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REVIEW PAPER

Trait-based ecological classifications for benthic algae: review and perspectives

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Abstract A high number of species often represents a relevant redundancy in terms of ecological adaptation strategies. Collecting species to groups based on their functional adaptations can handle this redundancy and obtain the "real" functional complexity of ecosystems. Functional traits are proxies of adaptation strategies under particular environmental conditions, and a set of functional traits are interpreted as life-strategies. Organisms with life-strategies occupying a similar niche can be collected in ecological groups (functional group/guild). In this study, we review the latest trait-based approaches and existing attempts at functional classifications in phytobenthos studies. Advantages and shortcomings of these classifications are discussed with perspectives of their utility in ecological status assessment.

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Introduction

Since its introduction, the binomial nomenclature of Linnaeus (1758) has remained the basic classification system of species in biology. Thus, species are the basic units of the taxonomical hierarchy and, consequently, of ecological studies. Although the concept of species is well established (De Queiroz, 2007), delimitation criteria and methods remain under continuous development. Especially among simple organisms (e.g., algae), the classical morphology-based identification is under change into a phylogeny-based delimitation stimulated by the rapid development of molecular techniques. At present, their taxonomy is unstable and quickly changing. Estimations on the total number of algal species vary from 30,000 to 1 million species. Mann (1999) mentions several tens of thousand species for diatoms alone. Later this number dropped to around 10,000 species (Mann & Vanormelingen, 2013). This diversity and the wide geographical and environmental distribution make these organisms useful tools for ecological assessment. Quality assessment methods based on benthic algae (with a strong bias towards diatoms) rely on taxonomic units (species or genus).

Autoecological indices [e.g., BDI (Prygiel & Coste, 1998), IPS (Cemagref, 1982), TDI (Kelly & Whitton, 1995), PIT (Schneider & Lindstrøm, 2011), AIP (Schneider & Lindstrøm, 2009)] are the most common method for ecological quality assessment used in the Water Framework Directive (European Commission, 2000). However, these indices carry uncertainties. Those thousands of taxa included in the databases of the indices comprise a number of rare species with hardly definable ecological profiles (Rimet & Bouchez, 2012a). In addition, the different European indices use different ecological profiles for the same species (probably because their profiles were defined from different ecoregions with limited range of environmental variables); this practice reduces the robustness of the estimations, especially for species present with low abundance per site and low frequency of occurrence (Besse-Lototskaya et al., 2011). Since indices are developed specifically for a particular ecoregion, their use in another ecoregion should be carried out with caution. Several "unreliable" species have been identified, i.e., they indicate trophic state changes from oligotrophic to hypertrophic, depending on the index (Besse-Lototskaya et al., 2011). Both taxonomic misidentification and species with different ecological optima can result in false assessments. Additionally, species' response to environmental parameters may depend on geographic or habitat-dependent distributions, resulting in different responses of the same species in different ecoregions. The rationale of such diatom indices have been often questioned (Kelly, 2013). As Kelly (2011) posed the question in a comment paper to Besse-Lototskaya et al. (2011): "Do we need diatom trophic metrics in Europe?". The question rose from the recognition that while the main debate between diatomists is about taxonomic issues, end users of quality evaluation methods do not get clear answers for their emergent environmental problems. His other main point is that often factors other than trophic condition acts as an underlying factor for casual relationship; however, this may correlate with nutrients. At first sight, it does not change the result but can bear problems when one must give advice or solutions to end users (Kelly, 2011).

The theoretical advantage of diversity metrics compared to autoecological indices is that they quantify the impact of pressures; in practice, this consists of mainly nutrient enrichment (e.g., eutrophication, organic pollution) on the structure of the entire community. They were already used successfully to indicate organic pollution (Stevenson & Bahls, 2002) and stream order (Stenger-Kovács et al., 2013b). There are also promising results on new generation diversity metrics that are proved to be sensitive and precise indicators (e.g., trophic level or pH) (Stenger-Kovács et al., 2016). On the other hand, studies on such metrics often contradict theoretical predictions, resulting in weak correlations and unclear patterns (Blanco et al., 2012). It suggests a more complex mechanism than simple correlations of how pressures affect diatom composition: response often evolves non-monotonic stressor gradients (Stevenson, 2014).

The fact that both autoecological and diversity indices are based on taxonomic units (species or genus) involves technical and theoretical issues. Accurate species-level identification is not always insured since it requires high-level experts in diatom identification to follow the continuously changing taxonomy, and it is time consuming (Berthon et al., 2011; Kermarrec et al., 2014). These issues entail the problem of disharmony in identification accuracy: variation in both space (differences between labs) (Kahlert et al., 2009, 2012) and time (Straile et al., 2013). The structuring impact of different ecoregions sets another challenge (Rimet et al., 2007). It is a particularly difficult task for countries with oversea departments under the EU legal system (France, Spain, Portugal) to apply their evaluation system to these regions with highly different geographical location and climate regimes. These regions may have unique algae flora and environmental conditions that require specific and robust assessment metrics. Species-based classification carries further drawbacks. The role of a member in an ecosystem depends on the morphological, physiological properties where it belongs to in order to adapt and compete in a particular habitat. These traits may include phylogenetically close species as well as distant ones. Even different strains or ecotypes of the same species can possess different traits. A well-known example is the toxic and non-toxic strains of cyanobacteria (Neilan et al., 1995). Regarding the selective factors in an environment and the possible adaptive strategies, one can see a high redundancy at the species level (Kelly, 2013). Ecological group cluster species with similar adaptive strategies corresponding to the real compartments of an ecosystem to potentially simplify its complexity (Salmaso et al., 2015). This concept among benthic algae has been promising, and the number of studies in this field in the last decade has increased (Fig. 1).

The aim of this review is to provide an overview of trait-based approaches and the ecological group concept in studies of benthic algae. We show a critical analysis of the status of existing ecological classifications and present their advantages and drawbacks (Table 1), including identification criteria, trait response to environmental factors, and utility. We propose perspectives that could be envisaged to improve trait-based ecological classification and its application in biomonitoring and quality assessment.

Trait-based approaches in light of environmental assessment

Traits are the basic units of developing any kind of ecological classification of organisms. According to Violle et al.'s (2007) definition, traits are "any morphological, physiological or phenological measurable feature at the individual level". This seems to be valid for all organisms regardless of the study objects (e.g., animals, terrestrial plants, phytoplankton, diatoms). In the case of complex and physiognomically diverse organisms such as vascular plants, a large set of easily identifiable traits exists. Now, several extended databases are accessible for terrestrial plants including hundreds of traits measured by standardized methods that allow for comparative studies (Kattge et al., 2011).

Regarding unicellular algae, applying trait-based approaches in the field of their ecological study has been a great challenge for scientists. Their simple structure, microscopic size, and potential observational difficulties hamper the identification of a large set of determinable traits with clearly associated ecological functions. However, trends show that this challenge can be accomplished. Phytoplankton studies already provide the knowledge of several categorized functional traits (e.g., morphological, physiological, behavioral, life-history) (Litchman & Klausmeier, 2008). Linking these traits to their appearance along environmental gradients was the basis of functional classification of phytoplankton (Margalef, 1978; Reynolds et al., 2002). The deficiency compared to plant functional groups is the lack of a global trait

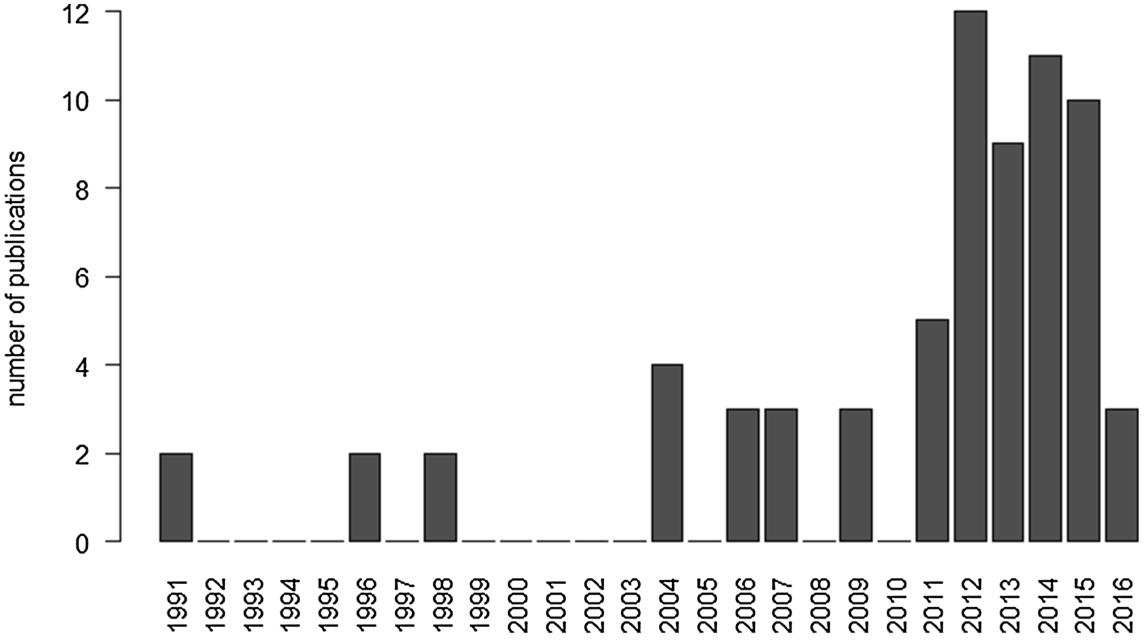


Fig. 1 Number of papers related to the concept of ecological guilds in benthic diatoms. The searched keywords were the following: "diatom(s)" or "phytobenthos" or "benthic alga(e)" in the title and "river(s)" or "stream(s)" in the topic, additionally with one of the following in the topic: "guild(s)", "functional group(s)", "adaptive strategie(s)", "life(-)form(s)", "growth(-)form(s)", "trait(s)", "life-strategie(s)"

database with guidelines and standardized measurements (Litchman & Klausmeier, 2008).

Table 1 Already existing functional classifications for benthic algae discussed in this review

Functional groups	Criteria	Number of groups	Number of traits	Algae groups	Number of taxa	Substrate	Origin of data	Efficiency	Reference
Guilds	Morphological, functional	3	1	Diatoms	104	Natural	Several points in White Creek (USA) and Mesta River (Bulgaria)	All guilds show habitat indication (however later studies shows contradictions)	Passy (2007)
Combined CSR strategy	Morphology	21	3	Diatoms + non-diatoms	78	Artificial	Several points in Wyre and Loud tributaries (UK)	Few new information considering the number of hypothetical groups	Law et al. (2014)
Trait-based conceptual framework	Morphological, physiological, behavioral, life-history based	0	21 in 7 categories	Diatoms + non-diatoms	91	Natural	Several sites in the Manuherikia River catchment area (New Zeland)	Ecologically well-justified traits showing good results, but no ecological groups are defined	Lange et al. (2016)
Eco-morphological functional groups	Morphological, functional	20	2	Diatoms	34	Artificial	Tócó stream (Hungary)	highlights "hidden" correlations within one guild	B-Béres et al. (2016)

A comprehensive database of traits is missing for benthic algae as well, but the terminology is used to refer to both simple measurable features (e.g., biovolume, size classes) and the more complex life-strategies (e.g., life-forms, guilds) (Virtanen et al., 2011; Laine et al., 2014). This trait-based approach is the basis of defining the so-called ecological groups (guilds or functional groups). The concept for phytobenthos has been under progress, and there are already some attempts for a possible complex ecological classification, as summarized in Table 1.

Diatom ecological guilds

The most widely known ecological classification is the ecological guilds of Passy (2007). Practically, the term "guild" is used as the synonym of "functional group" that is historically more preferred in plant biology than the former, which is preferred in animal biology (Blondel, 2003). "Guild" refers to a group of species that exploit resources in a similar way, resulting in stronger competition within the guilds than between them. In contrast, the base of the definition of functional groups is the similarity in the ecosystem functioning rather than in resource sharing. The criteria are more process oriented than structural. Since the way of resource utilizing is more diverse and apparent in animals (i.e., a set of feeding strategies), the term "guild" became more common in animal studies (Blondel, 2003). Since such attempts for classifications in phytobenthos studies import concepts and methods from phytoplankton studies where "functional group" is the accepted definition, we suggest keeping this terminology or the use of the more neutral "ecological groups".

The guild concept of diatoms states that the great diversity of benthic diatom growth forms (i.e., life-forms) shows high redundancy (i.e., niche overlap) along the main structuring environmental pressures: nutrient availability and flow disturbance. Using this redundancy, species were classified into three ecological guilds with distinct features in the changing habitat.

Unlike in the pelagic, in benthic habitats there is a steep vertical gradient of resources, i.e., nutrients and light within the biofilm characterized by canopy. The distance between individuals is spatially much closer than in the rather “dilute” phytoplankton. Passy’s classification can be regarded functional, including the way species attached to the substrate, thus how they cope with disturbance (e.g., flow velocity, grazing) and the way they utilize resources. Low-profile species positioned on the bottom layer of the biofilm attached strongly to the substrate with the whole valve surface, while the big, erected, or colonial high-profile species represent the canopy layer of the biofilm. Passy’s study on the guilds has been cited 101 times (Web of Science, 2016), indicating a strong interest on this topic. However, studies often show different results and interpretations of their findings that can be attributed to some deficiencies of clarity in the original guild classification.

The theoretical background of Passy’s findings about the negative correlation between resources and low-profile dominance is that due to their vertical position, low-profile species are exposed to resource limitation in a thick biofilm. Thick biofilm can develop under high nutrient values, and high-profile species have adaptive advantage to reach light and nutrients in the biofilm. The fact that in that case low-profile species are suppressed should not mean that they have an advantage under low-resource circumstances since their dominance under nutrient-poor conditions can be explained in several ways. First, if there is no difference in nutrient requirement between low- and high-profile guilds, the adaptive strategy of low-profile species against flow velocity can favor their growth even under low flow velocity. Second, low-profile species are frequently small species, and this “linked” trait may mean more effective nutrient uptake due to higher surface ratio or faster growth rate.

Passy is also inconsequent in this question. While she states that a low-profile guild is “likely to be resource-stressed but disturbance-free, i.e. it experiences resource limitations”, in the next statement, she states that this guild has “the ability to withstand resource limitation”. On the other hand, the “disturbance-stressed” high-profile guild is suppressed in high-disturbance habitats.

Several studies tested the response of guilds to environmental parameters, mainly, nutrients and physical forces (i.e., water flow) (Table 2). Rimet et al. (2015) examined the seasonal guild succession in the littoral benthic diatom assemblage in Lake Geneva (France–Switzerland). Their explanation of dominance of low and motile species driven by nutrient availability and grazing pressure supports Passy’s (2007) concept and is consistent with other studies (Berthon et al., 2011). However, the suggested reason of high-profile dominance during the nutrient-limited period by their competitive ability is somewhat in contradiction with Passy. In one of the cases, the same adaptation (i.e., competitive advantage for nutrients in a dense biofilm) results in their dominance in nutrient-rich habitats (Passy, 2007); in other cases, adaptation results in their dominance in nutrient-poor habitats (Rimet et al., 2015). Leira et al. (2015) suggested that high-profile forms may have advantages under low irradiance level caused by sediment resuspension and suppress the a priori shade-tolerant low-profile species. Additionally, they showed that even under low resources and light availability when the development of a three-dimensional biofilm was prevented, high-profile species dominated (Leira et al., 2015). Stenger-Kovács et al. (2013a) found an increasing trend in the abundance of low-profile guilds with the increasing irradiance due to seasonal change coupled with the removal of high-profile guilds due to floods. They argue that prostrate forms due to their vertical location in the biofilm utilize weaker irradiance better than high-profile species. The relative abundance of motile guild, however, correlated negatively with the irradiance. It is clear that a strong improvement is needed in defining how environmental factors affect diatoms in order to sort them into ecological groups. Regarding the resources, at least the separation between nutrients and light is essential. In a thick biofilm, both have gradients towards the same direction, but at larger scales, this is not the case. An interesting observation from Vilar et al. (2015) is that while low-profile species dominated low-nutrient, clear water, they were absent in an enclosure with artificially low turbidity. This is because low-profile species could colonize first in natural habitats after a strong disturbance event due to their resistance to flushing. Their dominance was due to the mass effect from the pre-disturbance period and not to their adaptation to the new environment. The motility of the motile guild enables them to find the best place in the microhabitat to avoid disturbance, i.e., resistance against moderate water discharge (Lengyel et al., 2015b) or reach the best position to acquire nutrients.

Passy’s use of the term disturbance is confusing: it is used to describe both the effect of water velocity and grazing. However, it would be welcome to make a distinction between stress and disturbance when one

Table 2 Traits already used for ecological classification, and factors for which they were tested. Ticks designate already tested relations

Categorized traits	Nutrients	Water flow	Light	Conductivity	Grazing	Organic pollution
Morphology						
Biovolume	✔	✔		✔		✔
Greatest axial length dimension	✔	✔	✔		✔	
Attachment mechanism	✔	✔				
Surface-to-volume ratio	✔	✔	✔			
Life-forms	✔	✔	✔			
Profile guilds	✔	✔	✔		✔	✔
Behavior						
Motility guilds	✔	✔	✔	✔		
Physiology						
Nitrogen fixation	✔					
Life-history						
Main reproductive techniques	✔					
Spore formation	✔	✔				

tries to classify ecological groups based on their adaptive features. The term “disturbance-stressed” that is used in her study is meaningless and is not used elsewhere in the scientific literature. This lack of separation is unfortunate especially because the study addressed to draw an analogy between the guild classification and Grime’s (1974) CSR strategy classification, which clearly defines that stress restricts production via the shortages of resources (nutrients, temperature stress, light limitation, etc.). Disturbance affects organisms through events that cause damage to the vegetation (e.g., grazing, floods, wind). The same factor can act both as stress and as disturbance. As discussed by Borics et al. (2013), it is the temporal frequency that differentiates them. While stress is a continuously acting pressure of the physical environment limiting resource utilization, growth rate, or reproduction of organisms (Grime, 1989), disturbance is considered as an unpredictable, stochastic event that interferes with the community development towards an ecological climax (Reynolds et al., 1993). Continuous nutrient limitation, high-velocity water flow, and grazing pressure all act as stress that enable the development of stress-adaptation strategies, while occasional disturbance events shift the community into an earlier successional phase, promoting recolonization. The remarkable difference in their effect on the community is that while stress decreases diversity, the effect of disturbance events on compositional diversity depends on its frequency and intensity, as formulated in the intermediate disturbance hypothesis (Hardin, 1960; Padisák, 1993; Lengyel et al., 2015a, b). Strongly stressed habitats represent ideal study sites for studying stress tolerance. For example, Central European saline lakes are characterized by high conductivity, high pH, and low light availability due to inorganic turbidity, fluctuating water level, and high daily temperature variation. These extreme conditions showed correlation with the dominance of the motile guild (Stenger-Kovács et al., 2014) that seems to be efficiently adapted to stressed environment, i.e., free-moving, shade-tolerance (Padisák, 2003). The adaptive advantage of low-profile species to high flow velocity circumstances is ecologically well founded. Passy (2007) found the strongest correlation between guilds, and this factor and subsequent studies confirmed it (Mackay et al., 2012; Stenger-Kovács et al., 2013a; Tang et al., 2013). The same morphological trait, i.e., strong attachment, being adnate helps to avoid grazing (Passy, 2007; Gottschalk & Kahlert, 2012) and thus hampers the distinction of these two pressures on the guild composition.

The classical CSR strategy classification combined with life-forms and applied to benthic algae

Another attempt to use the CSR classification (Grime, 1977; Reynolds, 2006) on benthic algae was made by Law et al. (2014). They used simple morphometric features to categorize benthic taxa: the surface area-to-volume ratio and the greatest axial linear dimension (GALD) of the cell. These features can be regarded as the proxy of adaptation to different resource levels; nutrients, light, or against water flow (Table 2). Colonists (C) are favored by higher level of nutrients and light, stress-tolerants (S) can withstand low level of nutrients, and ruderals (R) that can withstand low light level. The study combined these three categories with the life-forms used by Berthon et al. (2011), resulting in 21 variations. The use of life-forms is ecologically well justified since they represent easily measurable morphological traits that are good proxy of adaptive strategies. Similarly to other concepts, this also originates from terrestrial plant studies (von Humboldt, 1806; Raunkiaer, 1934; Gómez-Aparicio, 2009) and phytoplankton (Pianka, 1970; Margalef, 1978; Crossetti & de M. Bicudo, 2008; Dunck et al., 2013). A coherent classification of life-forms exists for diatoms (Round et al., 1990; Rimet & Bouchez, 2012b) that is based on their cellular structure (unicellular or colonial), attachment (e.g., not attached, adnate, attached by mucilage pad), and the type of aggregation (e.g., chain-, ribbon-, arbuscular colonies). This classification uses easily determinable traits (from living sample) with adaptive meanings (flow resistance, nutrient uptake). As an example, tube-forming diatoms appear to be effective indicators of low organic and trophic levels (Berthon et al., 2011). Other studies also confirm that species prone to tube-forming are found mainly in oligotrophic habitats (Rumeau & Coste, 1988; Leira et al., 2009). A similar relationship was shown for stalked diatoms (Berthon et al., 2011) with the interpretation of Pringle (1990) that these species are less adapted to uptake nutrients absorbed on the substratum but well adapted to exploit dissolved nutrients. This hypothesis was confirmed by an experimental study (Rimet et al., 2009). Although this classification involves diatoms only, recognition of simple life-forms would not involve special sample preparation; diatoms and non-diatoms could be classified together, since the interpretation of these traits, in this term, is not taxa specific, as shown by Law et al., (2014) and Lange et al. (2016). However, in the study of Law et al. (2014), life-forms alone did not give interpretable results tested against environmental factors that are, according to the authors, due to the potential of species utilizing more than one life-form. Tests with the CSR classification showed that S-category species with low surface-to-volume ratios and short GALD were associated with eutrophic conditions that are surprisingly the opposite of what is shown for phytoplankton (Reynolds, 1988). Colonists with higher surface area-to-volume ratios with short GALD were found in every treatment and ruderals with long GALD and high surface-to-volume ratios dominated oligotrophic conditions due to their competitive abilities. It is notable that while importing such concepts from phytoplankton studies can be successful, the two communities are quite different; in plankton, the organisms are relatively far from each other and the interaction between them is much less important than in the phytobenthos, where it is more important. Additionally, in the phytobenthos, a steep vertical gradient of the environmental constraints is present. Such differences raise limits in such direct application of the CSR classification. A combination of CSR strategies and life-forms gave better results (Law et al., 2014). Under eutrophic conditions, R-category motile species dominated, while under oligotrophic conditions, the S-category colonial species were abundant. Although this combination of classifications theoretically results in 21 groups, the study showed that most of them can exist only theoretically, and only two groups could indicate environmental gradients.

A conceptual framework on categorized traits

The application of trait categories presented first by Litchman & Klausmeier for phytoplankton (2008) was applied for benthic algae by Lange et al. (2016). The base is a matrix, where several traits grouped in trait categories are paired with their adaptive advantage category (e.g., resource acquisition, resistance to disturbance, predator avoidance). The advantage of this system is that it is applied for all benthic algae, not only diatoms. Cell size is one of the easiest measurable features with several ecological adaptive meanings proven by several former studies (Table 2). Large, erected cells are more sensitive to physical disturbances (e.g., flush, floods). Another example is that higher surface-to-volume ratios related to small size promote efficient nutrient uptake (Reynolds, 2006). Cattaneo (1987) and Morin et al. (2001) showed a significant positive correlation between cell size and nutrient concentration on environmental data, and a similar relation was shown by an experimental study

(Carrick & Lowe, 1989). A major part of the studies, however, focuses on only diatoms; thus, they demonstrate less convincing results. Lavoie et al. (2006, 2010) found no significant relation in the size (e.g., biovolume, surface) distribution along the P gradient; thus, they do not suggest this trait for assessment purposes. However, they refer to former studies on coastal waters (Busse & Snoeijs, 2002, 2003; Snoeijs et al., 2002) where a significant effect of salinity and wave movement on diatom size was shown (Table 2). Berthon et al. (2011) used size classes and showed some effect of trophic level and organic pollution on them but unfortunately without a clear ecological interpretation. Even if nutrients have no clear effect on diatom size, other factors are more relevant. Grazing proved to be a strong selective factor on diatom size (length), and the selected sizes strongly depended on the grazer species (Tall et al., 2006). Another study showed that water color (as a proxy of dissolved organic carbon) explained a major part of the size distribution of diatoms in Canadian rivers (Wunsam et al., 2002). A recent study examined the cell size structure of the two main phytobenthos algal group: desmids and diatoms in peatlands (Neustupa et al., 2013). While the cell size of desmids was strongly affected by the ombro-minerotrophic gradient, pH, and Ca ion concentration, diatom cell size was weakly related to these factors. In contrast, both biovolume and surface area of diatom cells were strongly correlated with conductivity. This example clearly suggests that benthic algae other than diatoms can provide additional information in a perspective of habitat assessment. Lange et al. (2016) tested their defined traits against farming intensity (as a proxy of nutrients) and water abstraction (effect of streamflow). Results on cell size showed dominance of small size cells under low-nutrient level, but increasing of nutrients induced the dominance of large, filamentous forms. An effect of the interaction of water abstraction and farming intensity was also shown. At high farming intensity (high nutrient concentration), high levels of water abstraction favored the development of small cells. They also demonstrated that farming intensity favored the development of non-attached but filamentous algae and that water abstraction with the risk of drying out the stream increased the dominance of small, resilient, and motile taxa (Lange et al., 2016). The tests on life-forms showed that a positive correlation of unicellular algae with water abstraction (i.e., low water flow stress) at high nutrient levels is in contrast with the presupposition that filamentous forms dominated under such circumstances. Probably, other factors overcame that effect; single-cell organisms have advantage under increased sedimentation, and they also have a greater chance to enter crevices in substratum particles (Lange et al., 2016). Nitrogen fixation as a physiological trait has been also tested and successfully indicated N-limited conditions. Two traits (i.e., reproduction techniques and spore formation) formed the category of life-history traits, and both proved to be successful indicators. The dominance of fragmentation over fission was present under high nutrient levels, which is explained with the dominance of filamentous forms under such circumstances. Spore formation showed negative response to nutrients but positive response to water abstraction.

Combined eco-morphological functional groups

The ecological classification by B-Béres et al. (2016) is a simple combination of the three ecological guilds of Passy (2007), which also adds a fourth guild of planktic species (Rimet & Bouchez, 2012b) and five size classes (Berthon et al., 2011), resulting in 20 combinations. The study was made in the framework of a colonization process and analyzed the effect of a disturbance event on the benthic diatom community as well. The study showed that the ecological guilds were not correlated significantly with the tested environmental factors. In contrast, in the combined eco-morphological groups, size classes highlighted differences within the same guilds. For example small, low-profile species were present in the beginning of the colonization, which stemmed from a fragmented mature biofilm and settled. Small species from the same guild dominated after a strong disturbance event (heavy raining) as the first colonizers. The study showed that the further refinement of existing classification can detect new niches.

Advantages and shortcomings in trait-based ecological classifications

Two of the four classifications involved non-diatoms in their study (Table 1), and in both cases it provided important additional information. Diatomists often forget about other taxa and draw their conclusions for the whole phytobenthos based only on diatom data. Even though diatoms can be often used as a proxy for the entire benthic algal community, in a perspective of assessment, studies on all groups may provide important additional information (Denicola & Kelly, 2014). The use of only diatoms has the practical advantage of a standardized sampling and preparation methods after which species can be easily identified based on clear morphological features. The question remains whether this advantage can compensate the loss of other information.

Kelly et al. (2008) tested the species–environment responses based on three kinds of datasets: only diatoms, diatoms and non-diatoms, and only non-diatoms. Results based on only diatoms were similar to results based on diatom and non-diatom data together, but both gave better correlation to environmental drivers (i.e., total phosphorus, dissolved inorganic carbon, conductivity, and calcium concentration) than non-diatoms alone. Even if non-diatoms represent a wider ecological scale, their indicator value is low due to the lower species richness (Kelly et al., 2008). On the other hand, it is clear that for a better understanding of the benthic communities, study of algae other than diatoms is inevitable. They have an important contribution, especially in eutrophic waters, and often dominate the algal community (Denicola et al., 2004). Although for now, most European countries use only diatom-based metrics in ecological quality assessment based on "macrophytes and phytobenthos" required by the WFD, there are countries using indices, including non-diatoms: Austria and Germany (Rott et al., 1997, 1999; Schaumburg et al., 2004), Czech Republic, and Norway (Schneider & Lindstrøm, 2009, 2011). The Norwegian examples demonstrate the utility of non-diatom benthic algae (mainly filamentous chlorophytes) as the indicator of trophic level (Periphyton index of trophic status, PIT—Schneider & Lindstrøm, 2011) and acidity (acidification index periphyton, AIP—Schneider & Lindstrøm, 2009). Schneider et al. (2012) showed that including non-diatom algae can provide additional information of the habitat. They found that while non-diatoms were mainly influenced by the channel substrate parameters, the diatom assemblage was influenced by both the substrate parameters and the riverbank characteristics. The authors explain those changes with the different dispersal characteristics. While filamentous Cyanobacteria or Chlorophyceae attach strongly to the substrate, diatoms generally disperse more easily due to the water flow. After the transport of diatom cells, habitat selection depends on the riverbank morphology, while non-diatom benthic algae are more dependent on the local substrates. Such important ecological differences have to be considered for the functional characterization of the phytobenthos. A simple measurable trait like the filament width of *Oedogonium* was found to positively correlate with the TP concentration (Schneider & Lindstrøm, 2011). Abundant appearance of *Mougeotia* indicates acidification (Graham et al., 1996a, b). It is possible that several already mentioned contradictions in studies trying to understand phytobenthos based on only diatom data were derived from such lack of information.

The number of groups is a critical point of functional classification. Comparative studies on phytoplankton functional groups show that the two most effective classification in terms of covering habitat diversity are the FG (Reynolds et al., 2002; Padisák et al., 2009) and MFG classifications (Salmaso & Padisák, 2007). They give similar results with their 40 and 31 groups, respectively. We suggest that a number of 20–40 groups would be ideal to cover habitat diversity. Although benthic diatom assemblages in rivers are different from planktic communities in lakes, a similar conclusion is considered valid: only a few groups are insufficient to cover the main habitat types. However, the existence of each group has to be clearly justified. Although the combination of the CSR strategies and life-forms resulted in 21 groups, most of them remained hypothetical. The study of Lange et al. (2016) does not define groups, but the number of ecologically meaningful traits has the potential to define several ecological groups.

The criteria of group definition are morphological in three cases (Table 1). It has the advantage of easy measurements and use, but it clearly limits the potential of defining a sufficient number of groups. An important task is collecting as much information as possible about the possible traits and their functional roles, as was previously done by Lange et al. (2016).

In further studies, it is important not only to look for correlations in environmental data but to confirm them by experiments where we can see not only correlations but causations too. Laboratory experiments on the effect of water flow, grazing, temperature, light intensity, nutrients, conductivity, etc. (e.g., Lange et al., 2011; Svensson et al., 2014; Cochero et al., 2015; Lengyel et al., 2015a) on particular species can provide useful information about the species preference that can be built in a trait database and help to define more realistic ecological groups. A particular symbiotic relation is represented between some species of cyanobacteria and species of diatoms (e.g., the genera *Epithemia* and *Rhopalodia*) (Janson, 2002). Having these symbiotic cyanobacteria is a very important trait of these diatoms. These heterocysts cyanobacteria can fix atmospheric nitrogen, which provides a clear competitive advantage in N-limited habitats (Stancheva et al., 2013; Lange et al., 2016).

Unfortunately, at present, due to the applied protocol for diatom sampling and preparation, we lack important information from monitoring data. Lack of data about non-diatom benthic algae can cause shortcomings regarding the functionality of the benthic community. During analyzing the samples, we know neither which cells were alive in the time of sampling nor which cells were already dead. Obviously, originally dead cells do not represent the conditions in the time of sampling. Although one study showed no difference between involving this information or not in assessing habitat conditions (Gillett et al., 2008), which was probably based on the habitat type (i.e., the current effect that washes away dead cells), results can change. We lose all visible information only in unprepared samples (e.g., type of attachment to substrate, colony-forming) after preparation. Even if we have information about this for several species, we can never be sure since some species can change their traits. Some *Cymbella* species can be unicellular and motile once and yet attached with a peduncle another time (Rimet & Bouchez, 2012b). *Encyonema silesiacum* can be found motile and tube-dwelling or colonial, and *Amphora lybica* can be attached with entire valve surface or stalked too (Law et al., 2014). This means that one species can be represented in two ecological groups depending on the environmental conditions in which they exist. In a particular case, a potential shift could be detected in ecological groups but not at the species level. Another example from phytoplankton is the planktic *Cylindrospermopsis raciborskii* that can be classified into two functional groups depending on whether it develops near the surface or forms a deep layer population (Padisák et al., 2009). For the mentioned reasons, more studies on traits are welcome, and data from investigation of unprepared samples are also necessary. In some cases where traits are missing for several species, phylogeny can also serve with solutions. Only if we have evidence that a particular trait is phylogenetically related can we assign this trait to all the taxa of that phylogenetic level (Keck et al., 2015; Larras et al., 2014).

We already possess knowledge of traits and their usability under particular conditions (Table 2). Most of our information is based on studies tested with nutrients and physical forces (flow, grazing), since they are the most common features that shape the benthic community. This information can be used to develop a conceptual framework similar to the one of Lange et al. (2016) and test them on a diverse dataset. One of the weakest points of this eco-morphological classification (B-Béres et al., 2016) is that their dataset originates from artificial substrata at one single sampling station containing only 34 diatom species. In contrast, the study of Lange et al. (2016) covers several sites in the catchment area of a river, with samples of diatoms and non-diatoms from natural substrate, containing 91 taxa in total.

Some shortcomings presented above can be derived from the problematics presented by Kelly (2012). We gain our information of the phytobenthos after a set of technical processes (e.g., sampling, sample preservation, preparation, microscopic examination, use of transfer function for quantifications); after that, the real picture of the community becomes an abstraction understood only by the experts. Kelly's proposition is a more holistic view with the help of 'guiding' images that not only provide a method for generating a more realistic view on the phytobenthos but also strengthens the bridge between scientists and end users.

Perspectives

We propose two basic, general methods for the development of functional groups. The first is based on an assignation of traits to species (Fig. 2). The chosen traits must be ecologically meaningful and justified by literature or experiments. These data are used to define groups of species that possess similar traits. The definition of such groups can be carried out by statistical methods, e.g., ordination techniques, clustering (Margalef, 1978; Usseglio-Polatera et al., 2000; Kruk et al., 2010; Law et al.,

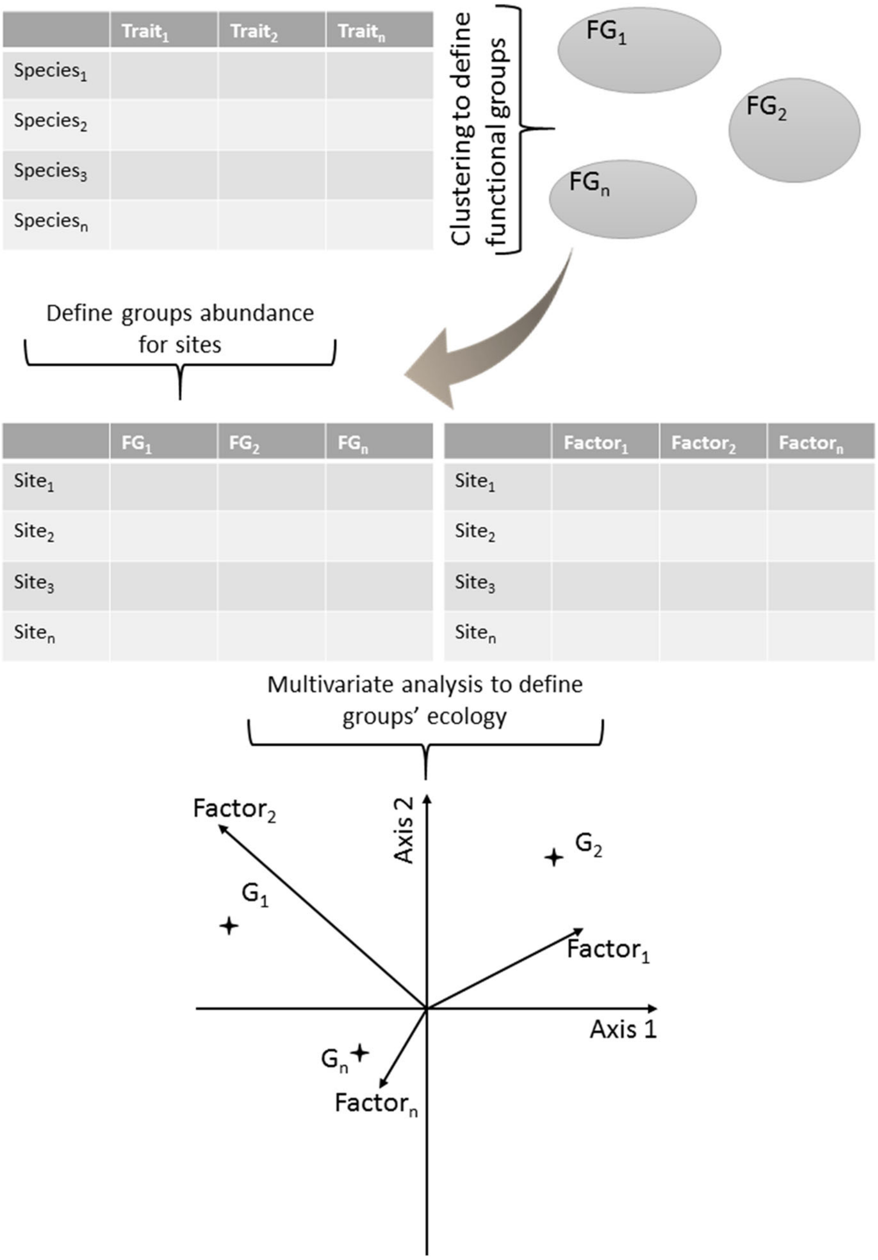


Fig. 2 Conceptual framework of defining ecological groups; definition of functional groups (FGs) are based on a species-trait database using statistical methods or expert knowledge. Datasets of FGs and environmental parameters are used to define the ecology of FGs via multivariate statistical methods

	$Trait_1$	$Trait_2$	$Trait_n$
$Species_1$			
$Species_2$			
$Species_3$			
$Species_n$			

	FG_1	FG_2	FG_n
$Site_1$			
$Site_2$			
$Site_3$			
$Site_n$			

	$Factor_1$	$Factor_2$	$Factor_n$
$Site_1$			
$Site_2$			
$Site_3$			
$Site_n$			

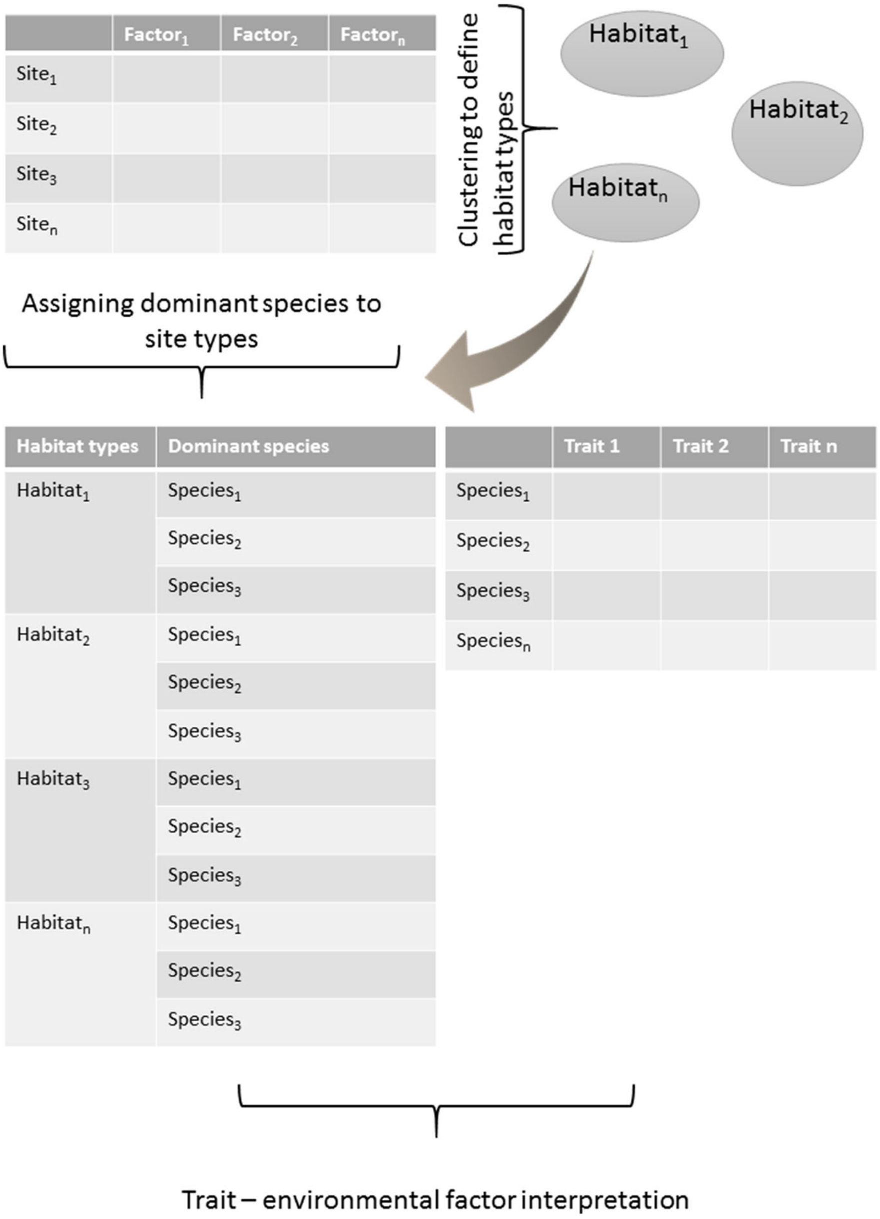
2014), or by expert knowledge (Passy, 2007; Salmaso & Padisák, 2007; Centis et al., 2010; B-Béres et al., 2016). The use of expert knowledge requires strong background knowledge in order to define ecologically meaningful groups. This concept was used for the ecological guilds (Passy, 2007) and the morpho-functional diatom groups (MFDG) (Centis et al., 2010), which is an adaptation of the morpho-functional group (MFG) classification developed for phytoplankton (Salmaso & Padisák, 2007) on planktic diatoms. The eco-morphological functional groups of B-Béres et al. (2016) is also based on presupposed combination of traits. Then, these groups must be tested on environmental data to see if they represent separated niches of the environment. This can be easily done by multivariate analyses, e.g., canonical correspondence analysis (B-Béres et al., 2016).

The other approach we propose (Fig. 3) is based on the Functional Group classification for phytoplankton

(Reynolds et al., 2002). It has a phytosociological base in analogy to "associations" of terrestrial plants. A particular habitat is represented by a set of environmental characteristics to which the occurring species are adapted, i.e., they possess functional traits that make the species competitive and therefore abundant there. A similar approach has not yet been tested for benthic algae flora. This approach also requires well-defined trait–environmental factor relations so that a new species can be classified in a functional group. The definition criteria for phytoplankton FGs is not only morphological but structural, functional, ecological (e.g., trophic preferences), habitat-based, and taxonomical.

The advantage of using trait-based classifications in ecological assessment is already recognized, and there is a trend in developing and using them for the purposes of the WFD (Hering et al., 2010; Reyjol et al., 2014). Several studies address developing such groups for the different "Biological Quality Elements" of the WFD: macrophytes (Orfanidis et al., 2003; Wells et al., 2007), fish (Logez et al., 2013),

Fig. 3 Conceptual framework of defining ecological groups; environmental data are used to define habitat types either with statistical methods or expert knowledge. Each habitat types possess dominant species with adaptive traits. Then, an interpretation of the trait–environment relation is required



	$Factor_1$	$Factor_2$	$Factor_n$
$Site_1$			
$Site_2$			
$Site_3$			
$Site_n$			

Habitat types	Dominant species
$Habitat_1$	$Species_1$
	$Species_2$
	$Species_3$
$Habitat_2$	$Species_1$
	$Species_2$
	$Species_3$
$Habitat_3$	$Species_1$
	$Species_2$
	$Species_3$
$Habitat_n$	$Species_1$
	$Species_2$
	$Species_3$

	Trait 1	Trait 2	Trait n
$Species_1$			
$Species_2$			
$Species_3$			
$Species_n$			

macroinvertebrates (Dolédec & Statzner, 2008; Borja et al., 2009), and phytoplankton (Padisák et al., 2006). The assemblage index to evaluate ecological status of lakes with their phytoplankton (Padisák et al., 2006) composition is based on the functional classification by Reynolds (Reynolds et al., 2002; Padisák et al., 2009). The index classifies Hungarian lakes into eight lake types according to their typology. Each phytoplankton codon has a factor number between 1 and 5 for each lake type indicating how favorable the presence of this codon in the particular habitat type. The final value is a simple average of the biomass contribution of each codon weighted by their factor value. A possible first step of integrating the approach in the Water Framework Directive can be the testing of already ecologically justified traits on the European river typology. There is a potential for defining particular trait compositions for the typological categories that can be further specified with further analyses. For example, we have already good knowledge of the trait versus nutrient or physical force, while less is known about how benthic algae communities are affected by the geochemical properties of the water body.

Another crucial point is the question of seasonality. Especially from the point of view of applied assessment, it would be necessary to standardize the sampling period. The most important requirement is representativeness. We have to look for the nearly competitively selected equilibrium period when the benthic community is the most representative. For example, for phytoplankton in lakes, Padisák et al. (2006) suggest the stable late summer period when the phytoplankton community reach a near steady-state condition, and this period also integrates the preceding events. Benthic communities are less intensively studied in terms of seasonality (King et al., 2006; Lengyel et al., 2015b). Although colonization time of the substrate by benthic algae strongly varies based on the environmental conditions, it can be measured in weeks. Generally, colonization experiments suggest 4 weeks for having a densely colonized substrate that we can sample. Therefore, sampling times should be long enough (∼4 weeks) after the last known strong disturbance event that can reverse the successional phases. It is important to avoid the comparison of habitats assessed by communities in different colonization phases, because we may detect the differences between the successional stages and not the habitats (King et al., 2006). Higher water temperature and light intensity enhance succession speed (Hoagland et al., 1982); hence, they practically can help to find an appropriate sampling time. Since in winter (under temperate climate and average altitude), the low temperature and light stress the community, these circumstances result in potentially low diversity assemblages with stress-tolerant species. This period is clearly not appropriate if the aim is to detect differences between the habitats caused by processes that are more complex. The spring period with its strong floods represent a likewise pressure avoiding the development of a mature biofilm, resulting in similar communities with different habitats. Hoagland et al. (1982) carried out a study investigating the successional and colonization process of a benthic algal community on artificial substrates in two reservoirs. They showed that the densest biofilm appeared in the summer, and the two reservoirs differed most in the summer based on their benthic community. Thus, we suggest that under a temperate climate, the summer–autumn period appears to be the appropriate time period for sampling. When algal succession is fast, the biofilm is dense, and the algal community may reach the competitively selected equilibrium state. We have to consider that sampling time is also climate dependent. Based on our own experiences on the tropical island of Mayotte, located 200 km east of Madagascar, the second half of the dry season (July–August) proved to be the best for assessing environmental conditions. In their paper, Hoagland et al. (1982) also showed that filamentous non-diatom algae become apparent in the last phase of succession that confirms the importance of investigating non-diatom benthic algae in a functional classification.

If we suggest an analogy between the species-based autoecological indices and the functional group indices, it would be worth considering using functional diversity metrics with species-based diversity metrics (e.g., richness, Shannon diversity, evenness). The first attempts on these metrics, which have been tested on virtual animal trait database, are promising (Schleuter et al., 2010).

The upcoming challenge for diatomists is to define ecologically meaningful functional traits that will be used for the development of an adequate number of functional groups for diatoms covering as many possible different habitat types. This classification can be the basis of a new quality evaluation system that is more robust and general, since it is based on traits and adaptations instead of species.

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