Abonyi, A., Z. Horváth & R. Ptacnik, 2018. Functional richness outperforms taxonomic richness in predicting ecosystem functioning in natural phytoplankton communities. Freshwater Biology 63(2):178–186 doi:10.1111/fwb.13051.

Authors[1]

András Abonyi

1 WasserCluster Lunz, Biologische Station GmbH, Dr. Carl Kupelwieser Promenade

    5, A-3293 Lunz am See, Austria

2 MTA-PE Limnoecology Research Group, University of Pannonia, Egyetem u. 10,

    H-8200 Veszprém, Hungary

3 MTA Centre for Ecological Research, Danube Research Institute, Karolina u. 29,

    H-1113 Budapest, Hungary

Zsófia Horváth

1 WasserCluster Lunz, Biologische Station GmbH, Dr. Carl Kupelwieser Promenade

    5, A-3293 Lunz am See, Austria

Robert Ptacnik

1 WasserCluster Lunz, Biologische Station GmbH, Dr. Carl Kupelwieser Promenade

    5, A-3293 Lunz am See, Austria

Corresponding author: András Abonyi, abonyi.andras@okologia.mta.hu

---

[1] AA and RP originally formulated the research idea; AA, RP and ZSH performed

data analyses and wrote the manuscript.

1

Abstract

1. Recent studies clearly support a positive biodiversity–ecosystem functioning (BEF) relationship in phytoplankton. As taxon richness does not quantify functional diversity, functional approaches have been developed to link community functioning to diversity. Compared to terrestrial plant communities, only a few studies have validated phytoplankton functional approaches in BEF relationships. Furthermore, the ability of functional and taxonomic richness measures in predicting ecosystem functioning of natural phytoplankton communities has not been compared yet.

2. Here, we analyzed the BEF relationship using taxonomic and functional (trait categories and response groups *sensu* Reynolds) approaches in a broad-scale phytoplankton dataset from Fennoscandia. First, we analyzed how taxonomic and functional compositions were related to local environmental predictors. We then compared how taxonomic and functional richness performed in predicting resource use efficiency (the yield in phytoplankton biomass standardized by total phosphorus) as an ecosystem functioning measure. Finally, we tested whether the relationship between ecosystem functioning and taxonomic richness is further enhanced once each of the functional richness measure is also considered.

3. Among the approaches, phytoplankton functional trait categories as community matrix showed the best correspondence with the local environment. The richness of phytoplankton response groups predicted ecosystem functioning significantly better than the taxonomic and the functional trait category richness – both in the full dataset and in almost all Fennoscandian countries. On top of taxonomic richness, only the residual variation in response group richness predicted ecosystem functioning positively in the entire dataset and in all individual countries.

4. Applying functional approaches, reduced complexity of data should come along with reduced ecological information. We showed however that both functional approaches represented some functional redundancy among taxa in a meaningful way, and enhanced our ability in predicting community composition from environmental predictors. Moreover, phytoplankton response group richness *sensu* Reynolds summarizes information on ecosystem functioning contained in the taxonomic data in a way that represents functional diversity better than the richness of functional trait categories.

5. Interestingly, the response group approach, which is exclusively derived from field observations rather than from quantified phytoplankton traits, outperforms taxonomic richness and trait category richness in predicting ecosystem functioning in our dataset. This may highlight that our ability to quantify phytoplankton traits is still limited. Existing phytoplankton functional approaches, however, can translate the taxonomic information into a reduced but reliable functional matrix already and predict ecosystem functioning better than taxonomic data.

Key words

biodiversity-ecosystem functioning, functional groups, functional trait categories, phytoplankton assemblages, response groups

Introduction

Recent studies clearly support a positive biodiversity-ecosystem functioning (BEF) relationship in phytoplankton communities (Naeem & Li, 1997; Ptacnik *et al.*, 2008b; Striebel, Behl & Stibor, 2009). Instead of asking how so many species may coexist in

phytoplankton (Hutchinson, 1961), the question has been reversed to how many species are needed to ensure ecosystem functioning (Ptacnik, Moorthi & Hillebrand, 2010). As taxonomic composition itself does not represent functional diversity, phytoplankton functional approaches have been developed (Salmaso, Naselli-Flores & Padisák, 2014). The potential of functional approaches in BEF, however, has rarely been compared with the taxonomic approach in natural phytoplankton communities.

Fridley (2001) highlighted that dominant mechanisms driving positive BEF are complementarity and sampling effect. Complementarity has been the most often recognized in terrestrial systems (Loreau & Hector, 2001). Complementarity means that more diverse communities allow for more efficient resource use. According to the sampling effect, the probability of species presence with effective functional attributes increases with an increase in the diversity of communities (Naeem & Wright, 2003). Better understanding of functional traits could help resolve such contradictions (op. cit.).

In an attempt to better understand mechanisms underlying the positive BEF relationship in a predictive way, there is a growing interest in functional diversity of communities (Hillebrand & Matthiessen, 2009). Functional diversity provides information about what species do in communities, and summarizes the value and range of traits that influence ecosystem functioning (Petchey & Gaston, 2006). In terrestrial plant communities, Flynn et al. (2011) showed that phylogenetic and functional diversity predicted ecosystem functioning better than functional group richness. Furthermore, trait-based models repeatedly predicted ecosystem functioning better than taxonomic richness in terrestrial plant communities (Tilman *et al.*, 1997; Díaz & Cabido, 2001). In spite of the growing interest in phytoplankton functional approaches, compared to terrestrial systems, only a few studies have validated trait-

based measures in terms of predicting BEF relationships (Zwart, Solomon & Jones, 2015). Furthermore, functional richness has so far never been used to describe BEF relationships in natural phytoplankton communities.

For phytoplankton, two outstanding and complementary functional approaches have been developed, namely (i) morphological, physiological and behavioural traits (functional traits - FTs) (Weithoff, 2003; Litchman & Klausmeier, 2008), which potentially impact fitness via growth and survival (Violle *et al.*, 2007); and (ii) characteristic assemblages described in the functional group concept *sensu* Reynolds (Reynolds *et al.*, 2002). Litchman and co-workers (Litchman *et al.*, 2007; Litchman & Klausmeier, 2008; Litchman *et al.*, 2010) have advocated the use of trait-based models to parameterize diversity-functioning relationships in phytoplankton, while the concept of Reynolds has never been used in a similar approach. It classifies taxa into ~40 groups based on their occurrence in context of a set of environmental conditions (Reynolds *et al.*, 2002; Padisák, Crossetti & Naselli-Flores, 2009). According to Violle et al. (2007), these groups summarize taxa with "response traits" to the environment in specific groups (hereafter response groups - RGs) rather than in functional groups.

The FT and RG compositions were repeatedly found to correlate well with local environmental predictors in individual lakes (Cellamare *et al.*, 2013; Cellamare *et al.*, 2016). Kruk et al. (2011) showed that the morphological trait composition of phytoplankton could be best predicted from local environmental parameters over the RG and taxonomic compositions. According to the FT and RG approaches, they are potentially complementary to better understand phytoplankton community structuring and the effect of functional richness on ecosystem functioning.

In a broad-scale phytoplankton dataset from Fennoscandian lakes and from the Baltic Sea, Ptacnik et al. (2008b) showed that resource use efficiency (RUE) scaled positively with taxonomic richness. Using the same dataset excluding the Baltic Sea, we test here how the richness of functional trait categories (FTR) and response group richness (RGR) perform as predictors of RUE compared to taxonomic richness (genus richness - GR). We first test whether the phytoplankton composition based on functional trait categories (FTC) and response groups (RGC) is better predicted by local environmental predictors than based on the taxonomic composition (genus composition - GC). Then we compare how GR, FTR and RGR each relate to RUE, and whether residual variations in FTR and RGR unexplained by GR further affect RUE in fitted linear models.

We hypothesize that (a) both functional compositions (FTC, RGC) are better predicted by local environmental parameters than the taxonomic composition (GC); (b) FTR and RGR richness predict ecosystem functioning better than GR; and (c) both the FTR and RGR residual variations affect RUE positively on top of GR in natural phytoplankton communities.

Material and Methods

Phytoplankton data and functional classifications

The phytoplankton dataset included samples from diverse monitoring programs through Fennoscandia, covering the period of 1988-2003 (Moe, Dudley & Ptacnik, 2008). Microscopic counting was carried out by Pål Brettum (Norway), Eva Willén (Sweden) and Liisa Lepistö (Finland); using the inverted microscope method

6

(Utermöhl, 1958). Algal biomass was based on approximated geometrical forms at species levels (Tikkanen & Willén, 1992), and expressed as fresh weight assuming a density of 1. Samples from acidified (pH<6) and high-altitude lakes (>300 m a.s.l.) were excluded, while we reduced the effect of seasonality by including only summer samples (July and August) with a latitude range ≤ 65°. The final dataset included 1016 samples.

Phytoplankton functional traits (FTs) and response groups (RGs) distinguish taxa mainly at the level of genera or order. By grouping taxa within the same functional unit, it effectively reduces the complexity of community data (Salmaso, Naselli-Flores & Padisák, 2014). Major morphological, physiological and behavioral characteristics of taxa were used to detail the phytoplankton functional trait composition (Weithoff, 2003; Litchman & Klausmeier, 2008) (see Table 1). Heterotrophic taxa (i.e. *Chilomonas, Gymnodinium helveticum, Katablepharis ovalis*) were included in our analysis. Taxa were considered mixotrophic if phagotrophy was formerly evidenced in the literature at genus level (Porter, 1988; Sanders & Porter, 1988).

The FT categories of each taxon were first specified based on presence-absence data (traits by species matrix; see Supplement 1). Then in each sample, the biomass contribution of taxa (species biomass by sites matrix) under each specific trait category was summed up (biomass in trait categories by sites matrix), and then used as the matrix of functional trait community composition (FTC). Phytoplankton taxa were furthermore classified into RGs *sensu* Reynolds (RGs by taxa matrix; see Supplement 2), and the summed biomass in each RG (biomass in RGs by sites matrix) was used as the matrix of response group community composition (RGC)..

Environmental data

Prior to analysis, we selected samples with a sufficient number of environmental predictors available. We included parameters that significantly affected the taxonomic and functional compositions of phytoplankton (see CCA in Statistical Analysis): total phosphorus (TP), total nitrogen (TN), pH, lake morphometry (lake surface area, mean depth) and altitude. Chemical parameters were analyzed based on the same water samples as phytoplankton compositions (Moe, Dudley & Ptacnik, 2008).

Phytoplankton taxonomic and functional richness measures

Taxonomic richness of phytoplankton was based on genus richness (GR). This makes our dataset more robust to differences in effort taken during phytoplankton identification in the three Fennoscandian countries. Functional richness was considered based on (i) the number of unique combinations of functional trait categories (FTR), and (ii) response group richness (RGR) *sensu* Reynolds present in each Fennoscandian lake phytoplankton sample. As several FT categories can be assigned for each taxon, the number of FT categories within a community would not be as informative as the number of unique combinations (all trait categories would be present in almost all samples). On the other hand, each taxon can be classified into one response group (RG) *sensu* Reynolds; therefore RGR is a condensed richness estimate, with peak RGR equal to the total number of RGs defined. We used the functionally singular taxa number (sing.sp) of the functional diversity-'FD' R package (Laliberté & Legendre, 2010; Laliberté, Legendre & Shipley, 2014) to calculate the

number of unique combinations of functional trait categories (FTR), and the number of response groups (RGR) in our dataset.

Resource use efficiency

Ecosystem functioning of phytoplankton was quantified as the yield in phytoplankton biomass standardized by the limiting resource, total phosphorus, also known as resource use efficiency (RUE; ln(chlorophyll-a: total phosphorus) (Ptacnik *et al.*, 2008b). RUE can be estimated both from algal biovolume or chlorophyll-a and shows consistent positive relationship with phytoplankton taxonomic richness (Ptacnik *et al.*, 2008b). Here, we use the RUE estimated from chlorophyll-a, being an independent estimate from the microscopic analysis.

Statistical analysis

Phytoplankton community (biovolume) data were cubic root transformed at taxonomic (genus composition - GC) and functional (FTC and RGC) levels to down-weigh dominant taxa in the analyses. Environmental predictors were ln-transformed to normalize their distributions (lake surface area, mean depth, altitude, TN, and TP). The relationships between community composition (GC, FTC and RGC) and local environmental predictors were assessed by three separate canonical correspondence analyses (CCA) based on selected samples with no missing data. Environmental parameters affecting the community composition significantly were first selected based on combined backward and forward selection in each analysis (function 'ordistep' in '*vegan*'). The significance of final models was tested by Monte Carlo

permutation test for each term in full models ('anova' command by 'terms' in 'direct' models in '*vegan*').

In order to rigorously compare the performance of taxonomic and functional richness measures as predictors of RUE, we performed a bootstrap analysis. Here we tested whether bootstrapped coefficients of determination of linear models predicting RUE based on functional richness measures (FTR and RGR) differed significantly from predictions based on genus richness (GR) ('*boot*' in R (Davison & Hinkley, 1997; Canty & Ripley, 2016) with 999 replicates). The bootstrapped coefficients of determination were then compared by Wilcoxon rank sum tests.

The relationships between taxonomic (GR) and functional richness measures (FTR, and RGR) were tested using generalized additive models (GAM) (Wood, 2011), selected according to the Akaike's information criterion (AIC). As functional richness is expected to strongly correlate with taxonomic richness, first we calculated the residual variation of FTR and RGR with GR from linear regression analysis, and subsequently regressed the resource use efficiency (RUE) against GR plus each of the residual variations. Thereby, we tested whether the fractions of FTR and RGR unexplained by GR does further affect ecosystem functioning.

Data analyses and visualization were performed in R (R Core Team, 2015), using the '*vegan*' package for multivariate analyses (Oksanen *et al.*, 2015).

Results

Relationships of community composition and local environmental predictors

In all CCAs, individual constraints affected the taxonomic (GC) and functional community compositions (FTC, RGC) significantly (Non-parametric permutation test, p<0.001 in all cases). The variation in phytoplankton composition explained by local environmental predictors increased from taxonomic (GC: 6.7%) to functional levels (FTC: 21.7%, RGC: 14.2%) based on the CCA analyses (Fig 1). Interestingly, while CCA separated samples of the three Fennoscandian countries based on taxonomic compositions, no similar pattern occurred based on the functional compositions (FTC and RGC; Fig 1).

Relationships between functional and taxonomic richness

The richness of functional trait categories (FTR) and response groups (RGR) both exhibited highly significant correlations with genus richness (GR) in the entire region and also in each Fennoscandian country (GAM, p<0.001, see Supplement 3). The relationship was almost linear for both FTR and RGR, but RGR exhibited a slightly saturating pattern with GR (see results of LM and GAM in Supplement 3).

Functional richness as predictor of resource use efficiency (RUE)

As independent predictors, both functional richness measures (FTR and RGR) strongly and positively predicted RUE in linear models in each Nordic country, and in the whole dataset (Table 2). Based on 999 bootstrapped coefficients of determination of linear models predicting RUE, RGR richness was the strongest predictor of RUE over FTR and GR in almost all regression models of individual countries, and also in the entire dataset (Fig 2, Table 3). The only exception was Norway, where RGR and

GR in predicting RUE did not differ significantly. Furthermore, FTR richness was a significantly weaker predictor of RUE than GR in almost all cases (except in Sweden). In agreement with the earlier analysis performed by Ptacnik et al. (2008b), RUE displayed the strongest relationships with FTR and RGR richness for Norwegian lakes, which at the same time had the lowest richness values (Fig 3 A, C).

The residual variation in the number of unique combinations of FT categories (FTR) unexplained by genus richness (GR) did not predict RUE significantly in linear models at the country level (Fig. 3B, Table 4A). Across the pooled dataset, however, FTR affected RUE negatively (LM, p<0.05). RGR richness unexplained by GR predicted RUE positively in linear models in all individual countries (LM, p<0.05 in all cases, except Finland p<0.001) and in the entire dataset (LM, p<0.001, Fig. 3D, Table 4B).

Discussion

Local environment predicts functional better than taxonomic composition

Aggregating the community matrix from taxonomic (genus composition - GC) to functional trait categories (FTC) and response groups (RGC) reduces drastically the complexity of the data. Instead of 239 genus variables, the matrix is compacted to 17 FTs and 30 RGs. The reduction of biological information should come along with reduced ecological information; hence one might expect a reduced link between the functional composition of phytoplankton and local environmental predictors. Compared to terrestrial plant communities, however, pelagic phytoplankton species

12

inhabiting different habitats are relatively similar functionally (Weithoff, 2003); a feature extensively studied based on morphological traits (Klais *et al.*, 2017), and size structure of phytoplankton communities (Naselli-Flores, Padisák & Albay, 2007; Naselli-Flores & Barone, 2011). Therefore, while the taxonomic composition may separate samples from different lake types and habitats (i.e. deep oligotrophic clear water lakes in Norway, small organic rich humic lakes in Finland, mixed typology in Sweden; CCA of the three Fennoscandian countries), the FT and RG approaches represent a considerable amount of functional redundancy in the taxonomic composition in a meaningful way. As a consequence, aggregating taxonomic data to functional data may lead to better correspondence between community composition and environment. Aggregated phytoplankton taxonomic data has already been found to better correspond to environmental predictors (Kruk *et al.*, 2011) and to trophic gradients (Ptacnik *et al.*, 2008a) than species-level taxonomic composition. Our finding support the idea that natural phytoplankton communities can be characterized by functional approaches that highlight some ecological similarities among taxa (Schippers *et al.*, 2001). We showed that both the FT and RG approaches successfully represent such functional similarities in natural phytoplankton communities. Our findings provide the first evidence from observational data for the hypothesis that reduced complexity using functional approaches could increase the ability of linking community composition to ecosystem functioning (McGill *et al.*, 2006; Litchman & Klausmeier, 2008; Litchman *et al.*, 2010).

Relationships between functional and taxonomic richness

Both functional richness measures (FTR and RGR) were highly correlated with taxonomic richness (GR). Especially the number of unique combinations of FT categories showed strong linear relationship with GR. On the other hand, the slight saturation of RGR with GR highlighted that the two functional approaches represent different aspects of community organization in phytoplankton. The strong linear relationship between FTR and GR suggests that based on trait categories either random or uniform occupation of niche space shapes community structure (Díaz & Cabido, 2001). Therefore, phytoplankton taxa may be equally complementary according to their combinations in FT categories, whereas species identity plays only a minor role in determining functional diversity (Petchey & Gaston, 2002). With the slightly saturating pattern in RGR with GR, however, one may expect more frequent niche overlaps (Ehrlich & Ehrlich, 1981), and therefore better representation of functional redundancy in communities (Díaz & Cabido, 2001). Accordingly, based on RGs, the chance of adding a new species with a unique functional role decreases as the number of species increases (Petchey & Gaston, 2002). While both functional richness measures increased almost linearly with taxonomic richness, the chance for the occurrence of functionally unique taxa is expected to decrease with increasing taxonomic richness. If one functional approach is able to successfully represent functional complementarity not explained by taxonomic richness, then that approach would be expected to predict ecosystem functioning more efficiently. As the RG approach allows the identification of polyphyletic species groups including taxa with either diverse or similar FT combinations, one may expect different representation of functional complementarity by FTs and RGs; hence their different abilities in predicting ecosystem functioning.

Functional identity matters to ecosystem functioning

We hypothesised that both functional richness (FTR and RGR) measures would predict ecosystem functioning better than GR. Our results showed that especially RGR performed better than GR, and the residual variation in RGR (the fraction not related to genus richness) enhanced the prediction of RUE. While the number of samples was uneven among countries, the by-country analyses performed in addition to the pooled dataset analysis highlighted that our results were quite robust. In spite of the overall high similarity of FTR and RGR richness with GR, only RGR predicted consistently and positively RUE. Kruk et al. (2011) argued that the local environment was responsible for the presence of species groups that shared similar adaptive features, i.e. similar trait compositions. The weaker relationship between RUE and FTR may emphasize the importance of dominance relationships and therefore the distribution of traits in communities (Hillebrand, Bennett & Cadotte, 2008). Furthermore, we were not able to weight traits according to their relative importance, which would lead to a decrease in the effective dimensionality of the trait space and increase in the relative importance of the species composition (Petchey & Gaston, 2002). Additionally, the information summarized in traits (similarly to the taxonomic composition) is often independent of the functional significance of traits that species possess (Naeem & Wright, 2003). In developing functional groups from traits, difficulties also occur as one or only a few species express some traits, while some species may express functional traits in several contexts under different conditions (op. cit.). Functional traits are ideally quantified empirically based on species-specific assays in lab-conditions, which is laborious with some obvious limitations. In our analysis, we have limited information i.e. about nutritional modes in mixotrophic taxa

15

(Mitra *et al.*, 2014). Likewise, in our FT classification, functional traits are represented as binary variables that simply categorize taxa i.e. as being non/motile. However, it is obvious that there is a considerable variability among motile taxa in terms of their swimming speed, tactile behaviour and escape responses to grazers.

Positive BEF relationships point out that more diverse communities fill available niche space better. According to Ptacnik et al. (2010), positive BEF scaling relationships imply that functional diversity of communities meets with a corresponding environmental dimensionality. In our analysis, ecosystem functioning scaled with all the three richness measures well (GR, FTR, RGR), implying that these approaches successfully represent communities filling niche space in a multi-dimensional environment. It is interesting to see, however, that RGR richness, which is exclusively derived from field observations rather than from quantified phytoplankton traits, outperforms GR and FTR in predicting ecosystem functioning along the entire E-W phytoplankton diversity gradient of Fennoscandia. This may suggest that RGR richness *sensu* Reynolds summarizes information on ecosystem functioning contained in the genus matrix in a way more directly linked to functional diversity than FTR.

By definition, traits should properly represent functional diversity of a biological community (Díaz & Cabido, 2001; Violle *et al.*, 2007). The fact that the heuristic RGs outperformed the FT approach suggests that our ability to quantify traits is still limited. Also, this may also point at a further limitation in the current use of traits. While traits are defined per species, trait-mediated effects that arise from interactions among taxa (see i.e. Klais et al. 2017) should also be considered.

The identification of reliable species associations in phytoplankton might be further enhanced by the future combination of different approaches, i.e. using trait-based

approaches to identify characteristic response groups in natural phytoplankton communities (Kruk *et al.*, 2017). In the future, trait-based approaches in phytoplankton ecology may favour the identification of ecologically relevant traits (Kremer *et al.*, 2016); the evaluation of continuous traits (Edwards *et al.*, 2012; Edwards, Klausmeier & Litchman, 2015), as well as the consideration of intraspecific variations in traits (Carmona *et al.*, 2016).

Conclusions and outlook

Here we asked whether our current understanding of phytoplankton composition based on existing functional approaches translates taxonomic information reliably into a reduced functional diversity matrix. The overall good correspondence between the taxonomic and functional richness measures and also in their abilities in predicting resource use demonstrate that existing metrics capture functional diversity in a meaningful way. Given the superior performance of the heuristically derived Reynolds functional group richness, our findings also motivate to further improve quantification of phytoplankton functional trait diversity. This will open towards effective modelling of ecosystem functioning in natural phytoplankton communities.

Acknowledgements

References

Canty A. & Ripley B. (2016) boot: Bootstrap R (S-Plus) Functions. R package version 1.3-18.

Carmona C.P., De Bello F., Mason N.W.H. & Lepš J. (2016) Traits without borders: Integrating functional diversity across scales. *Trends in Ecology & Evolution,* **31,** 382–394.

Cellamare M., Lançon A.M., Leitão M., Cerasino L., Obertegger U. & Flaim G. (2016) Phytoplankton functional response to spatial and temporal differences in a cold and oligotrophic lake. *Hydrobiologia,* **764,** 199–209.

Cellamare M., Tezanos Pinto P., Leitão M., Coste M., Boutry S. & Haury J. (2013) Using functional approaches to study phytoplankton communities in a temperate region exposed to tropical species dispersal. *Hydrobiologia,* **702,** 267-282.

Davison A.C. & Hinkley D.V. (1997) *Bootstrap methods and their applications,* Cambridge University Press, Cambridge.

Díaz S. & Cabido M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution,* **16,** 646-655.

Edwards K.F., Klausmeier C.A. & Litchman E. (2015) Nutrient utilization traits of phytoplankton. *Ecology,* **96,** 2311-2311.

Edwards K.F., Thomas M.K., Klausmeier C.A. & Litchman E. (2012) Allometric scaling and taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton. *Limnology and Oceanography,* **57,** 554-566.

Ehrlich P. & Ehrlich A. (1981) *Extinction: The causes and consequences of the disappearance of species,* Random House, New York.

Flynn D.F.B., Mirotchnick N., Jain M., Palmer M.I. & Naeem S. (2011) Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology,* **92,** 1573-1581.

Fridley J.D. (2001) The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos,* **93,** 514-526.

Hillebrand H., Bennett D.M. & Cadotte M.W. (2008) Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology,* **89,** 1510-1520.

Hillebrand H. & Matthiessen B. (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters,* **12,** 1405-1419.

Hutchinson G.E. (1961) The paradox of the plankton. *The American Naturalist,* **95,** 137-145.

Klais R., Norros V., Lehtinen S., Tamminen T. & Olli K. (2017) Community assembly and drivers of phytoplankton functional structure. *Functional Ecology,* **31,** 760–767.

Kremer C.T., Williams A.K., Finiguerra M., Fong A.A., Kellerman A., Paver S.F., Tolar B.B. & Toscano B.J. (2016) Realizing the potential of trait-based aquatic ecology: New tools and collaborative approaches. *Limnology and Oceanography,* **62,** 253–271.

Kruk C., Devercelli M., Huszar V.L.M., Hernández E., Beamud G., Diaz M., Silva L.H.S. & Segura A.M. (2017) Classification of Reynolds phytoplankton

functional groups using individual traits and machine learning techniques. *Freshwater Biology*, 1-12 (https://doi.org/10.1111/fwb.12968).

Kruk C., Peeters E.T.H.M., Van Nes E.H., Huszar V.L.M., Costa L.S. & Scheffera M. (2011) Phytoplankton community composition can be predicted best in terms of morphological groups. *Limnology & Oceanography,* **56,** 110-118.

Laliberté E. & Legendre P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology,* **91,** 299-305.

Laliberté E., Legendre P. & Shipley B. (2014) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Litchman E., De Tezanos Pinto P., Klausmeier C.A., Thomas M.K. & Yoshiyama K. (2010) Linking traits to species diversity and community structure in phytoplankton. *Hydrobiologia,* **653,** 15-28.

Litchman E. & Klausmeier C.A. (2008) Trait-based community ecology of phytoplankton. *Annual Review of Ecology, Evolution, and Systematics,* **39,** 615-639.

Litchman E., Klausmeier C.A., Schofield O.M. & Falkowski P.G. (2007) The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. *Ecology Letters,* **10,** 1170-1181.

Loreau M. & Hector A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature,* **412,** 72-76.

Mcgill B.J., Enquist B.J., Weiher E. & Westoby M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution,* **21,** 178-185.

Mitra A., Flynn K.J., Burkholder J.M., Berge T., Calbet A., Raven J.A., Granéli E., Glibert P.M., Hansen P.J., Stoecker D.K., Thingstad F., Tillmann U., Våge S.,

Wilken S. & Zubkov M.V. (2014) The role of mixotrophic protists in the biological carbon pump. *Biogeosciences,* **11,** 995-1005.

Moe S.J., Dudley B. & Ptacnik R. (2008) REBECCA databases: experiences from compilation and analyses of monitoring data from 5,000 lakes in 20 European countries. *Aquatic Ecology,* **42,** 183-201.

Naeem S. & Li S. (1997) Biodiversity enhances ecosystem reliability. *Nature,* **390,** 507-509.

Naeem S. & Wright J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters,* **6,** 567-579.

Naselli-Flores L. & Barone R. (2011) Fight on plankton! or, phytoplankton shape and size as adaptive tools to get ahead in the struggle for life. *Cryptogamie, Algologie,* **32,** 157-204.

Naselli-Flores L., Padisák J. & Albay M. (2007) Shape and size in phytoplankton ecology: do they matter? *Hydrobiologia,* **578,** 157-161.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'hara R.B., Simpson G.L., Solymos P., Stevens M.H.H. & Wagner H.H. (2015) vegan: Community Ecology Package. R package version 2.3-2. https://CRAN.R-project.org/package=vegan.

Padisák J., Crossetti L. & Naselli-Flores L. (2009) Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. *Hydrobiologia,* **621,** 1-19.

Petchey O.L. & Gaston K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters,* **5,** 402-411.

Petchey O.L. & Gaston K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters,* **9,** 741-758.

Porter K.G. (1988) Phagotrophic phytoflagellates in microbial food webs. *Hydrobiologia,* **159,** 89-97.

Ptacnik R., Lepistö L., Willén E., Brettum P., Andersen T., Rekolainen S., Lyche Solheim A. & Carvalho L. (2008a) Quantitative responses of lake phytoplankton to eutrophication in Northern Europe. *Aquatic Ecology,* **42,** 227-236.

Ptacnik R., Moorthi S.D. & Hillebrand H. (2010) Hutchinson reversed, or why there need to be so many species. *Advances in Ecological Research,* **43,** 1-33.

Ptacnik R., Solimini A.G., Andersen T., Tamminen T., Brettum P., Lepistö L., Willén E. & Rekolainen S. (2008b) Diversity predicts stability and resource use efficiency in natural phytoplankton communities. *Proceedings of the National Academy of Sciences,* **105,** 5134-5138.

R Core Team. (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL https://www.R-project.org/.

Reynolds C.S., Huszar V., Kruk C., Naselli-Flores L. & Melo S. (2002) Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research,* **24,** 417-428.

Salmaso N., Naselli-Flores L. & Padisák J. (2014) Functional classifications and their application in phytoplankton ecology. *Freshwater Biology,* **60,** 603–619.

Sanders R.W. & Porter K.G. (1988) Phagotrophic phytoflagellates. In: *Advances in Microbial Ecology.* (Ed K.C. Marshall), pp. 167-192. Springer US, Boston, MA.

Schippers P., Verschoor A.M., Vos M. & Mooij W.M. (2001) Does "supersaturated coexistence" resolve the "paradox of the plankton"? *Ecology Letters,* **4,** 404-407.

Striebel M., Behl S. & Stibor H. (2009) The coupling of biodiversity and productivity in phytoplankton communities: consequences for biomass stoichiometry. *Ecology,* **90,** 2025-2031.

Tikkanen T. & Willén T. (1992) *Växtplanktonflora,* Statens Naturvårdsverk (in Swedish).

Tilman D., Knops J., Wedin D., Reich P., Ritchie M. & Siemann E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science,* **277,** 1300-1302.

Utermöhl H. (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitteilungen der Internationalen Vereinigung für theoretische und angewandte Limnologie,* **9,** 1-38.

Violle C., Navas M.-L., Vile D., Kazakou E., Fortunel C., Hummel I. & Garnier E. (2007) Let the concept of trait be functional! *Oikos,* **116,** 882-892.

Weithoff G. (2003) The concepts of 'plant functional types' and 'functional diversity' in lake phytoplankton – a new understanding of phytoplankton ecology? *Freshwater Biology,* **48,** 1669-1675.

Wood S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology),* **73,** 3-36.

Zwart J.A., Solomon C.T. & Jones S.E. (2015) Phytoplankton traits predict ecosystem function in a global set of lakes. *Ecology,* **96,** 2257-2264.
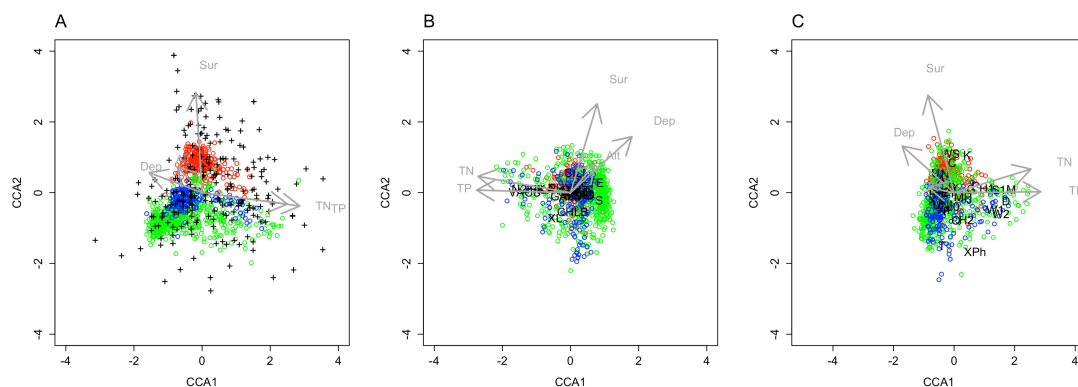
Legends for Figures

Fig. 1 Canonical Correspondence Analysis (CCA) predicting phytoplankton composition by local environmental predictors based on (A) genera (genus composition - GC); (B) functional trait categories (FT composition - FTC), and (C) response groups (RG composition - RGC) *sensu* Reynolds (n=929). Abbreviations: Sur: lake surface area, Alt: altitude, Dep: mean water column depth, TN: total nitrogen, TP: total phosphorus. Color codes: green: Norwegian, blue: Swedish, red: Finish lakes. Abbreviations for FTs (B): see Table 1. Abbreviation for FGs (C): alphabetic letters of response groups according to Reynolds et al. (2002)
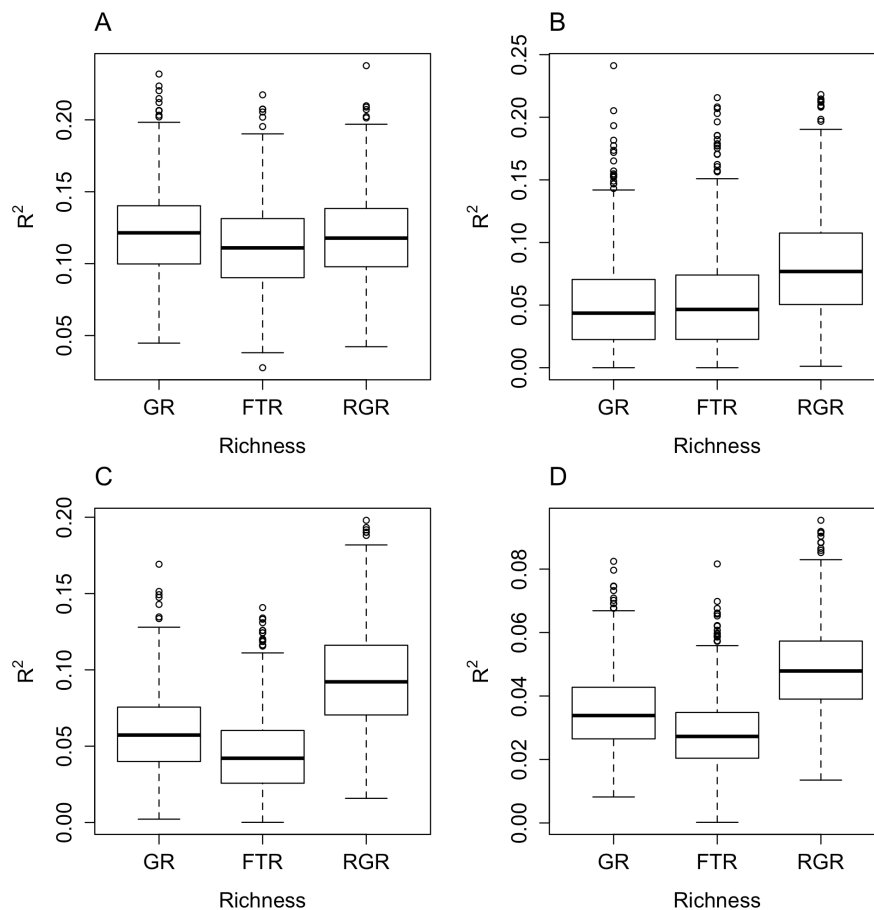
Fig. 2 Boxplots of 999 bootstrapped coefficients of determination of linear models predicting resource use efficiency (RUE) from genus richness (GR), number of unique combinations of functional trait categories (FTR), and response group richness *sensu* Reynolds (RGR) in (A) the Norwegian; (B) the Swedish; (C); the Finish; and (D) in the pooled dataset including all three Fennoscandian countries. Significance levels of Wilcoxon rank sum tests comparing the bootstrapped values of coefficients of determination based on the functional (FTR, RGR) and taxonomic (GR) approaches are given in Table 3.
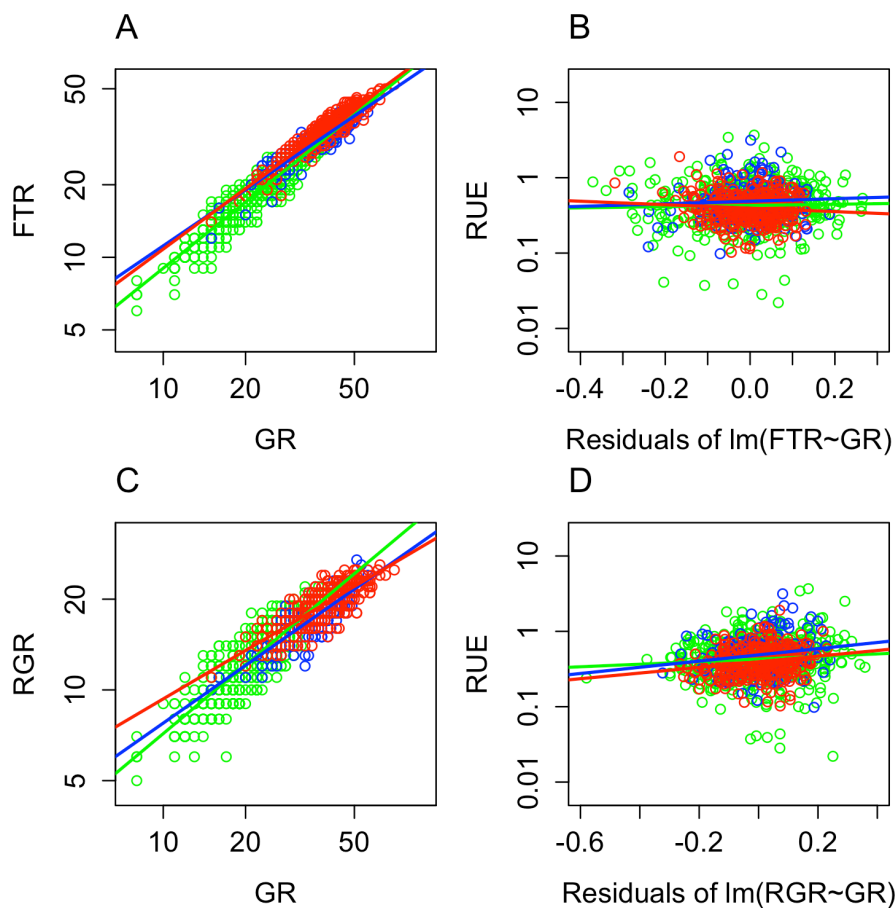
Fig. 3 Linear regressions in each individual Fennoscandian country between (A) the number of unique combinations of functional trait categories (FTR) and genus richness (GR); (B) RUE and the residual variation of FTR unexplained by GR; (C) response group richness *sensu* Reynolds (RGR) and genus richness (GR); and (D) RUE and the residual variation of RGR unexplained by GR. Color codes: green: Norwegian, blue: Swedish, red: Finish lakes. For resource use efficiency (RUE), see Ptacnik et al. (2008b). The number of samples are identical to those indicated in Table 2

Legends for Tables

Table 1 Morphological, physiological and behavioral traits of phytoplankton according to Weithoff (2003) and Litchman & Klausmeier (2008)

Traits	Categories	Abbreviation
Morphological traits		
Biovolume	<100 μm^3, 100-1,000 μm^3, 1,000-10,000 μm^3, >10,000 μm^3	Sma, Med, Lar, Xla
Greatest Axial Linear Dimension (GALD)	< 35 μm or > 35 μm	Gal
Life form	single-celled, colonial, filamentuous	Sin, Col, Fil
Physiological traits		
N_2-fixation	yes/no	N2f
Si requirements	yes/no	Sil
Mixotrophy (phagotrophy)	yes/no	Mix
Heterotrophy	yes/no	Het
Pigment composition	Chl-*b*, Chl-*c*, phycobiliproteins	ChlB, ChlC, Phy
Behavioral traits		
Motility	presence/absence of flagella	Fla
Vacuolated	yes/no	Vac

Table 2 Regression coefficients of linear models predicting resource use efficiency (RUE) from (A) genus richness (GR); (B) the number of unique combinations of functional trait categories (FTR); and (C) response group richness *sensu* Reynolds (RGR) in each individual Fennoscandian country and in the entire dataset. Significance levels for each coefficient are given in brackets. NO: Norwegian lakes, SE: Swedish lakes, FI: Finish lakes, All: the entire dataset including the three individual countries

Region	n	a	b
(A)		RUE=a+b*ln(GR)	
NO	537	-2.963 (<0.001)	0.695 (<0.001)
SE	158	-2.560 (<0.001)	0.517 (<0.01)
FI	321	-2.533 (<0.001)	0.438 (<0.001)
All	1016	-1.708 (<0.001)	0.257 (<0.001)
(B)		RUE=a+b*ln(FTR)	
NO	537	-2.833 (<0.001)	0.691 (<0.001)

Abonyi, A., Z. Horváth & R. Ptacnik, 2018. Functional richness outperforms taxonomic richness in predicting ecosystem functioning in natural phytoplankton communities. Freshwater Biology 63(2):178–186 doi:10.1111/fwb.13051.

SE	158	-2.844 (<0.001)	0.626 (<0.01)
FI	321	-2.369 (<0.001)	0.409 (<0.001)
All	1016	-1.581 (<0.001)	0.231 (<0.001)
(C)		RUE=a+b*ln(RGR)	
NO	537	-2.811 (<0.001)	0.775 (<0.001)
SE	158	-3.177 (<0.001)	0.859 (<0.001)
FI	321	-3.403 (<0.001)	0.836 (<0.001)
All	1016	-1.953 (<0.001)	0.405 (<0.001)

Table 3 Median values of the 999 bootstrapped coefficients of determination of linear models predicting resource use efficiency (RUE) from genus richness (GR), number of unique combinations of functional trait categories (FTR), and response group richness *sensu* Reynolds (RGR). The significance levels of Wilcoxon rank sum tests comparing the bootstrapped regression coefficients between the approaches are also given. NO: Norwegian lakes, SE: Swedish lakes, FI: Finish lakes, All: the entire dataset including the three individual countries.

Region	lm(RUE~GR)	lm(RUE~FTR)	Wilcoxon (GR, FTR)	lm(RUE~RGR)	Wilcoxon (GR, RGR)	Wilcoxon (FTR, RGR)
	median R^2	median R^2	p	median R^2	p	p
NO	0.1199	0.1099	<0.001	0.1160	n.s.	<0.01
SE	0.0439	0.0442	n.s.	0.0733	<0.001	<0.001
FI	0.0564	0.0394	<0.001	0.0912	<0.001	<0.001
All	0.0337	0.0261	<0.001	0.0476	<0.001	<0.001

Table 4 Regression coefficients predicting resource use efficiency (RUE) based on genus richness (GR) plus the residual variations of functional richness from the linear models of (A) lm(FTR~GR), whereas FTR is the number of unique combinations of functional trait categories; and (B) lm(RGR~GR), whereas RGR is the response group richness *sensu* Reynolds. Significance levels referring to the probability of the coefficients are given in brackets. NO: Norwegian lakes, SE: Swedish lakes, FI: Finish lakes, All: the entire dataset including the three countries

Region	n	b	c	Adjusted R^2
(A)		RUE=a+b*ln(GR)+c*Residuals of lm(FTR~GR)		GR+Res.FTR
NO	537	0.695 (<0.001)	0.183 (n.s.)	0.116
SE	158	0.517 (<0.01)	0.390 (n.s.)	0.035
FI	321	0.438 (<0.001)	-0.531 (n.s.)	0.058
All	1016	0.257 (<0.001)	-0.386 (<0.05)	0.037
(B)		RUE=a+b*ln(GR)+c*Residuals of lm(RGR~GR)		GR+Res.RGR
NO	537	0.695 (<0.001)	0.394 (<0.05)	0.123
SE	158	0.517 (<0.01)	0.949 (<0.05)	0.063
FI	321	0.438 (<0.001)	0.864 (<0.001)	0.087
All	1016	0.257 (<0.001)	0.539 (<0.001)	0.047