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

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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 multidimensional 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.

Keywords: Community ecology, Diversity index, Functional diversity, Global change, Lakes, Phylogenetic diversity, Rivers, Species traits, Streams

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. 2011). 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 1) are hosting relatively larger proportion of biodiversity compared to terrestrial systems and 2) 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 (Soininen 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.

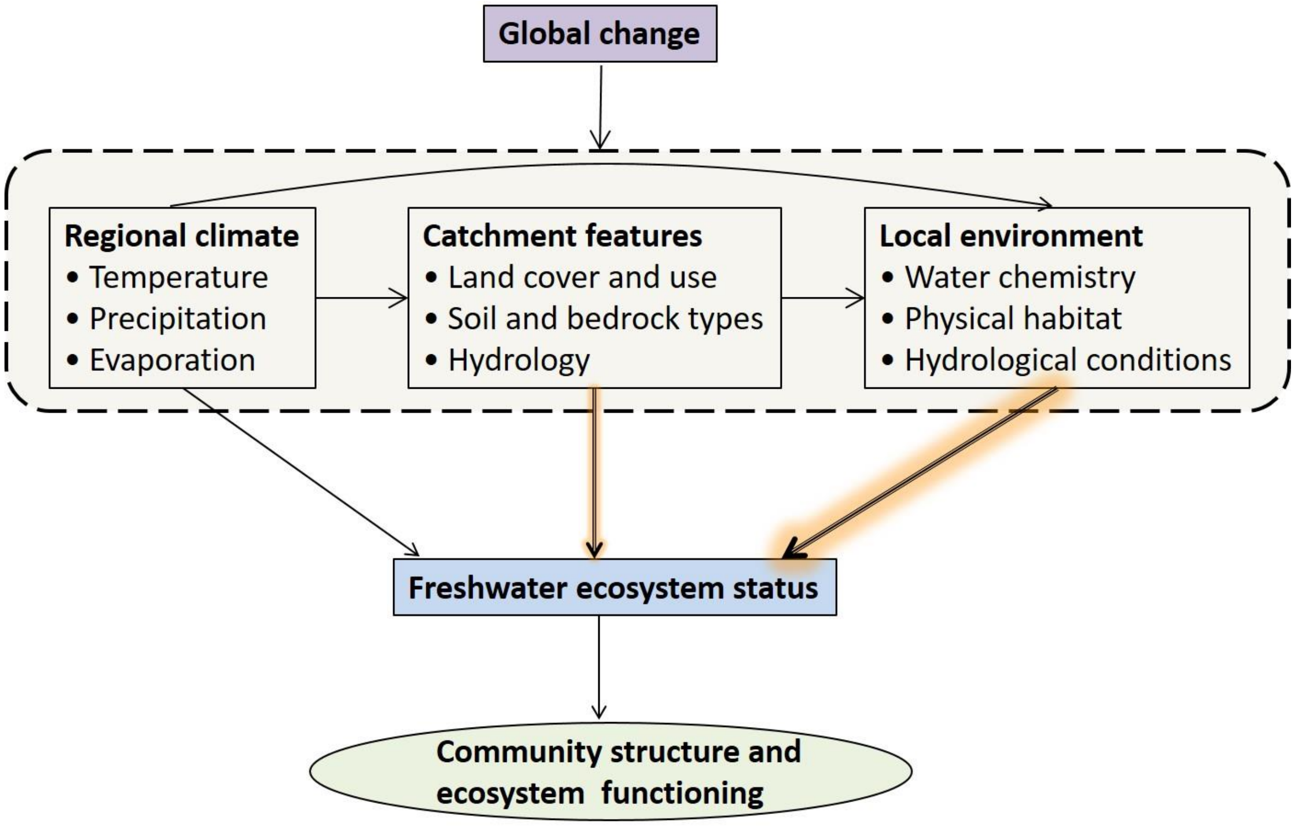

Fig. 1. Conceptual illustration of the relationships between environmental change and freshwater community structure and ecosystem functioning. Freshwater (abiotic) ecosystem status is influenced by different environmental variables, ranging in an increasing order of importance from regional climate 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.

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 considered are phylogenetically conserved (Winter et al. 2012). 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 a) developed a conceptual model of the possible relationships between environmental change and these three diversity facets in freshwaters, and b) 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, a functional or a 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 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, disassociating 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 in order 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 2016), 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 non-significant relationship. This kind of pattern has especially been found for taxonomic distinctness (e.g., Heino et al. 2007; Vilmi et al. 2016), 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 Maguirran 2006; Espanol et al. 2015).

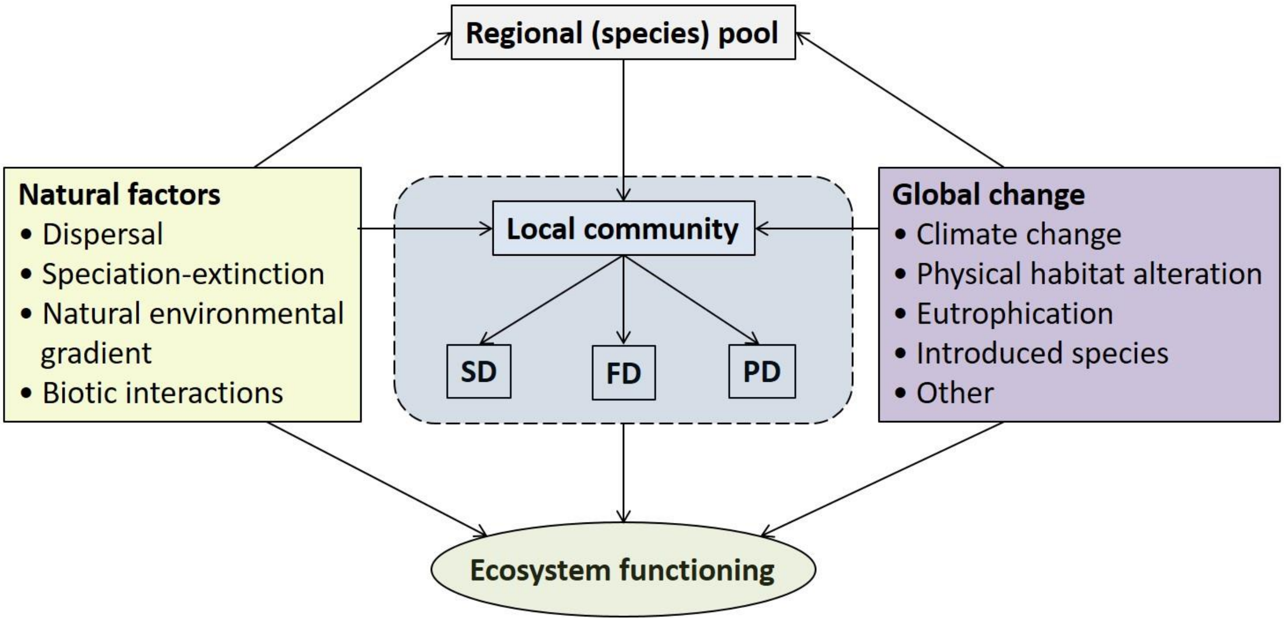

Fig. 2. The relationships between a local community and its environment in relation to ecosystem functioning. Local communities consist of a subset of species with suitable traits from the regional (species) pool that have passed through environmental filters (i.e., natural factors and global changes).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

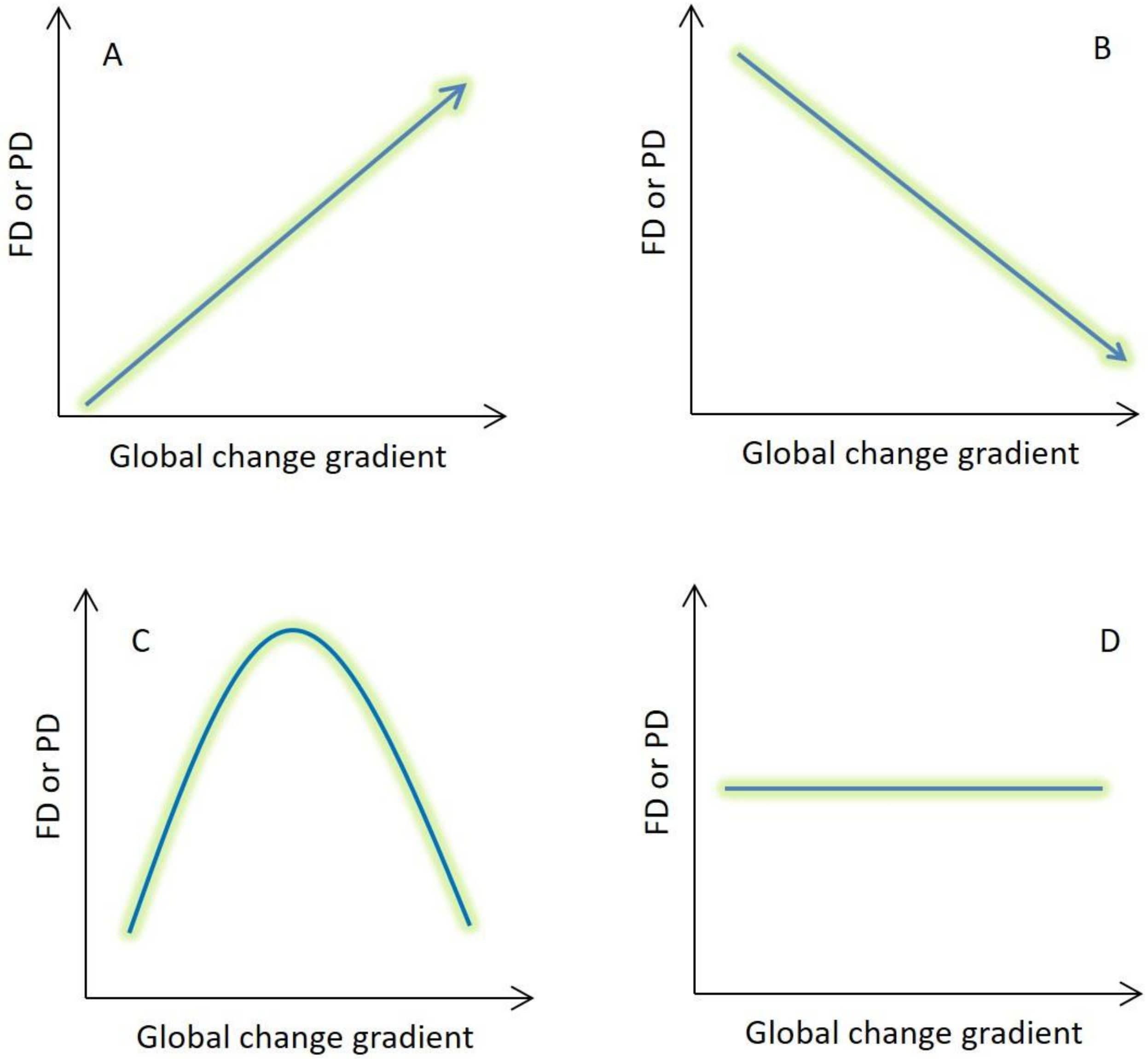

Fig. 3. Hypothesised relationships between functional diversity (FD) or phylogenetic diversity (PD) and an environmental change gradient. Depending on the length of the gradient and geographical location of study region, these relationships could be different. Environmental change may enhance diversity 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 chance 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 non-significant relationship (D).

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: 1) words that describe the trait-based, functional and phylogenetic diversity (funct* OR trait* OR phylogen* OR “taxonomic distinctness”), 2) words related to freshwater habitats (freshwater* OR lentic* OR lotic* OR lake* OR pond* OR stream* OR river* OR wetland* OR spring*), 3) words that are related to diversity (divers* OR biodiv*), and 4) words that indicate environmental change (environment* OR "climate change" OR eutrophication OR acidification OR "habitat loss" OR "nutrient enrichment" OR "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 in 13 February 2018 and 21 September 2018 to account for all published articles in year 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 year 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 neither included in the final set of articles. All authors collected information from articles that were likely suitable for comparative purposes (Table S1). The first author re-checked 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. 5), four main stressors (i.e., eutrophication, physical habitat alteration, non-native species and climate change, and their joint effects; see Fig. 6), and direction of stressor effect (i.e., no effect, increasing, decreasing and multiple responses). Finally, the first author compiled a consistent dataset including main information and variables from the final set of 100 selected articles matching our strict inclusion criteria (Table S2).

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. 4). 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 mid-2000s (e.g., McGill, Enquist, Weiher, & Westoby, 2006; Petchey, & Gaston, 2006; Villeger, Mason, & Mouillot, 2008), and freshwater ecologists have found these measures relatively well.

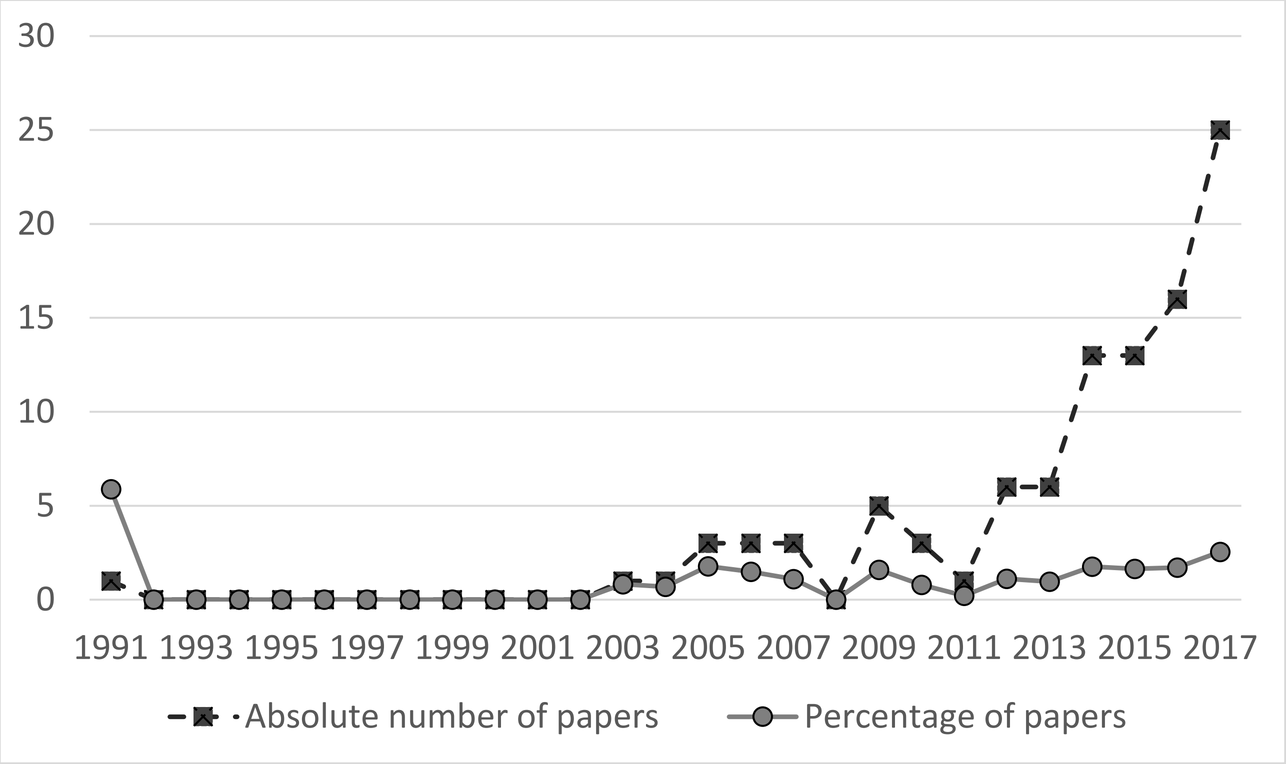

Fig. 4. Absolute and percentage (absolute number of selected papers in relation to all papers dealing with environmental change and functional, trait-based and phylogenetic diversity in terrestrial and marine systems) changes in the number of articles published that focus on the relationship between 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 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. 5; Fig. S1). 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). 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 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. Compared to 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 (six out of nine, 11 out of 13 and eight out of ten, respectively), but also some river and stream studies have appeared. All of the three organism groups have been under research mostly in North America, South America, Europe and China during the 2010s. Temporal aspects were considered in ca. 30% of all selected papers, 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). For macroinvertebrates (20 out of 47 studies), fish (11 out of 20), diatoms (nine out of 13) and macrophytes (five 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. 6). 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 six percentage of the papers each. 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 (two out of three), 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 (four out of seven). 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 that is why the responses of biodiversity measures to these two environmental changes were negative more often compared to 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 multidimensional, 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. 2016). 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).

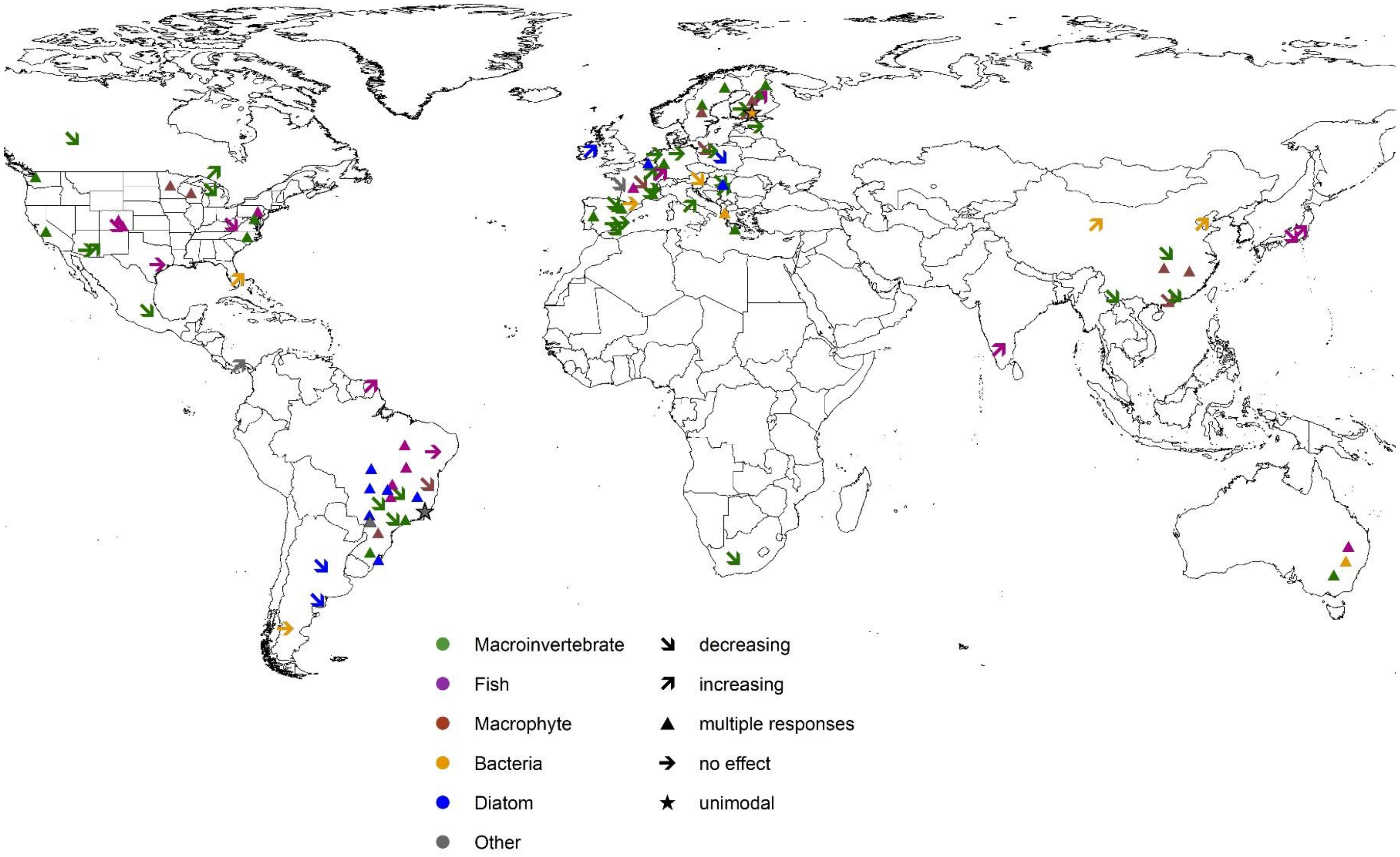

Fig. 5. A map illustrating the biological groups used to study the relationship between trait-based, functional and phylogenetic diversity and the direction of effect caused by environmental change effects based on our systematic review in the freshwater realm (n=100).

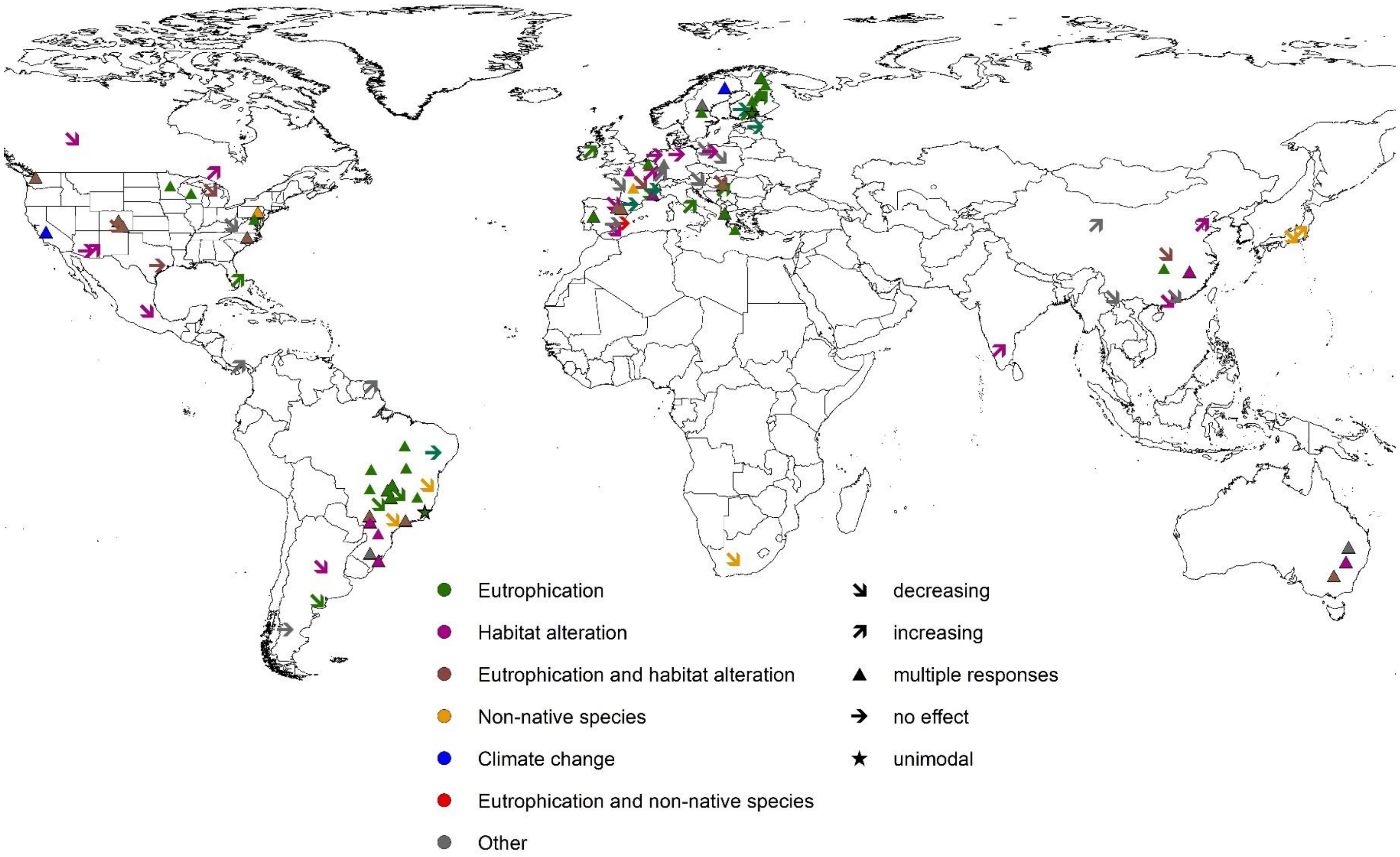

Fig. 6. A map illustrating the relationship between specific environmental change stressor and the direction of effect found in the different articles (n=100) selected in the systematic review.

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 (Stenberg 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. 2016). 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 to that of adjacent wetlands (Liu et al. 2013), whereas urbanization reduced functional diversity of aquatic insects in Neotropical streams (Gimenez and Higute 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 decrease strongly 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 due to either 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 suggested where the future research 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).

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 is 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

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. 4), 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 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 organism 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), increasing amount of evidence suggest 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, and 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. We found that only in one study biotic interactions were accounted for 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 exists for most of 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 PD 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 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 thermal tolerances and acclimation capacity of 82 fish species (Comte and Olden 2016). 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, climate niches did but local niches did not suggest niche conservatism for lake macrophytes in relation to their geographical distributions (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 their 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. 4). 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-art modelling tools (e.g., gap filling of species trait database, Schrodt et al. 2015) may offer help in building more comprehensive species trait databases for freshwater assemblages, especially when studying broad-scale 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 (Villeger 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 have 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 1) to detect which ecosystem functions should be monitored in freshwater bioassessment, 2) whether the restoration of freshwater systems has actually revived valuable ecosystem functions, and 3) 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.

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Supporting Information

Fig. S1.

Fig. S2.

Table S1.

Table S2.

Fig. S1. Tree diagrams showing (a) whether environmental change has had an increasing (in), decreasing (de), multiple (mu) or no (no) effect on different freshwater organism groups, and (b) whether different environmental change effects had increased, decreased, multiple or no effect on freshwater trait-based, functional and phylogenetic diversity. The size of a rectangle is proportional to the number of studies considered in the systematic review. Organism groups in the “Other” comprise of birds, frogs and anuran assemblages.

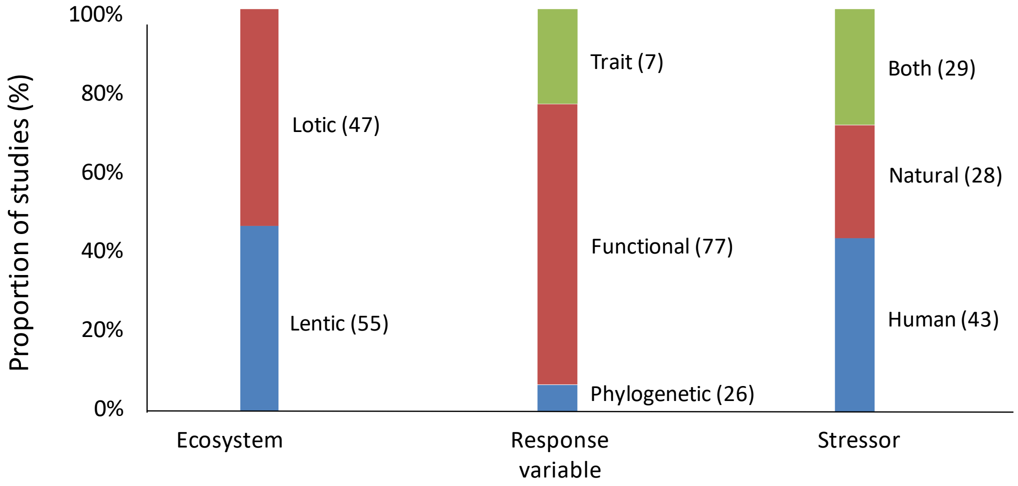

Fig. S2. Proportion of studies in different ecosystems (a), based on different response variables (b), and focusing on different stressors (c). The numbers within the bars refer to the number of studies.

Table S1. Information gathered from the selected articles.

- authors
- title
- journal
- publ. year
- country/place
- latitude
- longitude
- spatial scale
- temporal focus (contemporary/historical/paleo)
- observational/experimental
- data collected (year(s))
- ecosystem (lotic vs. lentic)
- pristine (yes/no)
- number of sites
- taxonomic group(s)
- tax group
- response variable(s)
- stressor (natural/human)
- specific stressor
- statistical methods
- number of species/taxa/OTUs
- effect (increasing/decreasing/U-shaped/hump-shaped/no effect/not applicable/multiple responses)
- main findings

- temporal variation (yes/no)
- spatial variation (yes/no)
- descriptive/predictive/both
- extra information

915 Table S2. List of included final articles based on our selection criteria with each article's author(s), title, journal and publication year given.

Authors	Title	Journal	Publication year
Azzanti, M	Sandy bottom macroinvertebrates in two moderately polluted stations of the River Treia (Central Italy): structural and functional organization	ANNALES DE LIMNOLOGIE-INTERNATIONAL JOURNAL OF LIMNOLOGY	1991
Ross, RM; Bennett, RM; Snyder, CD; Young, JA; Smith, DR; Lemarie, DP	Influence of eastern hemlock (Tsuga canadensis L.) on fish community structure and function in headwater streams of the Delaware River basin	ECOLOGY OF FRESHWATER FISH	2003
Castro, H; Ogram, A; Reddy, KR	Phylogenetic characterization of methanogenic assemblages in eutrophic and oligotrophic areas of the Florida Everglades	APPLIED AND ENVIRONMENTAL MICROBIOLOGY	2004
Devin, S; Beisel, JN; Usseglio-Polatera, P; Moreteau, JC	Changes in functional biodiversity in an invaded freshwater ecosystem: the Moselle River	HYDROBIOLOGIA	2005
Heino, J	Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams	FRESHWATER BIOLOGY	2005
Heino, J; Soininen, J; Lappalainen, J; Virtanen, R	The relationship between species richness and taxonomic distinctness in freshwater organisms	LIMNOLOGY AND OCEANOGRAPHY	2005
Abellan, P.; Bilton, D. T.; Millan, A.; Sanchez-Fernandez, D.; Ramsay, P. M.	Can taxonomic distinctness assess anthropogenic impacts in inland waters? A case study from a Mediterranean river basin	FRESHWATER BIOLOGY	2006
Bhat, A; Magurran, AE	Taxonomic distinctness in a linear system: a test using a tropical freshwater fish assemblage	ECOGRAPHY	2006
Salas, F; Patricio, J; Marcos, C; Pardal, MA; Perez-Ruzafa, A; Marques, JC	Are taxonomic distinctness measures compliant to other ecological indicators in assessing ecological status?	MARINE POLLUTION BULLETIN	2006
Campbell, WB; Novelo-Gutierrez, R	Reduction in odonate phylogenetic diversity associated with dam impoundment is revealed using taxonomic distinctness	FUNDAMENTAL AND APPLIED LIMNOLOGY	2007
Heino, Jani; Mykra, Heikki; Hamalainen, Heikki; Aroviita, Jukka; Muotka, Timo	Responses of taxonomic distinctness and species diversity indices to anthropogenic impacts and natural environmental gradients in stream macroinvertebrates	FRESHWATER BIOLOGY	2007
Marchant, Richard	The use of taxonomic distinctness to assess environmental disturbance of insect communities from running water	FRESHWATER BIOLOGY	2007

Eros, T; Heino, J; Schmera, D; Rask, M	Characterising functional trait diversity and trait-environment relationships in fish assemblages of boreal lakes	FRESHWATER BIOLOGY	2009
Gallardo, B; Gascon, S; Cabezas, A; Gonzalez, M; Garcia, M; Comin, FA	Relationship between invertebrate traits and lateral environmental gradients in a Mediterranean river-floodplain	FUNDAMENTAL AND APPLIED LIMNOLOGY	2009
Gallardo, B; Gascon, S; Garcia, M; Comin, FA	Testing the response of macroinvertebrate functional structure and biodiversity to flooding and confinement	JOURNAL OF LIMNOLOGY	2009
Leira, M.; Chen, G.; Dalton, C.; Irvine, K.; Taylor, D.	Patterns in freshwater diatom taxonomic distinctness along an eutrophication gradient	FRESHWATER BIOLOGY	2009
Tullos, DD; Penrose, DL; Jennings, GD; Cope, WG	Analysis of functional traits in reconfigured channels: implications for the bioassessment and disturbance of river restoration	JOURNAL OF THE NORTH AMERICAN BENTHOLOGICAL SOCIETY	2009
Michelan, TS; Thomaz, SM; Mormul, RP; Carvalho, P	Effects of an exotic invasive macrophyte (tropical signalgrass) on native plant community composition, species richness and functional diversity	FRESHWATER BIOLOGY	2010
Peru, N; Doledec, S	From compositional to functional biodiversity metrics in bioassessment: A case study using stream macroinvertebrate communities	ECOLOGICAL INDICATORS	2010
Pool, TK; Olden, JD; Whittier, JB; Paukert, CP	Environmental drivers of fish functional diversity and composition in the Lower Colorado River Basin	CANADIAN JOURNAL OF FISHERIES AND AQUATIC SCIENCES	2010
Strecker, AL; Olden, JD; Whittier, JB; Paukert, CP	Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity	ECOLOGICAL APPLICATIONS	2011
Arthaud, F; Vallod, D; Robin, J; Bornette, G	Eutrophication and drought disturbance shape functional diversity and life-history traits of aquatic plants in shallow lakes	AQUATIC SCIENCES	2012
Milosevic, Djuradj; Simic, Vladica; Stojkovic, Milica; Zivic, Ivana	Chironomid faunal composition represented by taxonomic distinctness index reveals environmental change in a lotic system over three decades	HYDROBIOLOGIA	2012
Pool, TK; Olden, JD	Taxonomic and functional homogenization of an endemic desert fish fauna	DIVERSITY AND DISTRIBUTIONS	2012
Schmera, D; Baur, B; Eros, T	Does functional redundancy of communities provide insurance against human disturbances? An analysis using regional-scale stream invertebrate data	HYDROBIOLOGIA	2012

Silver, CA; Vamosi, SM; Bayley, SE	Temporary and permanent wetland macroinvertebrate communities: Phylogenetic structure through time	ACTA OECOLOGIA	2012
Teresa, FB; Casatti, L	Influence of forest cover and mesohabitat types on functional and taxonomic diversity of fish communities in Neotropical lowland streams	ECOLOGY OF FRESHWATER FISH	2012
Angeler, DG; Allen, CR; Johnson, RK	Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales	JOURNAL OF APPLIED ECOLOGY	2013
Colzani, E; Siqueira, T; Suriano, MT; Roque, FO	Responses of Aquatic Insect Functional Diversity to Landscape Changes in Atlantic Forest	BIOTROPICA	2013
Liu, WZ; Liu, GH; Liu, H; Song, Y; Zhang, QF	Subtropical reservoir shorelines have reduced plant species and functional richness compared with adjacent riparian wetlands	ENVIRONMENTAL RESEARCH LETTERS	2013
Martinez, A; Larranaga, A; Basaguren, A; Perez, J; Mendoza-Lera, C; Pozo, J	Stream regulation by small dams affects benthic macroinvertebrate communities: from structural changes to functional implications	HYDROBIOLOGIA	2013
Matsuzaki, SS; Sasaki, T; Akasaka, M	Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages	GLOBAL ECOLOGY AND BIOGEOGRAPHY	2013
Paillex, A; Doledec, S; Castella, E; Merigoux, S; Aldridge, DC	Functional diversity in a large river floodplain: anticipating the response of native and alien macroinvertebrates to the restoration of hydrological connectivity	JOURNAL OF APPLIED ECOLOGY	2013
Arce, E; Archaimbault, V; Mondy, CP; Usseglio-Polatera, P	Recovery dynamics in invertebrate communities following water-quality improvement: taxonomy- vs trait-based assessment	FRESHWATER SCIENCE	2014
Barberan, A; Casamayor, EO	A phylogenetic perspective on species diversity, beta-diversity and biogeography for the microbial world	MOLECULAR ECOLOGY	2014
Boersma, KS; Bogan, MT; Henrichs, BA; Lytle, DA	Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying	FRESHWATER BIOLOGY	2014
Feld, CK; de Bello, F; Doledec, S	Biodiversity of traits and species both show weak responses to hydromorphological alteration in lowland river macroinvertebrates	FRESHWATER BIOLOGY	2014

Fernandez, C; Caceres, EJ; Parodi, ER	Phytoplankton Development in a Highly Eutrophic man-made Lake From the Pampa plain of Argentina-a functional Approach	INTERNATIONAL JOURNAL OF ENVIRONMENTAL RESEARCH	2014
Hitt, NP; Chambers, DB	Temporal changes in taxonomic and functional diversity of fish assemblages downstream from mountaintop mining	FRESHWATER SCIENCE	2014
Huang, QY; Briggs, BR; Dong, HL; Jiang, HC; Wu, G; Edwardson, C; De Vlaminck, I; Quake, S	Taxonomic and Functional Diversity Provides Insight into Microbial Pathways and Stress Responses in the Saline Qinghai Lake, China	PLOS ONE	2014
Jiang, Xiaoming; Song, Zhuoyan; Xiong, Jing; Xie, Zhicai	Can excluding non-insect taxa from stream macroinvertebrate surveys enhance the sensitivity of taxonomic distinctness indices to human disturbance?	ECOLOGICAL INDICATORS	2014
Kovalenko, KE; Brady, VJ; Ciborowski, JJH; Ilyushkin, S; Johnson, LB	Functional Changes in Littoral Macroinvertebrate Communities in Response to Watershed-Level Anthropogenic Stress	PLOS ONE	2014
Navarro, MB; Balseiro, E; Modenutti, B	Bacterial Community Structure in Patagonian Andean Lakes Above and Below Timberline: From Community Composition to Community Function	MICROBIAL ECOLOGY	2014
Romani, AM; Borrego, CM; Diaz-Villanueva, V; Freixa, A; Gich, F; Ylla, I	Shifts in microbial community structure and function in light- and dark-grown biofilms driven by warming	ENVIRONMENTAL MICROBIOLOGY	2014
Sternberg, D; Kennard, MJ; Balcombe, SR	Biogeographic determinants of Australian freshwater fish life-history indices assessed within a spatio-phylogenetic framework	GLOBAL ECOLOGY AND BIOGEOGRAPHY	2014
Timoner, X; Acuna, V; Frampton, L; Pollard, P; Sabater, S; Bunn, SE	Biofilm functional responses to the rehydration of a dry intermittent stream	HYDROBIOLOGIA	2014
Angeler, DG; Allen, CR; Uden, DR; Johnson, RK	Spatial Patterns and Functional Redundancies in a Changing Boreal Lake Landscape	ECOSYSTEMS	2015
Arrieira, RL; Schwind, LTF; Bonecker, CC; Lansac-Toha, FA	Use of functional diversity to assess determinant assembly processes of testate amoebae community	AQUATIC ECOLOGY	2015

Carvalho, RA; Tejerina-Garro, FL	Environmental and spatial processes: what controls the functional structure of fish assemblages in tropical rivers and headwater streams?	ECOLOGY OF FRESHWATER FISH	2015
Casatti, L; Teresa, FB; Zeni, JD; Ribeiro, MD; Brejao, GL; Ceneviva-Bastos, M	More of the Same: High Functional Redundancy in Stream Fish Assemblages from Tropical Agroecosystems	ENVIRONMENTAL MANAGEMENT	2015
Chmara, R; Banas, K; Szmeja, J	Changes in the structural and functional diversity of macrophyte communities along an acidity gradient in softwater lakes	FLORA	2015
Cibils, L; Principe, R; Marquez, J; Gari, N; Albarino, R	Functional diversity of algal communities from headwater grassland streams: How does it change following afforestation?	AQUATIC ECOLOGY	2015
Espanol, C; Gallardo, B; Comin, FA; Pino, MR	Constructed wetlands increase the taxonomic and functional diversity of a degraded floodplain	AQUATIC SCIENCES	2015
Fu, H; Zhong, JY; Yuan, GX; Guo, CJ; Ding, HJ; Feng, Q; Fu, Q	A functional-trait approach reveals community diversity and assembly processes responses to flood disturbance in a subtropical wetland	ECOLOGICAL RESEARCH	2015
He, FZ; Jiang, WX; Tang, T; Cai, QH	Assessing impact of acid mine drainage on benthic macroinvertebrates: can functional diversity metrics be used as indicators?	JOURNAL OF FRESHWATER ECOLOGY	2015
Pease, AA; Taylor, JM; Winemiller, KO; King, RS	Ecoregional, catchment, and reach-scale environmental factors shape functional-trait structure of stream fish assemblages	HYDROBIOLOGIA	2015
Queiroz, CD; da Silva, FR; Rossa-Feres, DD	The relationship between pond habitat depth and functional tadpole diversity in an agricultural landscape	ROYAL SOCIETY OPEN SCIENCE	2015
Saito, VS; Siqueira, T; Fonseca-Gessner, AA	Should phylogenetic and functional diversity metrics compose macroinvertebrate multimetric indices for stream biomonitoring?	HYDROBIOLOGIA	2015
Santos, AMC; Carneiro, FM; Cianciaruso, MV	Predicting productivity in tropical reservoirs: The roles of phytoplankton taxonomic and functional diversity	ECOLOGICAL INDICATORS	2015
Boersma, KS; Nickerson, A; Francis, CD; Siepielski, AM	Climate extremes are associated with invertebrate taxonomic and functional composition in mountain lakes	ECOLOGY AND EVOLUTION	2016
Carvajal-Castro, JD; Vargas-Salinas, F	Stream noise, habitat filtering, and the phenotypic and phylogenetic structure of Neotropical anuran assemblages	EVOLUTIONARY ECOLOGY	2016

Cilleros, K; Allard, L; Grenouillet, G; Brosse, S	Taxonomic and functional diversity patterns reveal different processes shaping European and Amazonian stream fish assemblages	JOURNAL OF BIOGEOGRAPHY	2016
Comte, L; Cucherousset, J; Bouletreau, S; Olden, JD	Resource partitioning and functional diversity of worldwide freshwater fish communities	ECOSPHERE	2016
Dalzochio, MS; Baldin, R; Stenert, C; Maltchik, L	How does the management of rice in natural ponds alter aquatic insect community functional structure?	MARINE AND FRESHWATER RESEARCH	2016
Dunck, B; Algarte, VM; Cianciaruso, MV; Rodrigues, L	Functional diversity and trait-environment relationships of periphytic algae in subtropical floodplain lakes	ECOLOGICAL INDICATORS	2016
Godet, L; Devictor, V; Burel, F; Robin, JG; Menanteau, L; Fournier, J	Extreme landscapes decrease taxonomic and functional bird diversity but promote the presence of rare species	ACTA ORNITHOLOGICA	2016
Lv, XF; Ma, B; Yu, JB; Chang, SX; Xu, JM; Li, YZ; Wang, GM; Han, GX; Bo, G; Chu, XJ	Bacterial community structure and function shift along a successional series of tidal flats in the Yellow River Delta	SCIENTIFIC REPORTS	2016
Matsuzaki, SS; Sasaki, T; Akasaka, M	Invasion of exotic piscivores causes losses of functional diversity and functionally unique species in Japanese lakes	FRESHWATER BIOLOGY	2016
Meziti, A; Tsementzi, D; Kormas, KA; Karayanni, H; Konstantinidis, KT	Anthropogenic effects on bacterial diversity and function along a river-to-estuary gradient in Northwest Greece revealed by metagenomics	ENVIRONMENTAL MICROBIOLOGY	2016
Mykra, H; Tolkkinen, M; Markkola, AM; Pirttila, AM; Muotka, T	Phylogenetic clustering of fungal communities in human-disturbed streams	ECOSPHERE	2016
Peter, H; Sommaruga, R	Shifts in diversity and function of lake bacterial communities upon glacier retreat	ISME JOURNAL	2016
Schriever, TA; Lytle, DA	Convergent diversity and trait composition in temporary streams and ponds	ECOSPHERE	2016
Stenger-Kovacs, C.; Hajnal, E.; Lengyel, E.; Buczko, K.; Padisak, J.	A test of traditional diversity measures and taxonomic distinctness indices on benthic diatoms of soda pans in the Carpathian basin	ECOLOGICAL INDICATORS	2016
Twardochleb, LA; Olden, JD	Human development modifies the functional composition of lake littoral invertebrate communities	HYDROBIOLOGIA	2016

Vilmi, A; Karjalainen, SM; Kuoppala, M; Tolonen, KT; Heino, J	Taxonomic distinctness along nutrient gradients: More diverse, less diverse or not different from random?	ECOLOGICAL INDICATORS	2016
Abgrall, C; Chauvat, M; Langlois, E; Hedde, M; Mouillot, D; Salmon, S; Winck, B; Forey, E	Shifts and linkages of functional diversity between above- and below-ground compartments along a flooding gradient	FUNCTIONAL ECOLOGY	2017
Almeida, BD; Gimenes, MR; dos Anjos, L	Wading bird functional diversity in a floodplain: Influence of habitat type and hydrological cycle	AUSTRAL ECOLOGY	2017
Ding, N; Yang, WF; Zhou, YL; Gonzalez-Bergonzoni, I; Zhang, J; Chen, K; Vidal, N; Jeppesen, E; Liu, ZW; Wang, BX	Different responses of functional traits and diversity of stream macroinvertebrates to environmental and spatial factors in the Xishuangbanna watershed of the upper Mekong River Basin, China	SCIENCE OF THE TOTAL ENVIRONMENT	2017
Nevalainen, L; Luoto, TP	Relationship between cladoceran (Crustacea) functional diversity and lake trophic gradients	FUNCTIONAL ECOLOGY	2017
Saulino, HHL; Trivinho-Strixino, S	The invasive white ginger lily (Hedichium coronarium) simplifies the trait composition of an insect assemblage in the littoral zone of a Savanna reservoir	REVISTA BRASILEIRA DE ENTOMOLOGIA	2017
Suarez, ML; Sanchez-Montoya, MM; Gomez, R; Arce, MI; del Campo, R; Vidal-Abarca, MR	Functional response of aquatic invertebrate communities along two natural stress gradients (water salinity and flow intermittence) in Mediterranean streams	AQUATIC SCIENCES	2017
Gimenez, Barbara C. G.; Higuti, Janet	Land use effects on the functional structure of aquatic insect communities in Neotropical streams	INLAND WATERS	2017
Soledad Morandeira, Natalia; Kandus, Patricia	Do taxonomic, phylogenetic and functional plant alpha- and beta-diversity reflect environmental patterns in the Lower Parana River floodplain?	PLANT ECOLOGY & DIVERSITY	2017
Teresa, Fabricio Barreto; Casatti, Lilian	Trait-based metrics as bioindicators: Responses of stream fish assemblages to a gradient of environmental degradation	ECOLOGICAL INDICATORS	2017
Garcia-Raventos, Aina; Viza, Aida; Tierno de Figueroa, Jose M.; Riera, Joan L.; Murria, Cesc	Seasonality, species richness and poor dispersion mediate intraspecific trait variability in stonefly community responses along an elevational gradient	FRESHWATER BIOLOGY	2017

Weithoff, Guntram; Gaedke, Ursula	Mean functional traits of lake phytoplankton reflect seasonal and inter-annual changes in nutrients, climate and herbivory	JOURNAL OF PLANKTON RESEARCH	2017
Heino, Jani; Tolonen, Kimmo T.	Untangling the assembly of littoral macroinvertebrate communities through measures of functional and phylogenetic alpha diversity	FRESHWATER BIOLOGY	2017
Alahuhta, Janne; Toivanen, Maija; Hjort, Jan; Ecke, Frauke; Johnson, Lucinda B.; Sass, Laura; Heino, Jani	Species richness and taxonomic distinctness of lake macrophytes along environmental gradients in two continents	FRESHWATER BIOLOGY	2017
Fu, Hui; Zhong, Jiayou; Fang, Shaowen; Hu, Jianmin; Guo, Chunjing; Lou, Qian; Yuan, Guixiang; Dai, Taotao; Li, Zhongqiang; Zhang, Meng; Li, Wei; Xu, Jun; Cao, Te	Scale-dependent changes in the functional diversity of macrophytes in subtropical freshwater lakes in south China	SCIENTIFIC REPORTS	2017
Sousa Rodrigues-Filho, Carlos Alberto; Gurgel-LourenOo, Ronaldo Cesar; Queiroz Lima, Sergio Maia; de Oliveira, Edson Fontes; Sanchez-Botero, Jorge Ivan	What governs the functional diversity patterns of fishes in the headwater streams of the humid forest enclaves: environmental conditions, taxonomic diversity or biotic interactions?	ENVIRONMENTAL BIOLOGY OF FISHES	2017
Sagouis, Alban; Jabot, Franck; Argillier, Christine	Taxonomic versus functional diversity metrics: how do fish communities respond to anthropogenic stressors in reservoirs?	ECOLOGY OF FRESHWATER FISH	2017
Machado, Karine Borges; Teresa, Fabricio Barreto; Nabout, Joao Carlos	Assessing the spatial variation of functional diversity estimates based on dendrograms in phytoplankton communities	ACTA BOTANICA BRASILICA	2017
Voss, K.; Schaefer, R. B.	Taxonomic and functional diversity of stream invertebrates along an environmental stress gradient	ECOLOGICAL INDICATORS	2017
Cardoso, Simone J.; Nabout, Joao Carlos; Farjalla, Vinicius F.; Lopes, Paloma M.; Bozelli, Reinaldo L.; Huszar, Vera L. M.; Roland, Fabio	Environmental factors driving phytoplankton taxonomic and functional diversity in Amazonian floodplain lakes	HYDROBIOLOGIA	2017

Santana, Lucineide Maria; Weithoff, Guntram; Ferragut, Carla	Seasonal and spatial functional shifts in phytoplankton communities of five tropical reservoirs	AQUATIC ECOLOGY	2017
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