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UCBL, Université Claude Bernard - Lyon 1, France
UPS, Université Paul Sabatier- Toulouse 3, France
ECOLOGIC, Ecologic GmbH Institut für Internationale und Europäische Umweltpolitik, Germany
EC-ERC, Commission of the European Communities - Directorate General Joint Research Centre, Italy
UD, University of Debrecin, Hungary
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BIOFRESH

Biodiversity of Freshwater Ecosystems: Status, Trends, Pressures, and Conservation Priorities

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Large scale collaborative project

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Introduction

Aim of the Deliverable was to produce a Manuscript on impacts of climate change on ecosystem functioning under Task 5.6. Impact of freshwater biodiversity change on ecosystem function (European, local scale).

The first manuscript summarizes results from a long-term study of the relationship between phytoplankton biodiversity and ecosystem functioning. We present models of ecosystem functions- algal biomass and nitrogen and phosphorous resource use efficiency, linking seasonal variability in ecosystem functioning to that in various physical, chemical, and diversity related drivers. Our study indicates, that throughout the seasons, phytoplankton biomass and nitrogen resource use efficiency are mainly linked to the diversity of phytoplankton communities. In contrast, resource supply determines the phosphorous use efficiency, except for spring with species evenness as the central driving factor. Overall, an increase in species evenness- regardless whether taxonomic or functional, is accompanied with a decrease in ecosystem functioning. Further, the shape of the ecosystem response to a particular driver and the temporal patterns in drivers' relative importance are shown to manifest larger variability across seasons, than across ecosystem functions

The second manuscript summarizes results from standardized and comprehensive field experiments conducted in streams across geographical regions. The presented data set reveals a remarkable convergence not only of litter decomposition rate but also of fungal decomposer and detritivore dynamics across climatic zones when data are normalized for temperature. This is an important advance towards a unified quantitative model of decomposer dynamics, litter decomposition as a central biogeochemical process, and organic matter turnover in stream networks in general. Such syntheses are essential given the recently discovered, unexpectedly large significance of streams in the global carbon cycle, in which particulate organic matter dynamics are not explicitly considered.

The relationship between phytoplankton diversity and ecosystem functioning: Testing ecological theory with observational data

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Introduction

One of the most crucial aspects of recent global change is the rapid decline of species diversity and its consequences for ecosystem functioning. The relationship between biodiversity and ecosystem function (EF) as a central issue in ecology became a fundamental research topic in ecology in the past decades. Traditionally, questions have been addressed by focusing on possible drivers such as biotic interactions, environmental fluctuations and natural or anthropogenic disturbances of observed patterns in species abundances, distributions and diversity in natural ecosystems. Numerous studies have addressed the relationship between single species or whole assemblages on ecosystem processes over the years, but they, however, mostly have not considered the role of biological diversity per se (Raffaelli et al., 2005) until consequences of BD loss on EF become emerging and made those consequences to the focal point of research interest. In this context, long-term grassland experiments by Tilman et al. (2001) were first to show that diversity loss is positively correlated with biomass loss. Meanwhile there is cumulative evidence, that the relationship between BD and EF can be transferred to various habitats and trophic levels (Hooper et al. 2005, Worm et al. 2006, Filip et al. 2012). However, the debate whether species diversity is a cause or a consequence of ecosystem processes is still in progress (e.g. Huston 1997; Grime 1998; Loreau et al. 2001). With the progress of this debate the possibility, that species richness can be both a cause of realized biomass production and a consequence of resource supplies that limit the potential production of a system received cumulative attention by heuristic studies investigating how BDEF relationships might operate at the same temporal and spatial scale are not contradictory as it was shown, that simultaneously resource supply can drive diversity and diversity can drive e.g. resource use (Loreau et al. 2001; Schmid 2002; Worm and Duffy 2003). Hence, changes in e.g. nutrient supply (water chemistry) or diversity are predicted to affect the outcome of EF, especially when ecosystem processes (e.g. primary production) are maintained by only a few species (Tilman 1999, Vinebrooke et al. 2003).

We examined various physical water parameters, chemical water parameters, parameters related to taxonomic diversity and those related to functional diversity as potential drivers of the following ecosystem functions: total algal biomass, resource use efficiency for phosphorous and nitrogen and uptake efficiency for phosphorous and nitrogen. The aim of our study was to determine the importance of possible EF drivers within seasons and in the long-term.

Study site and methods

Study site: Müggelsee is a shallow, eutrophic, polymictic lake in southeastern Berlin, Germany (52°26' N, 13°39' E) with an average retention time of 40 days. The lake has an area of 7.3 km², a mean depth of 4.9 m and a maximum depth of 8 m. Further physiographical and limnological characteristics of the lake are given in Driescher et al. (1993). Müggelsee has been extensively

studied with respect to responses toward variability in the climate and in external nutrient loading over the past three decades (Köhler et al. 2005, Adrian et al. 2006).

Data sampling and pre-processing: A set of physical, chemical and biological parameters was sampled at weekly (growing season) to biweekly intervals (winter), except for water temperature which was recorded daily between 8:00 and 9:00 AM. We aggregated daily water temperature measurements to the weekly scale and set the temperature to 0°C for periods with full ice cover. We avoided missing values replacement, except for the water temperature and transparency where we applied linear interpolation to fill data gaps (3% and 8% of the total data sample for water temperature and transparency, respectively). We excluded the sampled parameters with numerous missing values and those with negligible temporal variation from the analysis scope (i.e. conductivity, oxygen concentration, pH, dissolved organic carbon). We restricted our analyses to the time period from 1994 to 2010, a period not confounded by changes in the trophic state of the lake nor by changes in the taxonomic resolution of the phytoplankton analyses (Köhler et al. 2005). Given marked changes in phenology during the past three decades (Gerten & Adrian 2000, Adrian et al. 2006) seasons were standardized according to cardinal events (Adrian et al. 2006). Hence, spring onset was defined as ice-off date, while summer begins with the clear water phase (maximal Secchi depth after spring algal bloom) and ends in biweek 20 (end of September) as we lack a discrete and reliable biotic or abiotic marker (Wagner & Adrian 2009). There was no ice formation in the winter of 2006/2007, therefore we set the ice-off date to biweek 2, the earliest ice-off date in the past 30 years. Due to the seasonally specific sampling frequencies, differences in the length of the phenology adjusted seasons and data gaps the total number of considered sampling dates was 179, 309, 107 and 99 for spring, summer, autumn and winter, respectively.

Ecosystem functions

We focused on five ecosystem functions (EF): total algal biomass (AlgB; [mg/L]), resource use efficiency for phosphorous (RUE_P) and nitrogen (RUE_N) and uptake efficiency for phosphorous (UE_P) and nitrogen (UE_N) (Table 1). For AlgB calculations we excluded the biomass of all phytoplankton species without any taxonomic classification in the sampling record (on average 27% of total algal biomass), like e.g. organism groups classified as single centric diatoms. RUE_P and RUE_N were calculated as the ratio between AlgB and the soluble reactive phosphorus (SRP, [µg/L]) and the dissolved nitrogen (DN, [mg/L]), respectively. UE_P and UE_N were calculated as the ratio between total phosphorous (TP, [µg/L]) and SRP, and the ratio between total nitrogen (TN [mg/L]) and DN, respectively. SRP is considered to give in practice the best approximation of immediately bioavailable phosphorous fraction (see Scheffer, 1998), and is thus more suitable for our analyses than TP that includes fractions that are not convertible into bioavailable phosphorous.

Potential drivers of ecosystem functioning

We examined various (1) physical water parameters (Phys), (2) chemical water parameters (Chem), (3) parameters related to taxonomic diversity (TD) and (4) those related to functional diversity (FD) as potential drivers of ecosystem functions.

Physical parameters. Water temperature (WT, [°C]) is one of the most important drivers of physical, chemical and ecological processes in freshwater ecosystems (see Caissie 2006). The Müggelsee WT variability has a pronounced annual cycle with up to 6°C in the winter season and up to 28°C in the summer season. Water transparency (Secchi, [m]) generally affects littoral primary production, benthic productivity and population divergence (cf. Bartels et al 2012). The

Müggelsee Secchi depth was highest in summer and autumn, with values up to 5.4m.

Chemical parameters. We considered nitrate (NO_3N , [mg/l]), ammonium (NH_4N , [mg/l]), dissolved inorganic carbon (DIC, [mg/l]) and soluble phosphorous (SP, [$\mu\text{g/l}$]). At our study site NO_3N and NH_4N were highest in the winter (up to 3.09 and 0.81 mg/l, respectively), SP was highest in the autumn (up to 525 $\mu\text{g/L}$), while the DIC was highest in winter (up to 32.9 mg/L). As a side remark, the chemical parameters, which were used to define the EF, such as TP, SRP, TN, and DN were not considered as potential EF drivers. Overall, the ratio between the TN and TP (TN:TP) decreased across the study period, with the downward trend being most pronounced in summer and autumn.

Taxonomic diversity. We calculated taxonomic diversity (TD) as richness and evenness for both, phyto- and zooplankton assemblages (Magurran 2004). For phytoplankton species classified at the genus taxonomic level, the size classes (where available) were used to specify the TD at the species level. Besides the number of adults for the three main mesozooplankton classes (cladocerans, copepods and rotifers) the zooplankton data set included juveniles for each class, considered as independent species due to different feeding spectra and rates compared to the adults.

For phytoplankton species we studied the species level (SRic, SEve) and the class taxonomic level (CRic, CEve), while for zooplankton species we considered only the species level (ZpRic, ZpEve). Contrary to zooplankton richness, the seasonal patterns of phytoplankton species richness manifested a continuous decrease from 1994 to 2001 that was especially pronounced for the summer and spring season. This decline in species richness was mainly driven by species loss of the phytoplankton class Chlorophyceae.

Functional diversity. Phytoplankton functional diversity (FD) was determined from a multiple species trait matrix (e.g. cell shape, organization, cell protection, nitrogen fixation, silica demand etc.) and calculated as functional richness (FRic) and functional evenness (FEve) using the FD package developed by Laliberté and Legendre (2010). We choose species traits which reflect the species habitus, reproduction, growth and environmental demands, easily measurable and available in literature (Keddy 1992, McIntyre et al. 1999, Walker et al. 1999). Phytoplankton species are an important link of many aquatic food webs wherefore we focused on traits which also describe interactions of phytoplankton with other trophic levels of the aquatic food web like nutritional mode of phytoplankton species (mixotrophic phytoplankton species interaction with bacterial communities) or grazer resistance traits.

Both, functional richness and functional evenness, quantify different facets of functional diversity for a community with species distributed in a multidimensional functional space. While functional richness represents the amount of functional (niche) space filled by the community, functional evenness describes the evenness of abundance distribution in a functional (niche) trait space (Mason et al. 2005). Functional richness quantifies the smallest volume of the convex hull that encloses a set of points defined from the species traits matrix (see Laliberté and Legendre 2010 for details). Consequently, the functional richness is directly linked to the set of traits used within the calculation, implying that the values based on two different trait sets are not necessarily comparable. For instance, when traits describe resource use (e.g. for P) a low functional richness indicates a disuse of potentially available resources. When traits describe environmental tolerances (e.g. temperature tolerance) a low functional richness implies that under certain environmental conditions better adapted species dominate the community (Tilman 1996). Functional evenness is constrained between 0 and 1 and decreases when species abundance is less evenly distributed or functional distances among species are less regular. In other words, low FEve indicates the occurrence of a dominant species or trait composition.

Predictor selection and modelling

To avoid multicollinearity, pairwise correlations (r) between the predictors have to be below $|0.75|$. Within the predictor selection process we considered both, the multicollinearity condition and the ecological relevance of the parameter with respect to the studied EF. In cases of highly correlated predictors ($r \geq 0.75$), we selected the one manifesting statistically significant correlations (t-test, significance level $\alpha=5\%$) with all studied EF for more than 2 seasons. To enable results comparability across all combinations of the seasonal EF, the additional requirement of the predictor selection process was that the same predictors should be statistically applicable (i.e. no multicollinearity) across all studied seasons. Seasonal variations of EF were modelled using Generalised Additive Models (GAM) (library “gam”, Hastie, 2005). GAM is a non-parametric extension of generalized linear methods, which identifies non-linear relationships between the response variable and the predictors, well established for modelling of ecological processes (e.g. Leathwick et al. 2006, Franklin 2009).

To capture both, the overall relationship and the temporal changes in the explanatory power of the considered EF variability drivers, the modelling was performed using the seasonal data of the whole observation period (1994-2010) as well as sampling data from the 7 years long moving windows. The window length corresponds to the major interannual variability scale of the hydroclimatic variables across the study area, argued by the influence of the North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) (see Markovic and Koch 2013). To account for the uncertainty effects in the model output statistics, in addition to the models calibrated using the full observation dataset, the seasonal EF are modelled 100 times using randomly selected 70% of the data samples (e.g. for the 7 years windows we calibrated 6 EF's x 4 seasons x 101 models x 12 windows = 26 664 models). For goodness of the fit estimation we used the coefficient of determination (R^2) as well as the ratio between the root mean squared error and the standard deviation (RS), while searching for a parsimonious model involved use of the Akaike Information criterion (AIC) (see e.g. Wilks, 1995) through simultaneous forward and backward predictor selection. Within the alternative models, for each parameter we tested linear and cubic spline relationship with the EF, implying that in the final model, each parameter could appear linearly, as a non-parametrically estimated cubic spline or not appear at all. For comparisons between the model output statistics resulting from 100 runs of any two alternative models we used the two sample t-test (e.g. Wilks 1995) and the significance level α of 5%.

To quantify the relative predictor importance, we applied the variance partitioning (LMG) method (Lindeman et al. 1980) implemented within the R library “relaimpo” (Grömping 2006). The advantage of the LMG method is that it considers sequential sums of squares over all predictor permutations and thus considers the inter-correlations effects among the individual predictors (cf. Grömping 2006).

Results

Predictor selection

In view of the multicollinearity condition and parameter relevance in describing the EF's, we reduced the taxonomic predictor set to species richness and evenness, class evenness and zooplankton evenness. In particular, among the considered parameters describing the richness, species richness manifested the highest correlations with the studied EF (between 0.15 in spring and 0.23 in autumn) and was highly correlated ($r > 0.75$) with class richness and functional richness. We remark here that, owing to different sampling frequency and different sample length across seasons, the correlations between the predictors and the EF were statistically significant at significance level $\alpha=5\%$ if they are larger than 0.12, 0.09, 0.16 and 0.17 for spring, summer,

autumn and winter, respectively. Further, without violating the multicollinearity condition all chemical parameters except those used to define the nutrient and phosphorous related ecosystem functions (SRP, TP, DN and TN) could be considered in the modelling process (i.e. NO₃N, NH₄N, SP and DIC) as well as water temperature, Secchi depth and functional evenness. Since functional richness and species richness could not be simultaneously used in the modelling process due to correlations up to 0.83, we specified two modelling approaches with the initial predictor set including the above listed TD, Phys and Chem parameters and species richness (modelling approach 1), respectively functional richness (modelling approach 2).

Model performance. The goodness of the fit of the calibrated models as well as the average number of the factors identified as statistically significant drivers of the studied EF varied across seasons and across EF (see Table 2). The RMSE of our model approaches was always significantly smaller than the standard deviation of our data. The model performance was best for AlgB and RUE_N (mean R^2 from 100 model repetitions up to 0.84) and poorest for UE_N (e.g. R^2 for the winter varies between 0.45 and 0.79). The difference in the R^2 of the modelling approach 1 and the modelling approach 2 was generally small (up to 0.06), however statistically significant ($\alpha=5\%$) mainly in favour of the model 1 (see Table 2). The modelling approach 2 performed better than the modelling approach 1 only for UE_N in spring and RUE_P in winter but, as the difference in the R^2 of the two approaches (0.02) was though statistically significant, rather negligible in the absolute terms. The average number of statistically significant variability drivers was equal for both approaches and identified the AlgB as the EF with the highest complexity depending on species richness and evenness, class evenness, functional evenness, DIC, SP and water temperature while the variability in UE_P was generally related only to that of SP, DIC and zooplankton evenness. Thereby, the relationship between the EF and the studied drivers was mostly non-linear. Following the model output statistics we concluded the overall primacy of species richness over functional richness in describing the studied EF and considered only modelling approach 1 in the subsequent sections.

Drivers of ecosystem functions

Total algal biomass. Across all seasons AlgB was best explained by TD (Table 3), whereby species evenness had the largest explanation proportion (Table 3). When the phytoplankton community was evenly distributed AlgB was low. FD had less effect than TD on AlgB. However, AlgB was negatively affected by increased functional evenness throughout the seasons, indicating functional evenness as important as species evenness at least in spring (23%) and autumn (17%). The chemical and physical parameter played a minor role for the outcome of AlgB (Chem range 15-32%; Phys range 2.5-24%). Thereby, AlgB decreased at high levels of NH₄-N across all seasons (NH₄-N range 3-8%) (Fig. 1 a-d), DIC in summer (11%), autumn (7%) and winter (6%) and SP in spring (9%) and winter (23%). High Secchi depth transparency positively affected AlgB in spring (9%) and autumn (5%), while decreased AlgB in summer (2.5%). Enhanced water temperature in autumn (19%) and winter (5%) were accompanied by enhanced AlgB (Figure 1 a-d).

Resource use efficiency for P. The most important parameter group driving RUE_P was Chem (up to 77.1%, Table 3) indicating high RUE_P at low levels of SP, DIC and NH₄-N, except for spring where RUE_P was highest at low species evenness (38%) and zooplankton evenness (8%). RUE_P generally decreased at elevated functional evenness (16%) and was low at high SP levels (23%). Although RUE_P was low at high evenness, it was enhanced at high species richness levels (Figure 2 a-d).

Resource use efficiency for N. Across all seasons RUE_N was driven mainly by TD (Table 3). At low species and class evenness RUE_N decreased and vice versa. Furthermore an increase in zooplankton evenness was accompanied by decreased RUE_N in autumn and winter. Elevated levels of nutrients decreased RUE_N, whereby the relative importance of NH4N decreased during the year from being highest in spring (17%) to lowest in winter (6%). NO3N was shown to be an important chemical parameter especially in spring (17%) and autumn (13 %), while SP contribution was highest in winter (23%). The relative importance of DIC was rather modest (up to 7%) (Figure 3 a-d).

Resource uptake efficiency for P. Across all seasons Chem was the most important parameter group driving UE_P (Table 3). Elevated nutrient concentrations had a negative effective on NUE_P, with SP and DIC as the dominant parameters. Although TD, FD or Phys generally had a minor effect on NUE_P, elevated zooplankton evenness explained 10% of UE_P decrease in summer and 20% in autumn (Figure 4 a-d).

Resource uptake efficiency for N. The most important parameter group driving UE_N was Chem, signifying a decrease with increasing nutrient levels across all seasons (Table 3; Fig. 5). With a relative importance of up to 46% UE_N was mainly driven by NO3N, except in summer when NH4N was the most important variability driver (Fig.). TD, FD and Phys had minor effects on UE_N. However, from spring to autumn elevated species evenness negatively affected UE_N, while an increase in species richness enhanced UE_N. Additionally, an increase in functional evenness decreased UE_N in spring and summer. Furthermore, UE_N was enhanced by increasing water temperature, especially in autumn (21%) and summer (7%) (Figure 5 a-d).

Temporal variations in ecosystem function drivers' relative importance

The most prominent feature of the temporal patterns in the parameters groups' relative importance was an alternation between the relative importance of TD and Chem across all EF, with high TD importance when Chem importance is low and vice versa (Fig.6). Also, the temporal patterns of the parameter groups' relative importance were more similar across the EF of a single season than across the individual seasonal EF.

Total algal biomass over time and season was mainly driven by the variability in TD. Contrary to Phys, Chem and FD, whose relative importance in describing the variability in AlGB exhibited only a slight temporal variation, TD manifested an increasing pattern in spring and autumn and a pronounced oscillatory pattern in summer and winter. In the late 90s (summer and autumn) FD and Chem, respectively, dominated the outcome of AlGB.

Resource use efficiency for P variability was on average explained most by Chem. However, the relative importance of Chem oscillated over time and seasons, except for spring where its importance as ecosystem function driver manifested a pronounced decrease. At the same time the contribution of TD in driving RUE_P increased. Although being most important in spring and autumn, TD influence was low in summer and winter, except for 1997, where it was highest in winter. Neither FD nor Phys made significant contributions to the variability of RUE_P.

Resource use efficiency for N was mainly driven by TD, with TD relative importance increasing in spring and autumn and manifesting an oscillatory pattern in summer and winter. The importance of Chem (on average 30%), exhibited a slight decrease over time in spring and autumn, while the relative importance of FD and Phys was less than 20 % and with exception of the autumn was temporally invariant .

Uptake efficiency for P and N was mainly driven by the variability in Chem. In spring, however, the relative importance of Chem for UE_N decreased, while the opposite was true for winter. TD explained a minor part of variability in both ecosystem functions, whereby

oscillations over time and season were true for NUE_P, and an increase of importance of TD for UE_N occurred in spring in autumn, while it decreased in winter. FD and Phys had no relevant importance in driving both ecosystem functions, but so ever, Phys contributed up to 70% in autumn till the end of the 90s, decreasing since then.

Preliminary conclusions

Our study demonstrated that parameters related to phytoplankton taxonomic diversity and the water chemistry were the main drivers of the studied EF. The relative importance of these parameter groups in describing the EF alternated over time, with high importance of phytoplankton taxonomic diversity when the importance of the water chemistry was low and vice versa.

The role of biodiversity in ecosystem functioning

The paradigm of biodiversity and ecosystem functioning had been introduced when ecologists have viewed the relationship between species diversity and productivity, showing that diversity not only responds to but also controls the production of biomass (e.g. Chapin et al. 2000, Tilman 2000, Naeem 2002). Our study revealed that biodiversity was the most important driver of AlgB and RUE_N. Though less important compared to chemical parameters, biodiversity was shown to be relevant for RUE_P, UE_P and UE_N.

Overall, our study had shown that the most important biodiversity related EF drivers were species and functional evenness, with high EF when evenness was low and vice versa. In general, low evenness indicates a community where the contribution of a few species to the total biomass is relatively high, thus dominating the community composition. In Müggelsee the dominating species varied across seasons, e.g. diatoms dominated in spring, cyanobacteria in summer, leading to enhanced algal biomass production and RUE_N and demonstrating that an evenly distributed community was not efficient enough to use the given resources better than a single species (dominance effect, Fox 2005). We argue that the high relative importance of evenness for RUE_N was related to high competition for nitrogen, especially pronounced in the summer season. Nitrogen fixers have a substantial competitive advantage wherever nitrogen is limiting, and their activity reverse the limitation (Vitousek and Howarth, 1991). In summer the most dominant cyanobacteria species found in the Müggelsee was *Aphanizomenon flos-aquae*, which under nitrogen-limited conditions is capable of fixing atmospheric nitrogen. Consequently, the fixation of atmospheric nitrogen by cyanobacteria is an additional source of the nitrogen influx into Müggelsee.

Recently, the effect of biodiversity on ecosystem functioning was tested by Ptacnik et al. (2008), who investigated the effect of phytoplankton taxonomic (genus level) diversity on RUE_P using data sets from Scandinavian lakes and from the Baltic Sea. They showed that genus richness was positively connected to RUE_P in all data sets. Our study confirmed the positive influence of richness on ecosystem functioning, however only in summer for AlgB, RUE_N and UE_N and in winter for AlgB. Since seasonal effects were not considered in Ptacnik et al. (2008), our results are an extension of their study emphasizing the importance of seasonal data segmentation and consideration of multiple ecosystem functions. Here, we argue that consideration of seasonal effects is crucial to our understanding of the mechanisms and ecological significance of BDEF relationships.. Further, low relative importance of richness compared to evenness across the studied EF is partially attributed to the fact that diversity measures regarding evenness provide a significant amount of information on variance in diversity that is independent of variance in species richness alone (see Wilsey et al. 2005). It was shown, that species evenness is sensitive to anthropogenic alterations of nutrient cycles, consumer presence, climate, and land use, which can alter the dominance of ecological communities and result in consequences for EF (Hillebrand et al. 2008).

The temporal variations in TD importance were similar for spring and autumn, characterized by a level shift from lower than average values for time windows starting before 2001, and higher than average values for time windows from 2001 (for all EF except for RUE_P). This effect as well as

the temporal variations in the TD importance for the summer season is most likely associated with the continuous decrease of species richness up to 2001 (afterwards it remained at similar level as in 2001) and a decrease in TN:TP ratio from 2001. Regarding the community composition, Chlorophyceae was the species richest class up to 2001, while decrease in the TN:TP ratio was followed with the increase in the number and abundance of species in the class Cyanophyceae. The previous align with the studies suggesting that atmospheric N₂-fixing cyanobacteria are generally more abundant at low TN:TP ratios (see Scheffer, 1998).

The oscillatory character of TD relative importance in winter is strongly related to the temporal pattern of species abundance that was generally low except in years 1996, 1997 and 2009 where it was between 2 and 7 times larger than the average species abundance in winter across the whole study period. As a more detailed analysis of the temporal patterns in individual predictor importance was beyond the scope of this study, further investigation is needed.

The effects of biodiversity on EF can have different implications whether changes in species or functional diversity are considered as, for example a single species with a unique trait might have stronger effects on EF compared to several species with partly redundant traits (Downing 2005). Our study showed that species richness and functional richness are correlated and thus are equally relevant.

On the other hand species and functional evenness indicated different seasonal patterns. In spring species were generally evenly distributed with exception of the years 2004, 2006 and 2008 with exceptionally low evenness (below 0.4). Evenness was lowest in spring 2004 which was at the same time the period with the lowest observed TN:TP ratio. In contrast, functional evenness was on average above 0.5 indicating rather evenly distributed functional groups. In this context, a threshold for the effects of functional evenness on EF was identified, indicating that the negative effects of functional evenness becomes significant when the evenness value climb higher than 0.5- 0.69 depending on the EF.

Table 1: Range and standard deviation (SD) of the parameters considered as the potential drivers of the ecosystem functions. TD denotes the taxonomic diversity parameters, FD- functional diversity parameters, Phys-parameters related to physical and Chem- paramaters related to chemical water properties.

Parameter	Spring		summer		autumn		winter	
	range	SD	range	SD	range	SD	range	SD
<i>TD</i>								
species richness	6-41	0.56	6-48	0.39	5-32	0.55	5-29	0.45
class richness	3-10	0.12	2-9	0.08	2-9	0.14	3-9	0.13
species evenness	0.3-0.9	0.01	0.11-0.92	0.01	0.24-0.93	0.01	0.25-0.93	0.01
class evenness	0.2-0.9	0.01	0.03-0.93	0.01	0.14-0.97	0.02	0.22-0.95	0.01
zooplankton evenness	0.4-0.8	0.005	0.36-0.79	0.004	0.45-0.82	0.008	0.51-0.85	0.01
<i>FD</i>								
functional richness	0-0.7	0.17	0-0.76	0.2	0-0.63	0.16	0-0.55	0.14
functional evenness	0.38-0.91	0.01	0.15-0.84	0.006	0.14-0.75	0.01	0.29-0.87	0.01
<i>Phys</i>								
water temperature	0-19.3	0.36	6.3-27.8	0.17	4-18.5	0.34	0-6.2	0.14
Secchi depth	0.9-5.4	0.08	0.5-3.9	0.03	0.9-5.4	0.1	0.6-3.3	0.07
<i>Chem</i>								
SP	8-76	0.9	6-462	5.12	12-525	7.86	11-114	2.2
NO3-N	0-2.54	0.04	0-1.31	0.01	0-0.9	0.02	0.02-3.09	0.06
NH4-N	0.01-0.45	0.005	0.01-0.57	0.006	0.01-0.54	0.01	0.02-0.81	0.01
DIC	18.9-30.4	0.2	12.7-30.8	0.2	19.3-30.4	0.26	18.8-32.9	0.26

Table 2: Summary of the model output statistics. R^2 is the coefficient of determination given as a range and an average from 100 repetitive model runs per EF and season; SD is the mean standard deviation of the estimated R^2 's; RS is the mean ratio between the root mean squared error and the standard deviation of the particular ecosystem function; Npara is the mean number of the statistically significant model parameters across the repetitive model runs.

Modelling approach 1						Modelling approach 2				
EF	range R^2	SD	R^2	RS	Npara	range R^2	SD	R^2	RS	Npara
Spring										
AlgB	0.54-0.72	0.04	0.63	0.6	7	0.56-0.71	0.03	0.64	0.6	6
RUE_P	0.39-0.57	0.04	0.59*	0.64	6	0.4-0.63	0.04	0.57	0.65	5
RUE_N	0.44-0.62	0.03	0.64	0.58	6	0.45-0.59	0.03	0.63	0.61	6
UE_P	0.52-0.74	0.04	0.53	0.68	3	0.52-0.74	0.04	0.53	0.68	3
UE_N	0.46-0.71	0.05	0.51	0.70	5	0.46-0.67	0.05	0.53*	0.69	5
Summer										
AlgB	0.61-0.69	0.02	0.66*	0.59	8	0.58-0.68	0.02	0.64	0.6	9
RUE_P	0.48-0.6	0.02	0.56	0.66	5	0.46-0.61	0.03	0.56	0.66	5
RUE_N	0.53-0.65	0.02	0.65*	0.59	8	0.51-0.67	0.03	0.62	0.62	8
UE_P	0.6-0.68	0.02	0.57*	0.65	5	0.57-0.66	0.02	0.56	0.66	5
UE_N	0.51-0.62	0.02	0.54*	0.67	8	0.52-0.62	0.02	0.53	0.68	8
Autumn										
AlgB	0.56-0.8	0.04	0.69	0.55	7	0.59-0.8	0.04	0.70	0.55	7
RUE_P	0.51-0.73	0.04	0.70	0.53	3	0.52-0.75	0.05	0.71	0.52	3
RUE_N	0.52-0.82	0.08	0.73	0.51	7	0.53-0.8	0.07	0.72	0.53	6
UE_P	0.66-0.84	0.04	0.68	0.58	2	0.64-0.84	0.04	0.69	0.55	2
UE_N	0.51-0.81	0.09	0.63	0.61	4	0.54-0.85	0.09	0.63	0.60	4
Winter										
AlgB	0.66-0.89	0.04	0.82*	0.43	8	0.58-0.87	0.04	0.79	0.45	7
RUE_P	0.26-0.63	0.05	0.58	0.66	5	0.22-0.57	0.06	0.60*	0.63	5
RUE_N	0.69-0.86	0.03	0.81*	0.43	8	0.72-0.84	0.03	0.80	0.44	8
UE_P	0.67-0.9	0.04	0.78	0.48	2	0.64-0.88	0.05	0.78	0.47	2
UE_N	0.45-0.79	0.06	0.45	0.73	3	0.39-0.8	0.08	0.44	0.74	3

* Preferred model when the hypothesis of zero differences between R^2 for model 1 and 2 is rejected at $\alpha=5\%$

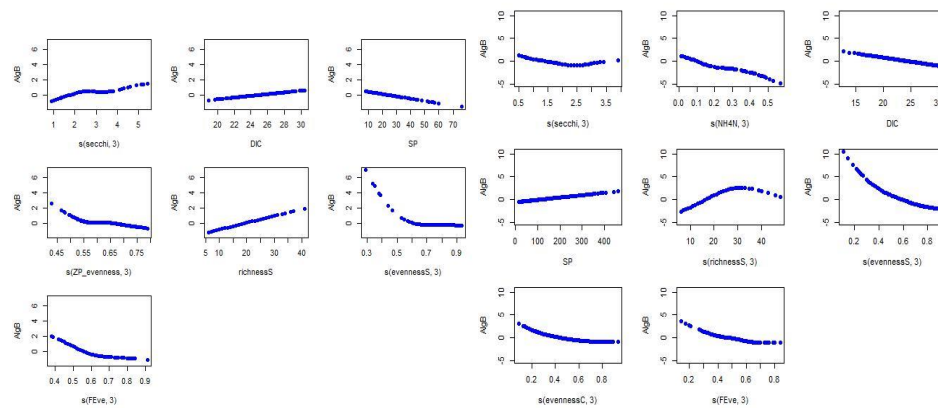
Table 3: The mean relative importance of the individual predictors and predictor groups in describing the EF's across the whole study period (1994-2010). The standard deviation of the relative importance of the individual predictor groups is denoted by SD.

EF	WT	Secchi	DIC	SP	NO3N	NH4N	SRich	SEve	CEve	ZpEve	FEve	Phys	SD	Chem	SD	TD	SD	FD	SD
Spring																			
AlgB	0.2	11.8	1.4	9.3	0.0	5.1	11.6	24.0	4.5	9.0	23.2	11.9	2.67	15.9	3.99	<u>49.0</u>	6.52	23.2	3.98
RUE_P	1.4	2.5	0.8	23.4	0.0	6.6	2.3	35.1	3.3	8.6	15.9	3.9	3.35	30.8	7.06	<u>49.3</u>	9.77	15.9	4.36
RUE_N	0.1	7.1	0.0	0.9	17.1	11.7	2.0	43.2	4.2	0.8	12.9	7.2	3.91	29.7	4.02	<u>50.2</u>	9.52	12.9	4.71
UE_P	0.0	0.1	15.2	82.2	0.0	0.7	0.0	1.0	0.0	0.5	0.2	0.1	0.30	<u>98.1</u>	3.46	1.6	3.12	0.2	0.64
UE_N	0.6	0.1	0.0	15.4	46.1	11.4	2.7	18.9	0.2	0.0	4.6	0.7	1.26	<u>72.9</u>	5.33	21.8	4.72	4.6	3.45
Summer																			
AlgB	0.8	2.4	11.4	0.8	0.1	5.9	11.4	40.7	21.1	0.6	5.0	3.1	1.77	18.1	2.96	<u>73.7</u>	2.8	5.0	1.01
RUE_P	0.2	0.2	33.3	42.1	0.0	1.7	0.2	3.3	10.8	8.1	0.2	0.4	1.27	<u>77.1</u>	5.75	22.3	5.66	0.2	0.9
RUE_N	0.1	2.6	8.1	0.3	7.3	14.2	11.6	34.6	16.7	0.0	4.6	2.7	1.37	29.9	3.69	<u>62.9</u>	3.67	4.6	1.05
UE_P	0.0	0.0	28.7	52.6	0.1	6.2	2.3	0.1	0.0	9.5	0.5	0.0	0.17	<u>87.6</u>	5.8	11.9	6.02	0.5	0.59
UE_N	7.2	0.0	7.2	4.3	18.4	29.1	10.7	17.4	0.2	0.0	5.4	7.2	4.41	<u>59.1</u>	5.45	28.3	3.66	5.4	1.42
Autumn																			
AlgB	20.0	3.7	7.7	0.7	0.3	8.2	0.9	22.4	15.1	3.9	17.1	23.7	5.48	16.9	5.07	<u>42.3</u>	8.35	17.1	4.98
RUE_P	3.1	4.4	57.0	1.3	0.5	3.0	0.2	0.8	0.1	29.6	0.0	7.5	9.94	<u>61.9</u>	13.01	30.6	18.26	0.0	0.27
RUE_N	8.6	2.3	2.3	0.1	13.2	8.3	0.3	27.3	15.4	12.5	9.7	10.9	8.41	23.9	7.07	<u>55.5</u>	10.28	9.7	6.69
UE_P	2.5	3.1	67.9	5.8	0.1	0.5	0.2	0.2	0.0	19.7	0.0	5.6	8.2	<u>74.3</u>	19.78	20.1	20.65	0.0	0.34
UE_N	21.5	0.1	1.2	0.3	43.3	18.1	0.2	12.2	0.6	2.7	0.1	21.5	9.82	62.8	8.35	15.6	8.88	0.1	0.26
Winter																			
AlgB	3.8	1.7	5.9	22.1	0.0	3.4	13.1	37.3	0.1	2.0	10.4	5.5	2.97	31.5	5.82	<u>52.6</u>	7.09	10.4	2.98
RUE_P	2.3	0.1	9.8	42.0	0.1	14.2	6.7	7.9	0.1	0.4	16.4	2.4	4.51	<u>66.1</u>	9.48	15.1	8.7	16.4	6.09
RUE_N	5.4	1.1	6.1	22.6	2.2	5.7	5.1	37.3	0.3	4.0	10.2	6.5	2.51	36.6	5.36	<u>46.7</u>	6.76	10.2	4.01
UE_P	0.0	0.0	1.0	88.0	1.9	5.8	1.0	0.1	0.1	0.2	2.0	0.1	0.48	<u>96.6</u>	4.8	1.4	3.2	2.0	2.78
UE_N	2.5	0.2	0.7	26.0	46.4	18.3	0.0	0.1	0.0	5.7	0.0	2.8	6.9	<u>91.4</u>	10.32	5.8	7.58	0.0	0.21

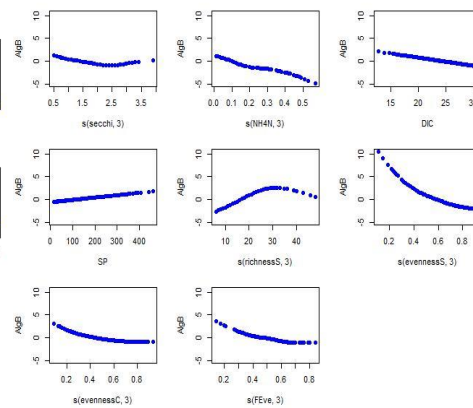
*Please see text for explanation of the abbreviations.

Figure 1 Response curves AlgB for the important parameters (a) spring, (b) summer, (c) autumn, (d) winter

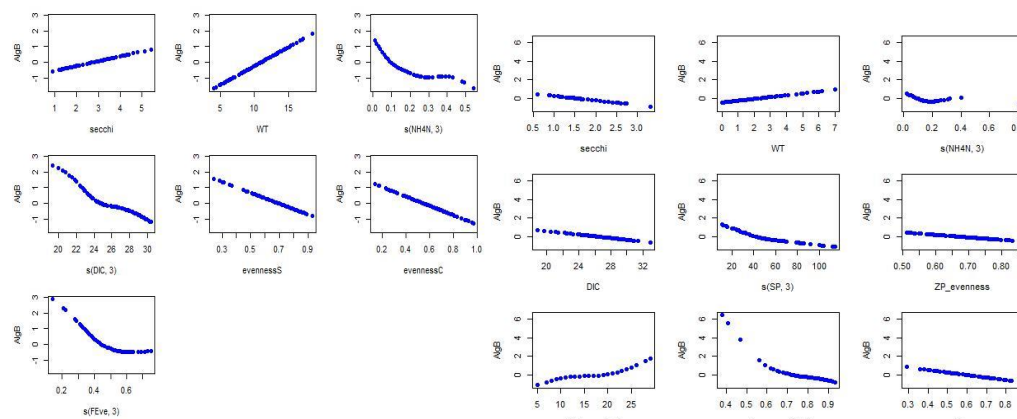
a) spring



b) summer



c) autumn



d) winter

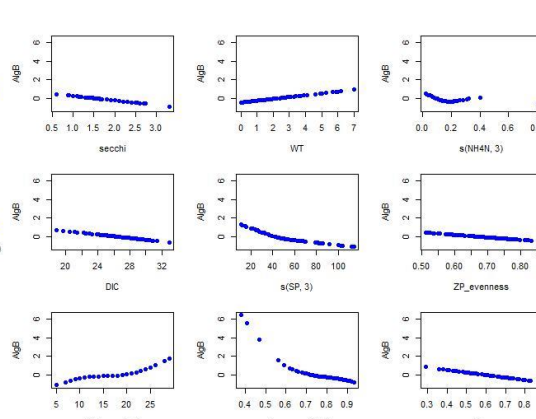
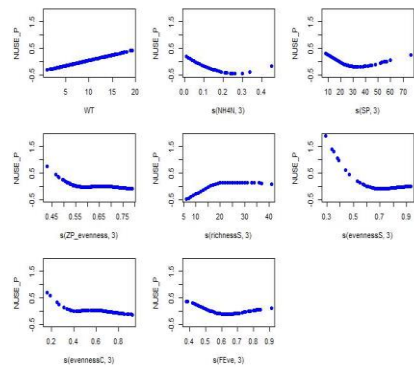
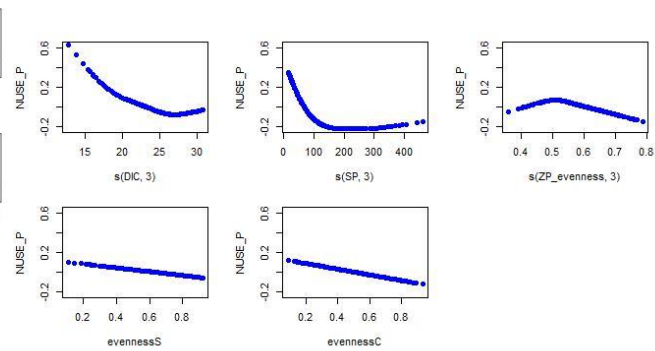


Figure 2 Response curves RUE_P for the important parameters (a) spring, (b) summer, (c) autumn, (d) winter

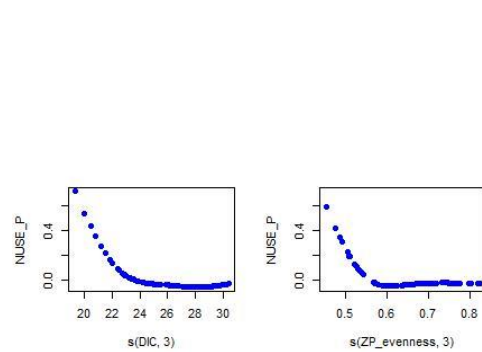
a) spring



b) summer



c) autumn



d) winter

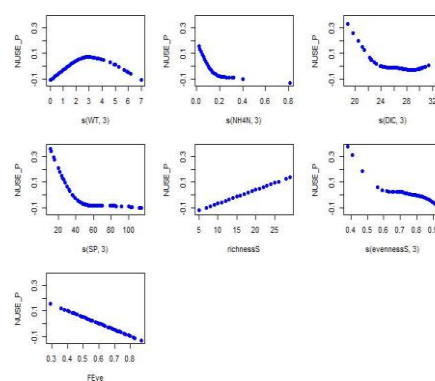
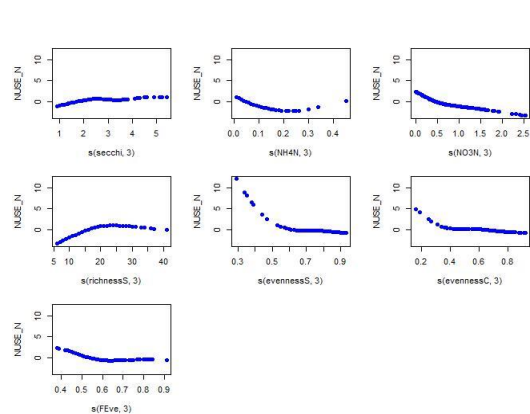
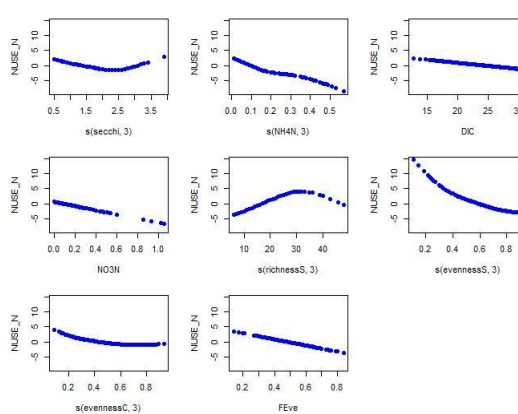


Figure 3 Response curves RUE_Nfor the important parameters (a) spring, (b) summer, (c) autumn, (d) winter

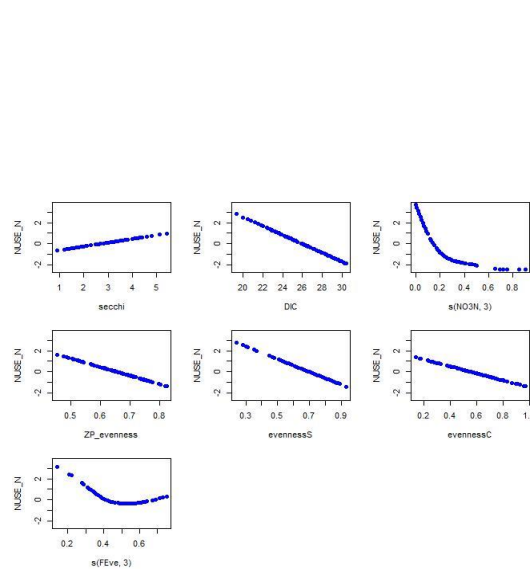
a) spring



b) summer



c) autumn



d) winter

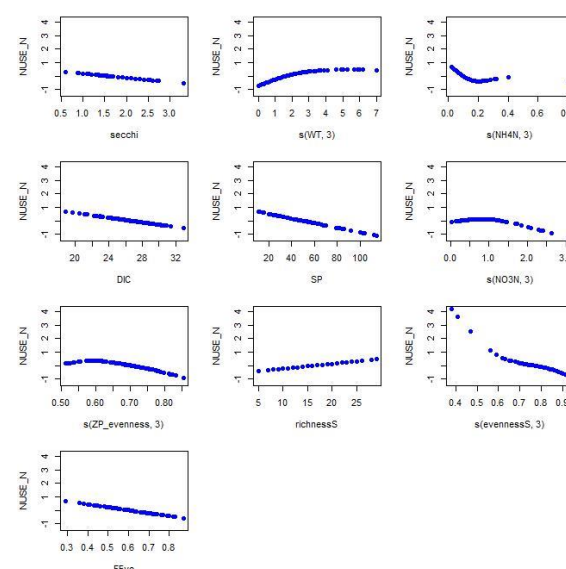
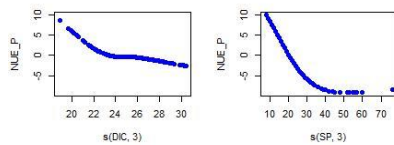
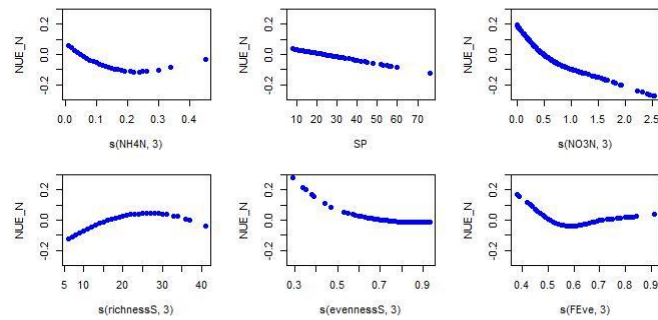


Figure 4 Response curves UE_P for the important parameters (a) spring, (b) summer, (c) autumn, (d) winter

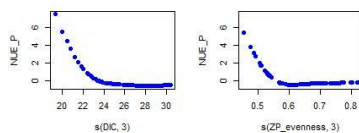
a) spring



b) summer



c) autumn



d) winter

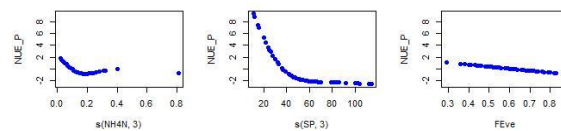
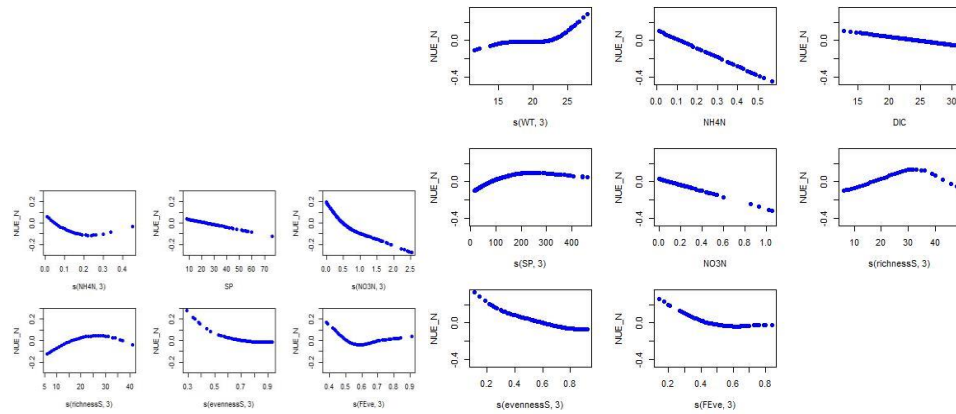


Figure 5 Response curves UE_N for the important parameters (a) spring, (b) summer, (c) autumn, (d) winter

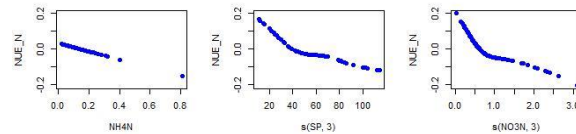
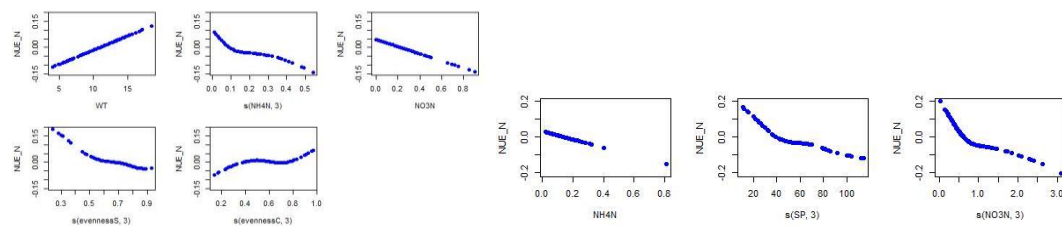
a) spring

b) summer



c) autumn

d) winter



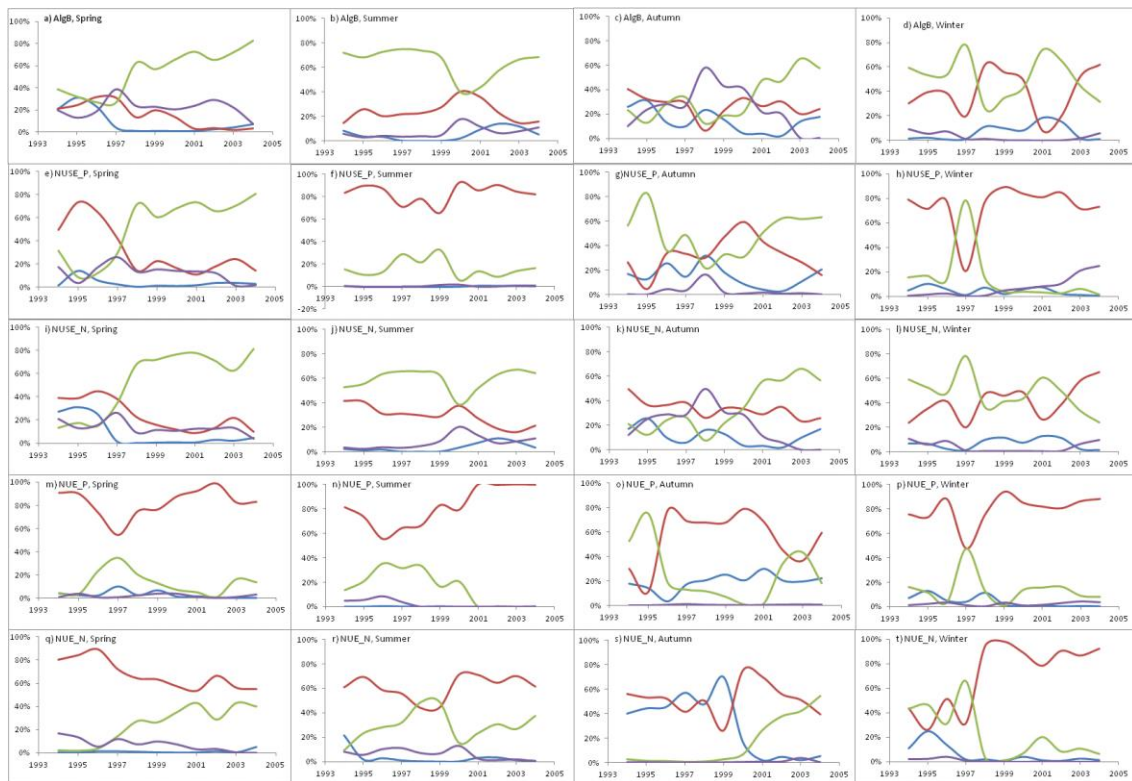


Figure 6: Temporal variations of the relative importance of the physical (blue line), chemical (red line), taxonomic (green line) and functional (purple line) drivers of EF's across seasons.

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