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Functionally similar species have similar dynamics

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Summary

1. Improving the mechanistic basis of biodiversity–ecosystem function relationships requires a better understanding of how functional traits drive the dynamics of populations. For example, environmental disturbances or grazing may increase synchronization of functionally similar species, whereas functionally different species may show independent dynamics, because of different responses to the environment. Competition for resources, on the other hand, may yield a wide range of dynamic patterns among competitors and lead functionally similar and different species to display synchronized to compensatory dynamics. The mixed effect of these forces will influence the temporal fluctuations of populations and, thus, the variability of aggregate community properties.

2. To search for a relationship between functional and dynamics similarity, we studied the relationship between functional trait similarity and temporal dynamics similarity for 36 morphotypes of phytoplankton using long-term high-frequency measurements.

3. Our results show that functionally similar morphotypes exhibit dynamics that are more synchronized than those of functionally dissimilar ones. Functionally dissimilar morphotypes predominantly display independent temporal dynamics. This pattern is especially strong when short time-scales are considered.

4. Negative correlations are present among both functionally similar and dissimilar phytoplankton morphotypes, but are rarer and weaker than positive ones over all temporal scales.

5. *Synthesis*. We demonstrate that diversity in functional traits decreases community variability and ecosystem-level properties by decoupling the dynamics of individual morphotypes.

Key-words: compensatory dynamics, competition, environmental forcing, functional diversity, functional traits, grazing, phytoplankton, plant population and community dynamics, synchrony, temporal dynamics

Introduction

Communities are structured in such a manner that a variety of species can share specific ecological properties and functional traits (Yodzis & Winemiller 1999; Cadotte, Bradley & Oakley 2008) – where a functional trait is defined as any measurable feature of an individual affecting its fitness directly or indirectly (Lavorel *et al*. 1997; Violle *et al*. 2007). Functional traits have been extensively used to describe, group and rank species according to their functions (Díaz & Cabido 2001; McGill *et al*. 2006) and, hence, their influence on ecosystem-level properties. However, the translation of functional traits into temporal dynamics remains a challenge, because of the many functional traits possessed by a species and the complex, non-linear ways in which these can interact with a changing environment. A promising avenue for studying the translation problem uses long-term data to elucidate the relationship between species' functional traits and their dynamics. Comprehending this relationship contributes to the understanding of how species impact the variability of aggregate community properties. If species with different functional traits exhibit unrelated dynamics through time, the community variability will be substantially lower than that of functionally less-diverse communities (Tilman 1996; Hooper *et al*. 2005). Here, we study the relationship between functional similarity and temporal dynamics similarity of phytoplankton morphotypes in Lake Constance, a temperate lake that follows a seasonal progression in which environmental forcing and competition alternate between cold, more externally driven months and warm, more internally driven months (Sommer *et al*. 1986).

Among the drivers influencing species' temporal dynamics, environmental forcing and competition play a major role (Weiher, Clarke & Keddy 1998). Previous theoretical and empirical research supports the existence of a strong relationship between species' functional traits and their response to environmental forcing. Species' functional traits are robustly related to fundamental and realized niches (McGill *et al*. 2006), and closely related species are known to co-occur more

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often than expected by chance (Díaz, Cabido & Casanoves 1998; Webb & Peart 2000; Helmus *et al.* 2010), suggesting that phylogenetically similar species co-occur in time or space because they are more likely to possess the traits that increase fitness (Bruggeman 2011). Alternatively, we would expect species that are functionally very different to show independent (uncorrelated) dynamics, because of varied responses to their environment.

Competition, on the other hand, may be observed in phytoplankton communities among functionally similar and different species as all species compete (to a varying extent) for the same essential resources (e.g. light and phosphorous are essential for photosynthesis and growth), regardless of their functional traits (Huisman *et al.* 1999). Competition may therefore yield a large range of dynamical patterns among competitors (Ricklefs 1987; Vandermeer 2004; Loreau & de Mazancourt 2008; Gonzalez & Loreau 2009). The traditional belief that competition should yield negative covariation among competitors (Hutchinson 1959; MacArthur & Levins 1967) was recently challenged by Loreau & de Mazancourt (2008), who showed that this result largely depends on the intensity of competition. Furthermore, competition-driven covariation can happen at different temporal scales than environmentally driven covariation so that species may show similar dynamics at one time-scale and different dynamics at another (Keitt & Fisher 2006; Vasseur & Gaedke 2007). Hence, detecting the relationship between functional and dynamic similarity requires statistical methods adequate to resolve patterns at different temporal scales (e.g. Micheli *et al.* 1999; Vasseur, Gaedke & McCann 2005; Downing *et al.* 2008).

We used long-term high-frequency measurements of phytoplankton, for which four functional traits reflecting the most important growth-determining factors (e.g. maximum growth rate, nutrient demands, susceptibility to grazing and sedimentation) were quantified for 36 morphotypes (Weithoff 2003). We determined correlations between the functional trait distances and the temporal dynamics distance of the morphotypes. This allowed us to study whether changes in functional distance are accompanied by changes in the similarity of temporal dynamics and, hence, whether a relationship between the functional traits of the morphotypes and their temporal dynamics exists. Because functional traits may impact the dynamics of populations at different temporal scales, we employ two different methods of time-series analysis (a moving-window correlation analysis and spline fitting) to distinguish short-term variation from general seasonal patterns.

Materials and methods

DATA ACQUISITION

Upper Lake Constance (Bodensee) is a large (472 km^2), deep (depth = 101 m), warm-monomictic temperate lake north of the European Alps. It underwent re-oligotrophication (Gaedke 1998), and mean annual phytoplankton biomass declined by a factor of 2 with phosphorous decline (Rocha *et al.* 2011), indicating that the long-term changes are small compared to the very pronounced seasonal dynamics (morphotypes vary in density by a factor of 10–1000 during the year). Plankton sampling was conducted weekly during the growing season and approximately fortnightly in winter, culminating in 820 sampling dates between 1979 and 1999 (for details see Gaedke 1998; Rocha *et al.* 2011). All measurements are provided per unit area and comprise the biomass within the uppermost water layer from 0 to 20 m depth, which roughly corresponds to the epilimnion and the euphotic zone. We log-transformed (base 2) the biomass measurements to account for their long-tailed residual distribution, given that the seasonal variation covered approximately two orders of magnitude (Gaedke 1998). In the present study, we use a taxonomic resolution of 36 morphotypes of phytoplankton comprising individual species or higher taxonomic units that are functionally identical or very similar under the functional classification employed here. We treated the non-detection of a morphotype at a particular sampling date as missing value. Morphotypes were classified based on their functional traits as well as upon their dynamics, as described below.

FUNCTIONAL CLASSIFICATION OF MORPHOTYPES

Selection of functional traits

For phytoplankton, net growth is the sum of intrinsic growth, sedimentation, grazing losses and some other typically less important loss factors. Building on a previous study on functional diversity in Lake Constance, we selected four traits reflecting these three main processes that determine the waxing and waning of individual populations, and the 36 morphotypes were classified according to volume, shape, motility and silica use (Weithoff 2003) [nitrogen fixation (Gaedke 1998) and mixotrophy were excluded owing to a lack of relevance (Gaedke 1998; cf results)].

First, according to allometric theory, size strongly influences many physiological activities such as maximum growth rate. For both colony-forming and single-cell phytoplankton morphotypes, the classification was performed according to individual cell size. Such a classification optimizes the predictability of weight-specific metabolic rates from cell size rather than the vulnerability to grazing and implies that edible and less-edible phytoplankton morphotypes strongly overlap in size. Secondly, the shape of a cell or colony (its surface-to-volume ratio) is important with respect to its ability to absorb nutrients, to its susceptibility to sedimentation and to filter-feeding zooplankton grazing. In combination with cell volume, a suitable measure for these processes is the longest linear dimension (LLD) of the organism. We log-transformed (base 2) the cell volumes and the LLD values to account for their large range (covering over 4 and 3 orders of magnitude, respectively) and to obtain a linear effect of characters. Third, motility was considered because mobile organisms can counteract sedimentation and migrate into favourable strata. In addition, motility affects nutrient deficiency as the movement of cells minimizes the hydrate envelope and, thus, the diffusive boundary layer for nutrients around the cells. Motility was classified as follows: 0, non-motile; 0.5, buoyancy regulation (through gas vacuoles); and 1, flagellated morphotypes, which can move in three-dimensional space (Lee 1999). Fourth, silica use was considered because it may be a limiting nutrient in Lake Constance. The use of silica decreases the carbon demand for cell walls and increases the specific weight, leading to higher sedimentation rates. Silica use can be classified as follows: 1 for diatoms, which need silica for their frustules; 0.5 for Chrysophyceae and Synurophyceae, which form statospores (e.g. Ochromonas), bristles and scales (e.g. Synura or Mallomonas); and 0 for all morphotypes that do not use silica (Lee 1999).

Distance matrix based on the traits

We have mixed variable types (continuous, ordinal and binary functional traits), and we thus opted for Gower's general similarity coefficient (Gower 1971). Gower defines a pair-wise distance value d_{jk} between two morphotypes, as follows:

$$d_{jk} = \frac{1}{N}\sum_{i=1}^{N} \mathrm{abs}\left(\frac{x_{ij} - x_{ik}}{\max(x_i) - \min(x_i)}\right)$$

where N is the number of functional traits considered, x_{ij} the value of trait i for species j and x_{ik} the value of the trait i for species k. It defines a pair-wise distance value, ranging from 0 to 1, in which 1 represents the highest functional distance amongst our morphotypes. We obtained a distance matrix for all pairs of morphotypes based on the four functional traits using R 2.9.0 (R Development Core Team 2009).

DYNAMICAL CLASSIFICATION OF MORPHOTYPES

Moving-window correlation of time series

Recently, progress has been made in quantitative methods that detect compensatory dynamics, and the importance of considering the variability at different temporal scales has been emphasized (Micheli *et al.* 1999; Downing *et al.* 2008 and reviewed in Gonzalez & Loreau 2009). With that in mind, we employed a non-overlapping moving-window Pearson correlation to search for the relationship between the temporal dynamics of pairs of morphotypes. The time-window length determines the portion of variance to be assessed. As the functional traits of morphotypes may act on their dynamics at different temporal scales, we examined time windows of 45-, 90-, 120-, 180- and 365-days, because, as revealed by spectral analysis (Rocha *et al.* 2011), cycles with these lengths generally contribute the most to the total variance present in total phytoplankton biomass and chlorophyll concentration.

We obtained a correlation value for each one of the non-overlapping windows along the time series of the morphotypes. To collapse this into a single measure of relatedness between the two time series, we calculated the mean of this series of correlations, hereafter referred to as 'ensemble average'. We included the correlations into the ensemble average only for windows that comprised at least four sampling dates in which both morphotypes were present, making sure that correlations are meaningful. We included the ensemble average of a given pair of morphotypes in the dynamics distance matrix only if at least 25% of all possible windows met this criterion. Otherwise, we considered the ensemble average as a missing value in the distance matrix. These criteria inevitably cause longer time windows to present more pairs of morphotypes with valid ensemble averages. We have accounted for this problem and also examined the results for only the pairs that are valid for all windows, which are presented separately in Fig. S1 in Supporting Information. For each time window, we obtained a distance matrix based on the ensemble average. Distance values may range from −1 (perfect compensatory dynamics) to 1 (perfectly synchronized), passing through 0, if the time series are entirely independent. All metrics were coded using R 2.9.0.

Spline fitting

In contrast to the moving-window correlation approach, which shows the relationship between the dynamics of morphotypes at shorter temporal scales, smoothing spline analysis shows the relationship between the recurrent seasonal patterns of morphotypes (Rocha *et al.* 2011).

We calculated the splines for the data points (t_i, x_i), t_i being the time lapsed since 1 January of the running year. Smoothing splines are estimated by maximizing the penalized likelihood function (Wahba 1990). The random effects are generic and are modelled parametrically by assuming that the covariance function depends on a parsimonious set of parameters. A generalized cross-validation was used for determining the smoothing parameter, which controls the trade-off between data fit (first term) and smoothness (second term) and is optimal when it minimizes the expected prediction error (Craven & Wahba 1978). For this analysis, we used the package *mgcv*in R 2.9.0. As an example, we show the spline fitting to the raw data of the morphotype *Synedra* spp. (Fig. S2). We obtained a distance matrix between pairs of morphotypes based on the Pearson correlation of the spline estimates of the individual morphotypes for times t_i.

COMPARISON OF THE DISTANCE MATRICES OBTAINED

We compare the distance matrix based on the functional traits with the set of six matrices based on the dynamics (five different time windows plus the splines) by using a Mantel test (package *vegan* in R 2.9.0). This test determines the correlation between the two distance matrices (the Mantel r, ranging from −1 to 1) and estimates the significance of the relationship using a permutation test. We tested the Mantel r observed for each comparison against the null hypothesis of $r = 0$ using 10 000 permutations. The square of the Mantel r quantifies the amount of shared variance between the two distance matrices, and it neither assumes nor provides any information about the distribution of observations around the trend.

INVESTIGATION OF RELATIVE TRAIT-IMPORTANCE

In the standard analysis, equal weight was given to each trait when computing the functional trait matrix based on the Gower distance. In addition, we performed an *a posteriori* test to determine which traits have the greatest ability to explain the similarities in population dynamics. Because our data generally indicated a negative correlation between functional trait similarity and temporal dynamics similarity, we attributed to each trait a weight and searched for the set of weights resulting in the most negative Mantel r (following the routine of Byrd *et al.* 1995). We assume that traits that obtain weights different from 0 for the majority of dynamics measures are important for generating dynamic patterns (Table 1). This analysis was performed using R 2.9.0.

Table 1. Minimization of mantel r and weights of traits yielding the strongest negative correlation

	Traits				
	Cell volume	LLD	Silica use	Motility	Mantel r
Window correlation (days)					
45	0.3	0.31	0.32	0.07	−0.49**
90	0.3	0.39	0.26	0.05	−0.28**
120	0.45	0.26	0.18	0.11	−0.29**
180	0.38	0.36	0.21	0.05	−0.29**
365	0.31	0.41	0.22	0.06	−0.27**
Splines	0.25	0.67	0.07	0	−0.24*

LLD, longest linear dimension. $^*P < 0.05$, $^{**}P < 0.01$.

Results

Functionally similar morphotypes presented more similar dynamics than functionally different morphotypes. The distance matrix based on functional traits was negatively correlated with the distance matrices based on the moving-window correlations (Mantel *r* of −0.46, −0.24, −0.23, −0.24, −0.2, for 45, 90, 120, 180 and 365-day windows, respectively, all with $P < 0.001$), showing that the distance matrices share between 4% and 21% of their variance (Fig. 1a–e). In addition to the significant Mantel *r*'s, we observe a trend in the graphs showing that the negative relationship is generated by positive ensemble averages when morphotypes are similar, decaying to ensemble averages close to 0 when morphotypes are different. The ensemble averages among individual pairs of morphotypes were mainly positive and only occasionally weakly negative. The Mantel *r* was influenced by the time-scale considered, and longer windows led to a weaker correlation and a smaller portion of shared variance between the morphotypes' distance in traits and their distance in dynamics.

As longer time windows comprise more sampling dates, a larger number of morphotype pairs contribute to the Mantel test, which may lead to differences based only on morphotype composition. To control for this, we performed all tests using matrices comprising all data and matrices comprising only the morphotype pairs present at all window lengths. Although the results (e.g. Mantel *r* tends to decrease with increasing window lengths) do not qualitatively change when fewer morphotype pairs contribute, the pattern between the functional traits and dynamics of the morphotypes is strengthened by the exclusion of the less-frequent morphotypes (the distance matrix based on traits shares 11–21% of its variance with the distance matrices based on temporal dynamics when focusing on the most frequently abundant pairs of morphotype). We not only incorporated all available morphotype pairs in the main results, but included results from the more restrictive inclusion rules in Fig. S1.

Splines depict a very smooth average annual pattern for the individual morphotypes in contrast to the biomass dynamics on which the moving-window correlations are based (Fig. S2).

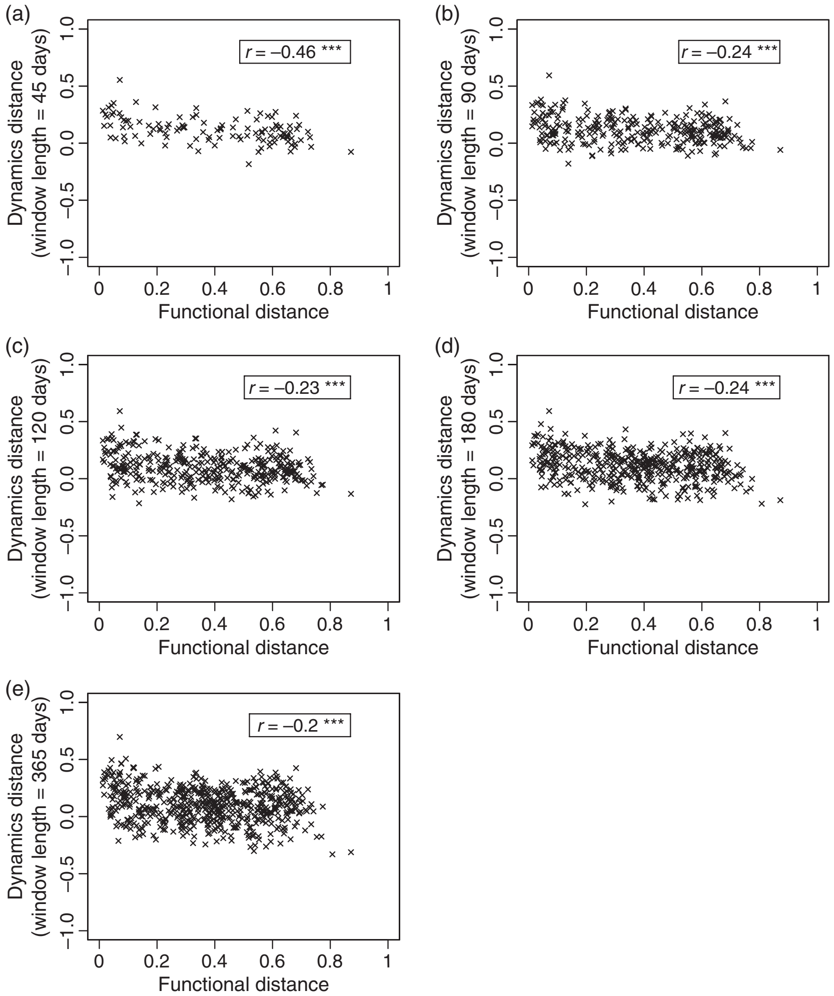

Fig. 1. Plots of functional trait distance vs. temporal dynamics distance at different temporal scales. Functional trait distances are measured for pairs of morphotypes using the Gower distance, and temporal dynamic distance is based on a moving-window correlation of window length (a) 45 days, (b) 90 days, (c) 120 days, (d) 180 days and (e) 365 days. The values of Mantel *r* are shown in the box within the plot area, and ***means $P < 0.001$.

For this reason, splines of pairs of morphotypes exhibit considerably higher absolute correlations ranging from near −1 to near 1 (Fig. 2). The distance matrix based on the splines is not significantly correlated with that based on the functional traits, and the values of the correlation coefficients do not decline with increasing functional distance. This suggests that different functional characteristics may result in similar overall annual dynamics and *vice versa*.

We performed an *a posteriori* test of the importance of individual traits for the relationship between functional trait similarity and temporal dynamics similarity. A null weight was attributed to mixotrophy in all cases, which led to the exclusion of this trait initially considered in the analysis. Hence, all analyses were performed using only the set of the four traits presented in our 'Materials and methods' section. Independently of the measure of dynamics distance, the highest weight was in all cases attributed to one of the two traits: either cell volume or LLD (Table 1). When summed, these two traits received a weight of at least 0.6. Aside from mixotrophy, the lowest weights were consistently attributed to the functional trait motility.

Discussion

WINDOW CORRELATION VS. SMOOTHING SPLINE ANALYSIS

Our results show that morphotypes with high functional trait similarity present dynamics that are more similar than those of dissimilar morphotypes. This relationship weakens as the time-scale over which correlations are determined increases (Fig. 1a–e and Fig. S1). Accordingly, the functional traits had no impact on the mean annual pattern of the dynamics of the morphotypes (depicted by the spline correlations, Fig. 2). These findings suggest that morphotype functional traits are more strongly driving the responses to short-term changes, such as those caused by light and nutrient availability, vertical mixing intensity, sedimentation and grazing pressure, which greatly influence phytoplankton dynamics in Lake Constance (Gaedke 1998; Huber & Gaedke 2006). The lack of a relationship at the annual scale suggests that some recurrent abiotic forces (e.g. annual deterioration of the underwater light climate, deep mixing) and biotic forces (e.g. intensive grazing during the clear water phase) affect all morphotypes in a similar manner, regardless of the functional traits we included here. At this scale and disturbance level, the potential for functional traits to drive differential responses is low, suggesting that considering the total variability in the temporal dynamics (and not only the average annual pattern) is fundamental to uncovering relationships between species' functional traits and the environment. Moreover, it indicates that the relationship between trait similarity and dynamics similarity is not constant throughout the year.

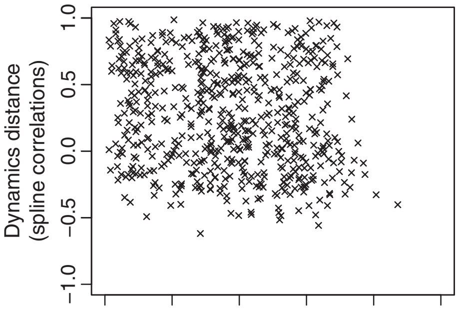

Fig. 2. Plots of functional trait distance vs. temporal dynamic distance depicted by the correlation of splines fit to the annual seasonal patterns of the morphotypes. Mantel *r* is not significant.

IMPORTANCE OF FUNCTIONAL TRAITS

Despite a significant correlation, the percentages of shared variance between the distance matrix based on traits and distance matrices based on temporal dynamics are rather low, which may arise for two reasons. First, a multitude of functional traits may drive dynamics at a variety of different temporal scales, making the functional classification of morphotypes challenging. We used the functional traits that were considered most relevant for our morphotypes (Weithoff 2003); however, these are obviously an incomplete subset of the set of traits actually impacting dynamics. Given this limitation, our results are conservative and reassuring of an existent relationship. Secondly, morphotypes that occur less frequently in the community contribute less to the pattern than more frequent ones (Fig. 1 and Fig. S1), which can be due to the fact that fewer values are taken into account in the ensemble average, decreasing its reliability.

Our investigation of the importance of individual traits for determining morphotype dynamics showed that all traits but mixotrophy contributed to the relationship between functional and dynamics similarity, leading to the exclusion of this trait in the final analysis. This may be due to the fact that mixotrophy is only relevant during a short time during the year and increased during the long-term period of re-oligotrophication (1979–2000) (Kamjunke, Henrichs & Gaedke 2007) and that our methodology, which averages within the year and across all years, is not suitable for grasping these changes. Motility is consistently attributed a low weight, showing a weak effect on the dynamics. This functional trait is direct or indirectly associated with several factors that may have a temporally variable impact on dynamics (e.g. nutrient deficiency, sedimentation, probability of predator encounter). Cell size and shape were the most important traits, when summed, for all measures of temporal dynamics. This is in line with numerous other studies showing that size is the single most informative attribute of the morphotypes (Reiss 1991; Litchman *et al.* 2010; cf. Materials and methods). Interestingly, the relationship between functional similarity calculated for individual functional traits and dynamics similarity was not significant for any of the four traits considered here, showing that the combined effect of these functional traits is decisive for predicting dynamics similarity (results not shown).

FUNCTIONAL DISTANCE AND THE RATE OF COMPETITIVE EXCLUSION

Species with similar functions are expected to have similar competitive abilities, slowing the rate at which competitive replacement may occur (Agren & Fagerstrom 1984). Alternatively, this process should be faster among functionally more different species. This alone could lead to a negative Mantel *r*, as negative covariances among functionally similar species would only be observed over long time-scales but could be present among functionally different species on the short-term patterns studied here. We accounted for this by aggregating very similar species into one morphotype and found no indication of differential speed of competitive replacement among morphotypes, as negative correlations were present equally among functionally similar and different morphotypes. This confirmed that the degree of synchrony encountered among functionally similar morphotypes is conferred by functional trait similarity and is a real feature of the dynamics. It has important consequences at this time-scale for ecosystem-level processes regardless of our ability to detect slow competitive replacement.

COMPARISON WITH PREVIOUS WORKS

Temporal dynamics of morphotypes are mainly positively correlated, but negative correlations also occur, especially over long time-scales. This is in agreement with previous studies, which revealed that synchronous dynamics dominated within the phytoplankton community in Lake Constance and that at certain instances some compensatory dynamics were present; notably, negative correlations were found among cryptomonads and non-cryptomonads during extended spring blooms (Tirok & Gaedke 2007), and during the growing season when grouping the entire phytoplankton into edible and less-edible and eliminating (Vasseur, Gaedke & McCann 2005; Vasseur & Gaedke 2007) or reducing (Huber & Gaedke 2006) the impact of the annual cycle. In accordance with Huber & Gaedke (2006) who showed that grazing represents an important environmental driver in our system, which desynchronizes pairs of edible and less-edible phytoplankton during the growing season, we also found negative correlations among these pairs for the most frequently encountered morphotypes. These negative correlations spread along the whole gradient of the functional distance employed here, which is because of the fact that our functional classification of morphotypes not only is restricted to grazing susceptibility but also considers nutrient demands, motility and susceptibility to sedimentation. In contrast to previous studies, we opted to consider the total variance present in the morphotype time series, which made our approach unbiased but led to a weakening of negative correlations previously identified for Lake Constance phytoplankton. Considering only portions of the variance and the effects of seasonality on this relationship represents a promising area for future research.

The prevalence of synchronized dynamics among individual morphotype pairs relative to compensatory dynamics in our results concord with the study by Houlahan *et al.* (2007), which showed that synchronous dynamics are far more common in communities of competing species. We cannot, however, reject that compensatory dynamics exist in our community, as we use species' absolute abundances, which are expected to covary with fluctuations in community size even if competitive interactions are present (Loreau & de Mazancourt 2008). In Lake Constance, this is highly relevant as the community biomass varies by approximately two orders of magnitude (Rocha *et al.* 2011). Moreover, our results are in agreement with previous studies, which show that closely related species are likely to occur in similar habitats because of environmental filtering (Díaz, Cabido & Casanoves 1998; Webb & Peart 2000; Helmus *et al.* 2010). These studies used phylogenetic relatedness as a proxy for trait information, when predicting community and species responses to their environment, assuming that closely related species exhibit similar responses to the environment. Phytoplankton traits are to some extent evolutionarily conserved, but deviations and exceptions exist (Bruggeman 2011), and there can be a large discrepancy between phylogenetic relatedness and the expression of phenotypic traits. By combining highly resolved temporal dynamics with species traits rather than phylogeny, our study enriches our understanding of the mechanisms directly determining species' temporal dynamics.

Conclusions

For the phytoplankton community in Lake Constance, we show that differences in morphology, behaviour, physiology and susceptibility to grazing imply differences in temporal dynamics. With increasing functional differentiation, dynamics move from more synchronized to independent, suggesting that a more diverse set of traits will reduce variability of community-level properties such as biomass production, respiration or remineralization. Moreover, our data suggest that the functional relationships among species can be used to assess the impact of the loss of functional diversity. We show that a loss of functional diversity would lead to increased variability at the community level. Understanding how functional differences drive differences in dynamics in this and other systems will ultimately lead to better predictions for the consequences of anthropogenic changes.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Figure S1. Plots of functional trait distance vs. temporal dynamics distance at different temporal scales, only for the pairs of species that are valid for all window lengths.

Figure S2. Spline (black line) and raw time series (grey dots) of *Synedra* spp. morphotype.