013; Matsuzaki et al. 2016). The relationship between biodiversity and ecosystem functioning is assumed to be linearly positive, but global change effects may disturb this relationship (Woodward et al. 2010; Cadotte et al. 2011). In the examples we found, a single human-induced stressor was correlated with biodiversity, producing a decreasing trend. For instance, increased water level led to decline in functional diversity of macrophytes in a subtropical reservoir compared with that of adjacent wetlands (Liu et al. 2013), whereas urbanization reduced functional diversity of aquatic insects in Neotropical streams (Gimenez and Higuera 2017). In the other study, introduction of non-native fish species decreased functional diversity of native fish assemblages over time (Matsuzaki et al. 2016). However, multiple global change effects can act simultaneously in influencing ecosystem functioning, such as in the case of climate warming and eutrophication in freshwaters. The joint effects of different global change factors are likely to strongly decrease overall species richness and trait diversity by filtering out species not only located in different parts of the functional space but also acting additively, or even acting in synergy, leading to rapid extinctions when the effects of the stressors overlap in functional space (Mouillot et al. 2012). For example, Olden et al. (2006) found that native fish communities experienced two shared pressures mediated by functional traits; species were filtered out because of vulnerable traits associated with environmental changes or competition with exotic species sharing similar traits. This further complicates our attempts to investigate how global change affects biodiversity and, subsequently, ecosystem functioning.

### Research gaps and future study directions

We have demonstrated a link between trait-based, functional, and phylogenetic diversity and environmental change in freshwater ecosystems through the conceptual model and the systematic review. The latter also offered us details on the current research status and knowledge gaps. Next, we presented gaps in the knowledge of the relationship between freshwater biodiversity and environmental change, and we suggested where the future research

**Table 1.** Summary of the known research gaps and suggestions for possible future research directions based on our systematic review on trait-based, functional, and phylogenetic biodiversity of freshwater organism groups.

Research gap	Suggestion for future study direction
Low number of community-based studies	More studies on the trait-based, functional, and phylogenetic biodiversity as related to environmental change are required.
Species dispersal	Alternative methods (e.g., dispersal proxies such as different distance metrics) to account for dispersal in multi-species communities are needed.
Biotic interactions	Biotic interaction measures (e.g., Joint Species Distribution Models) should be included in future studies.
Lack of phylogenetic information	True phylogenies of freshwater organisms are desperately required and (or) development of additional phylogeny proxies are needed.
Conservatism of species traits	Conservatism of species traits needs to be evaluated for different organism groups before phylogeny can be used as a proxy for functional diversity.
Lack of information on species functional traits	More research focus should be devoted to functional species traits and how they are actually related to freshwater ecosystem functioning.
Understudied organism groups	More investigations especially on the biodiversity of macrophytes, diatoms, other algae, and bacteria are needed.
Understudied global change stressors	Studies are required on the effects of climate change and non-native species on different freshwater organism groups.
Geographical bias in research	Additional studies from Africa, Southern Asia, and Russia are needed.
How restoration affects trait-based, functional, and phylogenetic diversity	Review whether restoration affects the relationships between trait-based, functional, or phylogenetic diversity and environmental change.

efforts should focus. The research gaps are related to a low number of biodiversity studies, species dispersal, lack of information on true phylogenies, niche conservatism of species traits, lack of data on species functional traits, understudied organism groups and global change stressors, geographical biases in research, and lack of summarized information how restoration affects the relationships between trait-based, functional, and phylogenetic diversity and environmental change (Table 1).

We surprisingly found only 100 papers out of 1475 (7%) matching our selection criteria. The majority of the papers in the initial selection phase concerned studies with space-for-time substitutions, testing of ecological theories only, without any specific stressors, with purely predictive purposes, with single species only, and without original peer-reviewed contribution (i.e., review and conference abstract). Fortunately, there has been a clear increase in the absolute number of published papers during the past couple of years (Fig. 6), suggesting that community-based studies on the relationship between biodiversity and environmental change are building up. This is an encouraging trend because the species traits of a biological community rather than that of, for example, a single species influence the ecosystem functioning (Flynn et al. 2011; Mouillot et al. 2012).

One of the hot subjects in freshwater ecology is how dispersal may affect local communities (Heino et al. 2015). The importance of dispersal is highlighted in the differently connected freshwater systems, including organisms with different dispersal abilities. Dispersal interacts with environmental change so that anthropogenic disturbance affects poorly dispersing organisms more severely than species with efficient dispersal traits, because poorly dispersing organisms cannot track variation in environmental changes as rapidly as strong dispersers. In addition, organisms in isolated freshwater systems (e.g., springs, ponds, and lakes) are likely to be more strongly impacted by the joint effects of limited dispersal and anthropogenic disturbance than those in more continuous ecosystems (e.g., streams and rivers) (Soininen 2014), but more research is needed to assess this idea further. Our systematic review revealed that dispersal was rarely included, if at all, in the study of the biodiversity measures considered. For example, in the partitioning of functional beta diversity, dispersal limitation was the principal force structuring tropical fish assemblages due to low functional turnover (Cilleros et al. 2016). Although passively moving organisms with small propagules (e.g., macrophytes, diatoms, bacteria) could be expected to be less dispersal limited than

actively dispersing large species (e.g., macroinvertebrates and fish), the increasing amount of evidence suggests a low level of congruence among the findings of freshwater studies. However, conflicting results suggest (De Bie et al. 2012; Soininen 2014) that freshwater organisms' dispersal depends on biological group, region, and spatial scale under study, as well as their combinations; thus, different ways to determine dispersal for these case-specific situations are required (Heino et al. 2017).

Biotic interactions among species in a community can also strongly affect diversity measures. Only one study accounted for biotic interactions in freshwaters though they were not important predictors of functional diversity of stream fish in a semiarid region of Brazil (Rodrigues-Filho et al. 2017). Recently emerged statistical tools of Joint Species Distribution Modelling (JSDM) may offer valuable assistance in including species interactions to the models (e.g., Pollock et al. 2014). At the moment, different JSDM methods are emerging, with the basic difference whether direction of interaction is available or not. Inclusion of biotic interactions to the diversity models may also partly overcome low explained variations often found for freshwater communities.

In addition to the dispersal and biotic interaction proxies, comprehensive and true phylogenies rarely exist for most freshwater organism groups. The only biological group for which comprehensive evolutionary history has often been revealed through DNA analysis is bacteria (Barberan and Casamayor 2014). As demonstrated in our review, the majority of freshwater studies on phylogenetic diversity has been based on proxies for true phylogeny, such as taxonomic distinctness (Clarke and Warwick 2001). However, these phylogeny proxies have not managed to quantify the relationship between phylogenetic diversity and environmental change very well. Thus, we advise researchers to determine the true phylogeny of freshwater assemblages, if possible, or develop alternative proxies for phylogenetic diversity. These possible proxies should be able to function properly in complex situations of natural and anthropogenic environmental effects on phylogenetic diversity so that different effects can be distinguished.

Phylogeny can be used as a proxy for functional diversity if the species traits considered are phylogenetically conserved (Flynn et al. 2011). We found that the influence of niche conservatism on the species traits was explicitly considered in two selected papers out of 27 studying phylogenetic diversity. Carvajal-Castro and Vargas-Salinas (2016) assessed whether male body size and call frequency of Neotropical anuran assemblages were conserved and



found a strong phylogenetic signal. In another work, trait conservatism was evidenced only at short phylogenetic distances for stream fungi (Mykrä et al. 2016). In the very few published papers of niche conservatism for the freshwater realm beyond our review, a significant phylogenetic signal was discovered for many of the ecological optima of 217 diatom species (Keck et al. 2016) and for thermal tolerances and acclimation capacity of 82 fish species (Comte and Olden 2017). However, the strength of the signal has varied or even lacked among the studied species and species traits (Litsios et al. 2012; Keck et al. 2016). Moreover, local niches did not suggest niche conservatism for lake macrophytes in relation to their geographical distributions, whereas climate niches did (Alahuhta et al. 2017b). These findings indicate that niche conservatism in the freshwater realm should be more closely examined for species traits before we can reliably use phylogeny as a proxy for trait-based or functional diversity for freshwater organism groups.

Although other diversity measures (i.e., trait-based and functional diversity) were under intensive research, the species traits used are not necessarily related to ecosystem functioning. Schmera et al. (2017) reviewed functional diversity measures of macroinvertebrates and found that none of the published papers actually quantified any ecosystem functioning. Instead, the reviewed publications were focussed purely on perspectives of biodiversity that may affect ecosystem functions in general (Schmera et al. 2017). Similar to this study, ecosystem functioning was investigated only in a relatively few papers in our systematic review. For instance, the relationship between phylogeny of methanogen bacteria and eutrophication were studied in the Florida Everglades (Castro et al. 2004). In a second work on bacteria, ecologists investigated if an increase in water temperature would influence heterotrophic metabolic activities of biofilms grown under light or dark conditions (Romani et al. 2014). In a third example, linking primary producers to consumers, functional composition of plant communities had a central role in structuring Collembola assemblages along a flood gradient (Abgrall et al. 2017). Lack of species traits related to pure ecosystem functions may also be related to a rather slow emergence of species trait databases including information on freshwater assemblages especially for less-studied organism groups (see also Fig. 6). This general finding on the small number of papers studying actual ecosystem functions emphasises that more efforts should be devoted to the validation and development of freshwater species traits and investigations of true ecosystem functions. In addition, state-of-the-art modelling tools (e.g., gap filling of species trait database, Schrodte et al. 2015) may offer help in building more comprehensive species trait databases for freshwater assemblages, especially when studying broadscale patterns.

Moreover, there is currently a consensus on which measures should be determined when ecosystem functioning effects are assessed using functional diversity measures. Functional richness, evenness, and divergence have been identified as complementary indices to account for different aspects of functional diversity affecting ecosystem functioning (Villegger et al. 2008; Mouchet et al. 2010). Our systematic review revealed that these three functional diversity approaches have been the main foci of freshwater ecologists only in the past couple of years. Although the use of several biodiversity indices inevitably leads to increasing “multiple response effects”, we urge scientists for the sake of comparability among different studies to continue to use at least these three elements of functional diversity in the future studies on freshwater ecosystems.

Macroinvertebrates and fish were the biological groups investigated in most freshwater diversity studies, covering 65% of all the selected studies. For the other biological groups, including macrophytes, diatoms, and bacteria, there were much fewer investigations. More research is needed on these understudied biological assemblages to gain more profound understanding on the relationship between biodiversity and environmental change.

To our surprise, climate change and non-native species were clearly less widely investigated than other global change stressors. This is rather alarming considering that climate change likely severely affects freshwater biodiversity and ecosystem functioning (Heino et al. 2009; Moss et al. 2011; Jourdan et al. 2018). Moreover, the majority of climate change studies focussed on individuals or species populations, instead of entire communities and whole ecosystems (Woodward et al. 2010).

We also found a geographical bias in the published literature, as Europe, North America, South America, and China were the dominant study regions. Because the evidence seems to suggest that the correlations between freshwater diversity and environmental change are dependent on a study region and the background characteristics of those regions, more research is required from poorly studied regions such as Africa, Southern Asia, and Russia. However, we acknowledge that freshwater diversity in relation to the environmental change has been investigated especially in Russia, but results from these studies have not reached English-language dominated contemporary scientific literature.

Our review focussed on the relationships between trait-based, functional, or phylogenetic diversity and environmental change in freshwater ecosystems. Another important aspect would be to investigate how restoration affects these relationships. Environmental change can be seen as a cause of deterioration, whereas restoration is a desirable means, with which global change impacts on trait-based, functional, and phylogenetic biodiversity are repaired close to an original or a desirable state. This topic is beyond our present review, but we urge other scientists to summarize how restoration affects ecosystem functioning measured using these diversity indices as proxies (see e.g., Collier 2017).

Finally, trait-based, functional, and phylogenetic diversity measures not only provide basic scientific knowledge on how environmental change affects freshwater biodiversity and ecosystem functioning, but also act as early warning signals of the intensifying global change effects in the vulnerable freshwater ecosystems. This is because they can possibly a priori be used to detect disturbance impacts before species loss and extinctions actually take place (Mouillot et al. 2012). In addition, freshwaters as vulnerable sentinel systems can provide early warnings of wider-scale environmental change across different ecosystems (Woodward et al. 2010). Lastly, the biodiversity measures we considered can help us to detect (i) which ecosystem functions should be monitored in freshwater bioassessment, (ii) whether the restoration of freshwater systems has actually revived valuable ecosystem functions, and (iii) whether protected areas are conserving different facets of biodiversity and ecosystem functioning in addition to taxonomic diversity (e.g., Saito et al. 2015). We hope that our current review will stimulate more research on the less well-known facets and topics of biodiversity in highly vulnerable freshwater ecosystems.

#### Conflict of interest statement

The authors have no conflict of interest to report.

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