



Does ecosystem variability explain phytoplankton diversity? Solving an ecological puzzle with long-term data sets

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ABSTRACT

Explaining species diversity as a function of ecosystem variability is a long-term discussion in community-ecology research. Here, we aimed to establish a causal relationship between ecosystem variability and phytoplankton diversity in a shallow-sea ecosystem. We used long-term data on biotic and abiotic factors from Helgoland Roads, along with climate data to assess the effect of ecosystem variability on phytoplankton diversity. A point cumulative semi-variogram method was used to estimate the long-term ecosystem variability. A Markov chain model was used to estimate dynamical processes of species i.e. occurrence, absence and out-compete probability. We identified that the 1980s was a period of high ecosystem variability while the last two decades were comparatively less variable. Ecosystem variability was found as an important predictor of phytoplankton diversity at Helgoland Roads. High diversity was related to low ecosystem variability due to non-significant relationship between probability of a species occurrence and absence, significant negative relationship between probability of a species occurrence and probability of a species to be outcompeted by others, and high species occurrence at low ecosystem variability. Using an exceptional marine long-term data set, this study established a causal relationship between ecosystem variability and phytoplankton diversity.

1. Introduction

Phytoplankton is a taxonomically and functionally diverse group of organisms (Bonachela et al., 2015) comprising tens of thousands of species (Mutshinda et al., 2013). Their ability to utilize solar energy makes them fundamental for ocean productivity and they are responsible for half the global primary production (Field et al., 1998). Phytoplankton are the energy source for larger heterotrophic zooplankton and thus, transfer energy upwards to higher trophic levels (Steele, 1970). They, therefore, play essential roles in food webs and global biogeochemical cycles (Bonachela et al., 2015). Changes in phytoplankton dynamics create an impact on species growth rate and photosynthetic response (Duarte et al., 2006).

Many abiotic factors (e.g. light availability, temperature, salinity, pH and nutrients) and biotic factors (e.g. predators, parasites) are regulators of phytoplankton community structure (Wiltshire and Boersma, 2016; Wiltshire et al., 2015). In addition, meteorological and climatic factors, such as wind intensity and direction, the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO) and El Niño due to their impact on hydrography and ocean stratification are also important for long-term changes in the abundance and diversity of

plankton.

The global marine environment is changing rapidly (IPCC, 2007), and significant correlations between changes in marine environment and species abundance and diversity have been reported (Aebischer et al., 1990; Beaugrand and Reid, 2003). Large changes in phytoplankton species distribution in the North Sea over the last decades have been identified (Wiltshire et al., 2015). Phytoplankton colour index seems to have shown a marked increase in this region during the mid to late 1980s (Edwards et al., 2001; Reid et al., 1998). Changes in phenology (Greve et al., 2005; Wiltshire and Manly, 2004) and species composition (Beaugrand, 2003) have also been observed in this area. Although we know that these biotic changes are accompanied by variations in environmental conditions, it remains challenging to establish a causal relationship between environmental variability and community structure change.

The majority of the factors which affect biodiversity show an increasing trend and global diversity shows a decreasing trend (Butchart et al., 2010). Contrastingly an analysis of algal species diversity based on the Helgoland Roads Time Series data set (Wiltshire and Dürselen, 2004) shows that, over the recent years, there is a significant increase in the species diversity (Fig. 1). Therefore, an important question which

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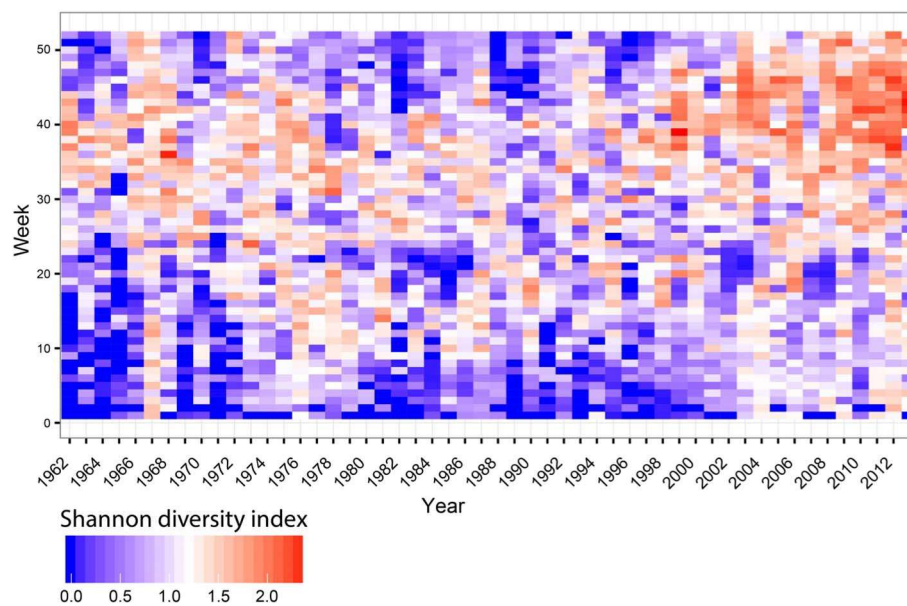


Fig. 1. Long-term weekly mean phytoplankton diversity at Helgoland Roads. Diversity is measured as Shannon diversity index from quality controlled counts data of 26 species from the Helgoland Roads Time Series station.

needs to be addressed is what has caused this phytoplankton diversity increase at Helgoland Roads.

Several ideas have been developed over the past few decades to explain shifts in species diversity. The intermediate disturbance hypothesis (Connell, 1978) is one of the most overarching concepts of non-equilibrium community theory and explains high species diversity (Graine, 2005; Grime, 2007). The intermediate disturbance hypothesis (IDH) predicts that species diversity peaks at the intermediate levels of disturbance. At low disturbance competitive exclusion reduces diversity. High disturbance produces high stress on species and increases mortality, therefore reduces diversity. Disturbance at intermediate levels prevents competitive exclusion, permits the coexistence of successful competitors and maximizes species diversity (Flöder and Sommer, 1999). This “disturbance” is a result of heterogeneity of the environment in the form of ecosystem drivers, such as nutrient supply, temperature, salinity, light availability and biotic factors (i.e. species interactions, parasites, predation etc.).

We hypothesized that algal diversity at Helgoland Roads is related to disturbance associated with environmental variables. The IDH is able to predict high diversity at the intermediate level of disturbance and therefore, one can assume that this high species diversity at Helgoland Roads might be related to an intermediate level of disturbance. This disturbance is the heterogeneity in the ecosystem drivers which we termed “ecosystem variability” in our study.

Many studies provide analytical methods for the link of ecosystem variability to species diversity (e.g. Flöder and Sommer (1999), D’Odorico et al. (2008), Dornelas (2010) etc.). A number of studies based on field data were reported in Padisák et al. (2013). Here we carry out a study linking ecosystem variability to marine biodiversity based on a marine time series of species abundance at Helgoland Roads in the North Sea. The objectives of this study are:

- (i) the estimation of long-term ecosystem variability as a function of biotic, abiotic and climatic factors,
- (ii) to test if the intermediate disturbance hypothesis (IDH) can explain recent increase (after the 1990s) in algal species diversity at Helgoland Roads, and
- (iii) to explain the observed relationship of phytoplankton diversity - ecosystem variability.

2. Materials and methods

2.1. Data source

We used the quality-controlled data of phytoplankton abundance, nutrient concentrations, Secchi depth, temperature and salinity from the Helgoland Roads long-term data sets (Raabe and Wiltshire, 2009; Wiltshire and Dürselen, 2004). The Helgoland Roads Time Series station (54°11.3′ N, 7°54.0′ E) is located between two islands, i.e. Helgoland and Düne, in the North Sea. Long-term monitoring of biological, chemical, and physical parameters has been carried out continuously on a work daily basis since 1962. This data set is one of the longest aquatic data sets in history (Wiltshire and Dürselen, 2004). Water samples are collected from the surface and preserved for further analysis of nutrients, phytoplankton and zooplankton. The nutrients (silicate, phosphate, ammonium, nitrate and nitrite) are measured immediately using the standard colorimetric methods after Grasshoff (1976) on a filtered sub-sample from the daily Helgoland Roads surface water sample (Wiltshire et al., 2010). The phytoplankton sub-sample from the Helgoland Roads sample is preserved in a brown glass bottle with Lugol’s solution. The samples are subsequently counted under an inverted microscope using Utermöhl settling chambers and individuals are identified to species level when possible, or otherwise differentiated into defined size classes (Wiltshire and Dürselen, 2004; Wiltshire et al., 2010). Secchi depth and temperature are measured directly on station (Wiltshire et al., 2015). We also used three climatic variables i.e. the NAO (data available from <https://www.ncdc.noaa.gov/teleconnections/nao/>), the AMO (data available from <https://www.esrl.noaa.gov/psd/data/timeseries/AMO/>) and the Tropical Pacific sea surface temperatures in the El Niño 3.4 region (data available from http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml) for our study.

2.2. Phytoplankton diversity estimation

We used species richness and the Shannon diversity index as a measure of phytoplankton diversity. The Shannon diversity index (Shannon and Weaver, 1949) depends on both species richness and evenness (Pielou, 1966), and is the best measure of their joint influence (Fager, 1972). In addition, this index is not strongly affected by rare species (Stirling and Wilsey, 2001), it is sample size independent

(Sanders, 1968), and has been developed as a test statistic that is neutral with respect to physical, functional, and biotic interactions (Caswell, 1976). Therefore, this index is widely used as a measure of biodiversity.

We estimated species richness R as the sum of total number of species present in each sample. The Shannon diversity index (H') was calculated for each sample using the following equations:

$$H' = - \sum_{i=1}^R p_i \ln(p_i) \quad (1)$$

$$p_i = \frac{N_i}{N_{total}} \quad (2)$$

where, p_i is the relative abundance of species i , N_i is the number of individuals in species i and N_{total} is the total number of individuals in the community.

Based on the counts in the Helgoland Roads long-term phytoplankton data set, a taxon list of 261 taxa has been assembled (Kraberg et al., 2015). Numbers for all the species listed at the Helgoland Roads Time Series Station are not continuously available from 1962. Details on the gaps in species abundance data are explained in Wiltshire and Dürselen (2004). However, due to the potential of this data set for examining plankton biodiversity against the backdrop of global change a list of species was made by Wiltshire and Dürselen (2004) to use for comparisons of their long-term occurrence. We used 26 of these species data to estimate the long-term phytoplankton diversity shifts at Helgoland Roads. These 26 species represent different groups and growth types (i.e. fast and slow growing species), and they are merely a sub-community of the overall counts. The reduced community with 26 species means a removal of large number of species from the entire community which is a kind of thinning. This may cause difficulties in comparing trends across different species numbers. Removing an extremely rare species typically leads to a smaller or similar diversity, while the removal of a dominating species can have the opposite effect of increasing diversity.

Diversity index estimated from the sub-community should be, on average, equal to the value of diversity index when different species numbers are compared. To examine if our sub-community of 26 species meets these criteria, we performed following analyses:

We took data on observed phytoplankton species abundance from the Helgoland Roads Time Series station for the time period of 1990 to present. For this time period we have continuous observations of species abundance. Ten replicate sub-communities each of sizes $N = 30, 50, 70, 90, 110$ and 130 species were randomly sampled from the phytoplankton species of Helgoland Roads. Then, Shannon index was calculated for each replicate sub-community. Estimated Shannon index from each replicate sub-community were averaged as a ratio to the 26 species sub-community. The ratio < 1 or > 1 indicates that Shannon index of replicate sub-community is smaller or greater than our 26 species sub-community, respectively. The ratio equal to 1 indicates that our 26 species sub-community has perfect performance to describe the diversity of the replicate sub-community.

Overall, it can be seen that the ratio for most of the replicate sub-communities is close to 1 even when large number of species were considered (Fig. S1). Average ratio across 10 replicates drew for sub-communities each of sizes 30, 50, 70, 90, 110 and 130 species indicate that all of them are located within the $\pm 10\%$ deviation from the ratio 1. This indicates that our 26 species sub-community has nearly perfect performances to describe the diversity of entire community. In addition, we found significant positive correlations of Shannon index of 26 species with the Shannon index estimated from replicates of 30, 50, 70, 90, 110 and 130 species ($r = 0.78, 0.82, 0.75, 0.72, 0.71, 0.68$ respectively). Therefore, as a representation of long-term shifts in phytoplankton diversity at Helgoland Roads consideration of 26 species is reasonable.

2.3. Ecosystem variability estimation

Ecosystem variability was examined by using the annual mean data on biotic, abiotic and climatic factors (i.e. sum of phytoplankton species abundance data, temperature, salinity, Secchi depth, silicate concentrations, nitrate concentrations, phosphate concentrations, NAO, AMO and El Niño index). To reduce the high dimensionality, we first performed a principal component analysis (PCA) of these multivariate data series. The first axis of the PC explained most of the variance (61.44%). Therefore, we took PC1 as a representation of the ecosystem. Then the “local variance” was calculated directly on the first PC to examine the long-term ‘ecosystem variability’ by following Beaugrand et al. (2008). The ‘local variance’ explains the heterogeneity of a value of an observation with respect to the value of another observation (Beaugrand et al., 2008).

To calculate the ‘local variance’, we borrowed the technique derived from the method of point-cumulative semi-variogram (PCSV) which is developed by Şen (1998). The PCSV function is proposed for identifying the spatial behaviour of any variable around a reference site (Şen and Habib, 1998). This method measures the dissimilarity between a concerned observation with another (Beaugrand and Ibañez, 2002) and therefore, provides valuable information for describing the heterogeneity between observations (Şen and Habib, 1998).

2.4. Markov chain model

Markov chain model is the simplest model to analyze multispecies data and the transition matrix of this model summarizes essential parameters related to the community dynamics in a way that few models can achieve. In ecology, Markov chain model is used to estimate the probabilities of species to move from one ecological state to another (Wootton, 2001). The ecological states in the model depend on the major mechanisms that the investigator believes are important (Wootton, 2001). For example, occurrence and absence of a species can represent two different ecological states if the investigator is interested to estimate the probability of a species being present and absent respectively.

Here, we used a Markov chain model to estimate the dynamical processes of species i.e. probability of species occurrence (i.e. probability of a species being present at time $t + 1$ which was absent at time t), probability of species being absent (i.e. probability of a species being absent at time $t + 1$ which was present at time t) and probability of a species to be outcompeted by other species. The Markov chain model used for this study is shown in Eq. (3) where C_t denotes a column vector containing proportional abundance of community c_j at time t and C_{t+1} contains proportional abundance of community c_j at time $t + 1$. The column vector C_t satisfies the conditions $0 \leq c_j \leq 1$ and $\sum_j c_j = 1$. In transition matrix P at i^{th} row and j^{th} column, the probability (p_{ij}) defines a point in ecological state j at time t , being at state i at the next sampling at the time $t + 1$. In Eq. (3), P is a matrix with $S + 1$ rows and $S + 1$ columns where S is the number of species in the model. Columns and rows contain transition probabilities of points which either start from or end in “empty space” (i.e. absence of species), respectively. We considered 26 species (S), thus, we had 27 ecological states ($S + 1$) in the transitional probability matrix. Twenty-six species represent 26 ecological states ($S = 1, 2, \dots, 26$) and ($S + 1$)th state or 27th state represents the “empty space”.

$$C_{t+1} = PC_t \quad (3)$$

where

$$P = \begin{pmatrix} p_{11} & \dots & p_{1j} & & p_{1S} & p_{1(S+1)} \\ p_{S1} & \dots & p_{Sj} & & p_{SS} & p_{S(S+1)} \\ p_{(S+1)1} & \dots & p_{(S+1)j} & & p_{(S+1)S} & p_{(S+1)(S+1)} \end{pmatrix}$$

Probability of species i occurrence was estimated according to

Wootton (2001) as:

$$p(\text{Occurrence of species } i) = p_{i(s+1)}$$

Probability of species j being absent was estimated according to Wootton (2001) as:

$$p(\text{Absence of species } j) = p_{(s+1)j}$$

Total probability to outcompete species j by other species was estimated according to Wootton (2001) as:

$$\left(1 - p_{jj} - p_{(s+1)j} = \sum_{i=1}^s p_{ij}; i \neq j \right)$$

The transition matrix P was determined from the observations C through Eq. (3) by performing Markov chain Monte Carlo (MCMC) simulations (Gilks et al., 1995) in OpenBUGS software (Thomas et al., 2006). We linked OpenBUGS software with the statistical computing software R (R Development Core Team, 2010) by R2OpenBUGS package (Sturtz et al., 2005) for the MCMC simulations. We ran 20,000 MCMC iterations with three parallel chains. To remove the dependence on the starting values we discarded the first halves from each Markov chain as burn in.

3. Results

3.1. What are the long-term trends in biodiversity and ecosystem variability?

We first estimated the long-term trends in species richness (Fig. 2a), Shannon index (Fig. 2b) and ecosystem variability (Fig. 2c). The polynomial regression analyses of year versus species richness, Shannon index and ecosystem variability explained 87% ($p < 0.0001$), 49% ($p < 0.0001$) and 43% ($p < 0.001$) of variations, respectively. Our trend analyses revealed significant inter-annual variation in all these three variables. Species diversity increased until around mid-1970s before undergoing a decline during the 1980s. From the beginning of the 1990s we observed an increase in species diversity. Overall, the 1980s represented a period of high ecosystem variability with a comparatively less variable period during the 1970s and from the beginning of 1990s to onwards.

3.2. Does ecosystem variability explain increase in phytoplankton diversity?

We carried out linear regression analyses of ecosystem variability versus species richness and Shannon index (Fig. 3) data. We found that ecosystem variability is an important predictor of long-term change in phytoplankton diversity. Ecosystem variability explained 47% and 40% of variations in long-term species richness and Shannon index respectively at Helgoland Roads. We also found a significantly negative relationship between ecosystem variability and both the species richness ($r = -0.68$, $p < 0.0001$) and the Shannon index ($r = -0.63$, $p < 0.0001$).

3.3. What causes high diversity at low ecosystem variability?

Diversity only peaks at the intermediate level of variability if a negative relationship exists between probability of species absence and occurrence (Petraitis et al., 1989). Our analysis (Fig. 4) indicates non-significant negative relationship ($r = -0.095$, $p = 0.63$) between the probability of species absence and occurrence. In addition, species selected for our study differs from each other in-terms of their occurrence probabilities which should be same for all species to support the prediction of the IDH. Thus, species interactions found in the community contradicts the underlying mechanistic assumptions of IDH and therefore, diversity might not peak at the intermediate level of variability.

We found a significant negative relationship between probability of

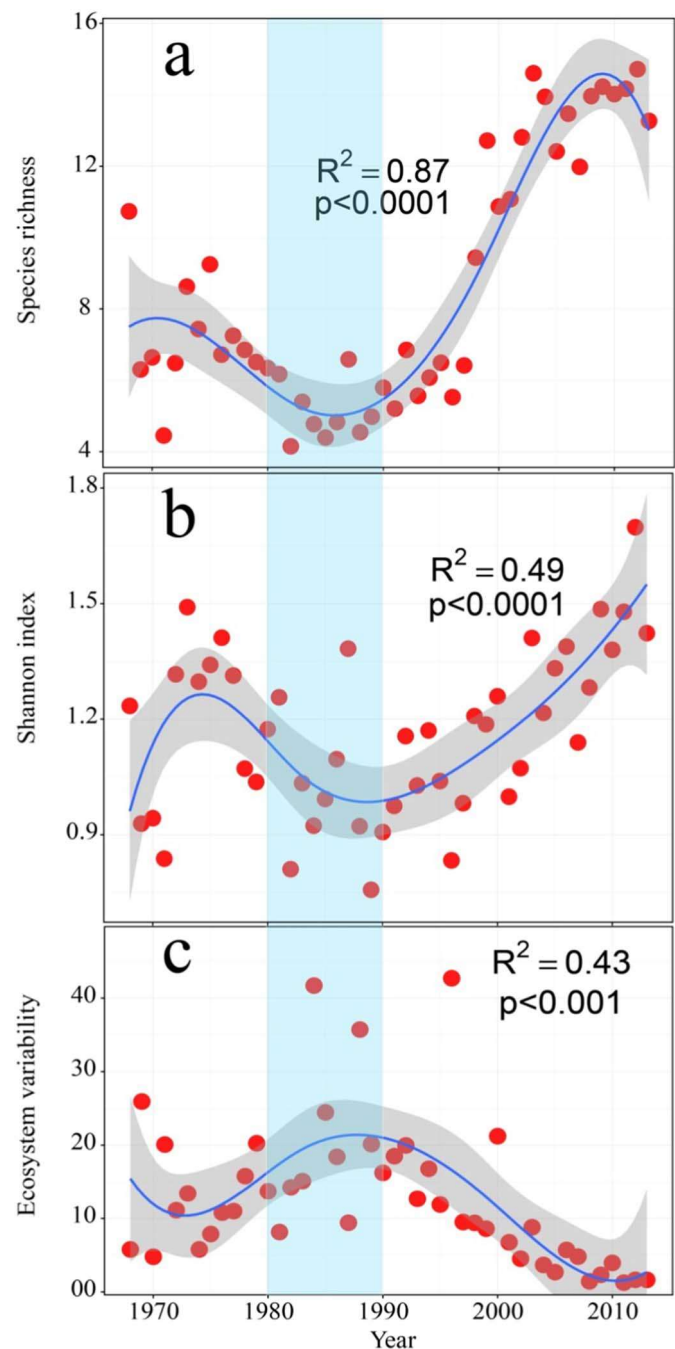


Fig. 2. Long-term annual mean of (a) species richness (b) Shannon index and (c) ecosystem variability at the Helgoland Roads Time Series station. Red dots indicate the values of respective variable at different years, grey shade indicates 95% confidence interval and blue solid line indicates the trend estimated as the function of time. The vertical shaded block indicates the decline of species diversity (a, b) and high variability in ecosystem (c) during the 1980s. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species occurrence and probability to outcompete (Fig. 5; $r = -0.81$, $p = 0.0001$). We also found that higher probability of phytoplankton occurrence is related to low ecosystem variability (Fig. 6a; $r = -0.58$, $p < 0.001$) while there is a non-significant relationship exists between ecosystem variability and probability of a species to be outcompeted by other species (Fig. 6b; $r = 0.13$, $p = 0.38$). Negative relationship between species occurrence and probability of a species to be outcompeted by other species, and high occurrence probability at low ecosystem variability reduce species competition at low ecosystem variability and thus, exclusion of species does not occur. Therefore,

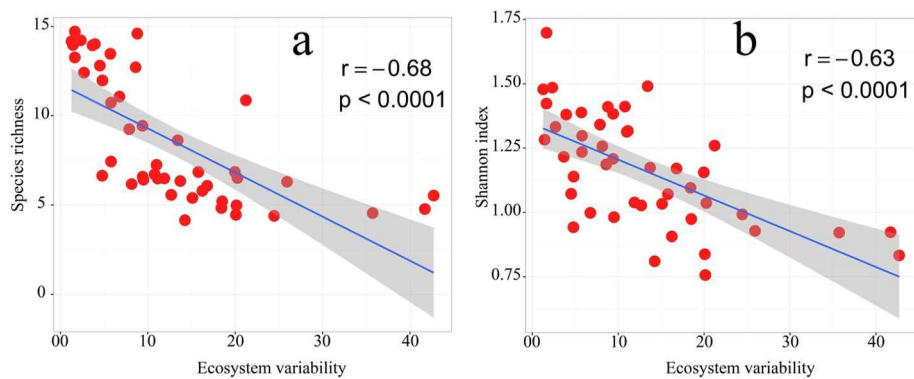


Fig. 3. Relationship between ecosystem variability and, (a) species richness and (b) Shannon index. Red dots in both plots indicate the values from each year, shaded grey lines indicate 95% confidence interval and blue lines indicate the linear trends. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

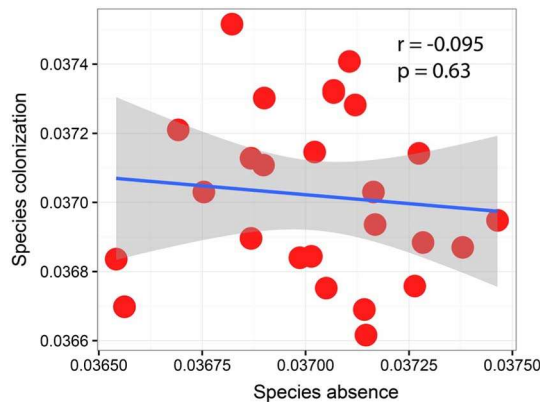


Fig. 4. Linear regression to compare the species absence probability and occurrence. Shaded grey lines indicate 95% confidence interval and blue lines indicate the linear trend. Each red dot indicates the average of each species over the study period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

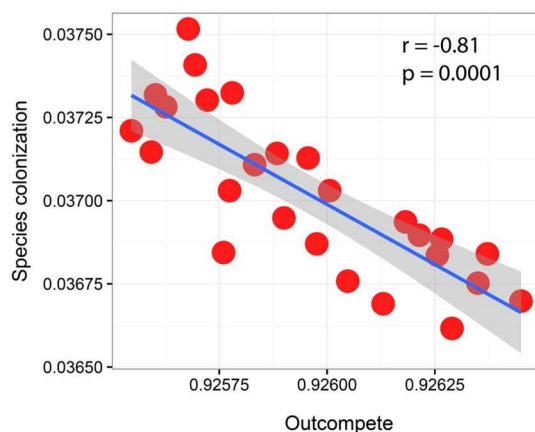


Fig. 5. Linear regression to compare the species occurrence probability and probability to outcompete. Shaded grey lines indicate 95% confidence interval and blue lines indicate the linear trend. Each red dot indicates the average of each species over the study period (1968–2014). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species diversity increases at low ecosystem variability rather than there being a decrease.

4. Discussion

We analyzed long-term quality-controlled Helgoland Roads phytoplankton, temperature, salinity, Secchi depth and nutrient data, and three climate variables (i.e. NAO, AMO and El Niño). First we estimated

the long-term ecosystem variability and then explained long-term phytoplankton diversity change as a function of ecosystem variability.

The southern North Sea has undergone considerable change in the last decades, and many examples exist describing changes in the environment (Beaugrand et al., 2008; Beaugrand et al., 2014; Boersma et al., 2015; Edwards et al., 2002; Siegismund and Schrum, 2001). Three temporally persistent shifts were identified in the 1960s, 1980s and during the period 1996 to 2003 in the North Sea and the three shifts impacted 40% of the plankton species or taxa considered in a study of Beaugrand (2014). In our study, we identified the 1980s as period of high ecosystem variability at the Helgoland Roads Time Series station while a comparatively less variable period in the ecosystem was identified afterwards (Fig. 2c). Beaugrand et al. (2008) also identified that the 1980s overall was a period of high variability with a low variability in the recent years in the North Atlantic region. Similar change in the late 1980s in long-term records of Mediterranean ecological and hydro-climate variables were also observed (Conversi et al., 2010). The hydrography of the southern North Sea has changed significantly in the last 50 years (Scharfe, 2013), especially around Helgoland, showed a change in phenology of the phytoplankton (Wiltshire et al., 2015). This known shift during the 1980s was also previously described by Wiltshire et al. (2008) for the same data sets in terms of average phytoplankton winter densities and average cell size.

During the 1980s, we observed a decline in phytoplankton diversity while a positive trend is observed from the beginning of 1990s (Fig. 2a & 2b). Reid et al. (2016) have confirmed that the 1980s shift in the ecosystem represented a major change in many of the Earth's biophysical systems. A collapse of global biodiversity occurred during the 1980s (Rockström et al., 2015). In a Costa Rican cloud forest, amphibian and reptile populations declined in 1987 (Pounds et al., 1999). From 1984 to 2004, the International Union for Conservation of Nature (IUCN) recorded 27 extinctions of species (Pereira et al., 2012). All these studies mentioned above support our findings of decline in phytoplankton diversity during the 1980s.

From our analyses, we know that phytoplankton diversity at Helgoland Roads has increased significantly over the past years. However, a definite single cause of this increase has yet to be elucidated. Previous studies on this data set found a strong decrease in the densities of calanoid zooplankton (Boersma et al., 2015) and an increase in diatom biomass (Wiltshire et al., 2010). Therefore, lower herbivore densities would release the predation pressure of zooplankton on the algae, and that this may lead to higher algal densities at Helgoland Roads (Wiltshire and Boersma, 2016). However, in this study we focused on long-term change in the phytoplankton diversity at Helgoland Roads in relation to ecosystem variability. Our study found ecosystem variability as an important predictor of phytoplankton diversity at Helgoland Roads, but due to significantly negative association between these two variables finding of our study contradicts with the prediction of the IDH (Connell, 1978; Grime, 1973). Findings of many experimental studies supported the prediction of the IDH (Flöder and

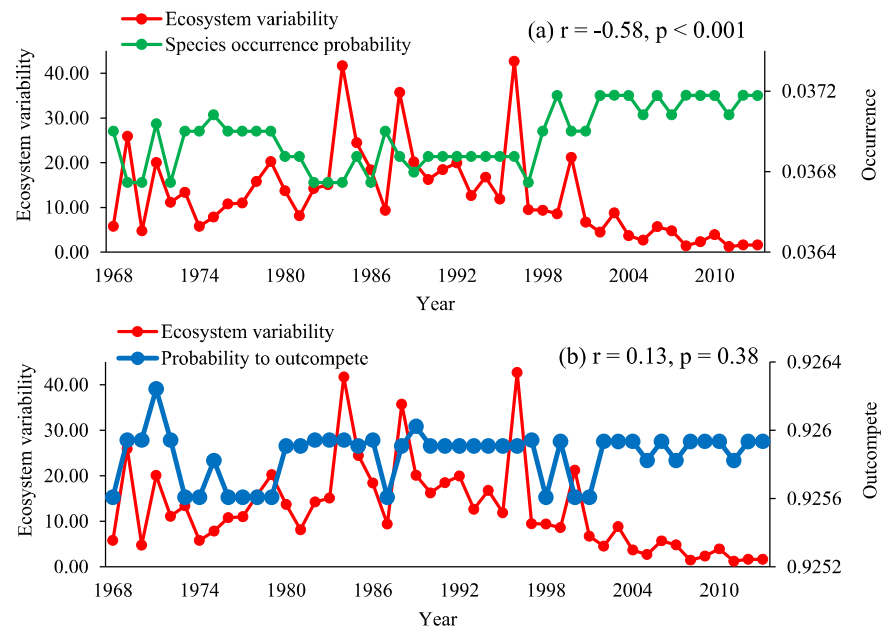


Fig. 6. Relationship between (a) long-term ecosystem variability and species occurrence (each data point indicates the mean of 26 species for a year) probability and (b) long-term ecosystem variability and probability to outcompete by other species (each data point indicates the mean of 26 species for a year).

Sommer, 1999; Gaedeke and Sommer, 1986; Robinson and Sandgren, 1984; Sommer, 1995). However, field based studies rarely found the predicted peak in diversity at intermediate disturbance levels (Fox, 2013). Some studies found completely different patterns i.e. monotonic increases and declines with increasing disturbance intensity (Mackey and Currie, 2001). Collins (1987), Collins and Gibson (1990) and Robinson and Minshall (1986) found diversity decreases with the increase in variability while diversity increases at comparatively less variable ecosystem which are in line with our findings.

Due to contradiction of our finding with most commonly cited prediction of the IDH, we explored the reasons of why diversity peaked at low ecosystem variability. Existing studies suggest that biodiversity only peaks at the intermediate level of variability if there is a negative relationship exists between species absence and occurrence (Petraitis et al., 1989). Our study did not find significant negative relationship between these two parameters (Fig. 4) and thus no peak in biodiversity at the intermediate level of variability might happen. The IDH considered the “equal chance hypothesis” which assumes that the species occurrence probabilities are very similar (Connell, 1978), but in our case species differ in-terms of their occurrence probabilities (Fig. 6). This might be another reason that diversity did not peak at the intermediate level of variability.

Negative relationship between species occurrence and probability of a species to be outcompeted by other species promote biodiversity, and this relationship is also a powerful explanation of species coexistence (Cadotte, 2007). We also found a similar negative relationship (Fig. 5), which indicates that species has higher ability to co-exist. Both diversity and species occurrence probability declined with the increase of ecosystem variability (Figs. 3 and 6, respectively) and these indicate that species are generally inferior to occur at highly variable ecosystem. Moreover, these species are skewed toward the competitive end of probability to outcompete and occurrence probability. This means increasing ecosystem variability should reduce diversity (Cadotte, 2007). In addition, negative relationship between species occurrence and probability to outcompete, and high occurrence probability at low ecosystem variability prevent exclusion of species at low ecosystem variability. Thus, many species can occur in a less variable ecosystem and therefore, increase the diversity. Following the loss of diversity from disturbance or highly variable condition, species increase owing to

recruitment and species are able to occur in cleared patches (Hughes et al., 2007). After in the decline of species diversity during the 1980s due to high ecosystem variability, species might had a window for their occurrence in the system afterwards with an ability that was not enough to exclude other species. Therefore, coexisted in a less variable ecosystem and enhanced diversity.

In conclusion, going back to our title: Does ecosystem variability explain phytoplankton diversity? The answer is “yes”. We found that, ecosystem variability is an important predictor of long-term shifts in phytoplankton species diversity at Helgoland Roads. The increasing diversity trend of the last two decades is related to low ecosystem variability. The occurrence of more species at low ecosystem variability without causing the loss of other species indicates the niche differentiation, tend to reduce competition so that exclusion does not occur and directly increases species diversity.

The search for the causal explanation of species diversity and ecosystem variability is one of the key questions in modern community ecology research. In this study we considered annual mean data of biotic, abiotic and climatic factors for ecosystem variability analysis. It would be interesting to consider in addition the seasonality in the analysis. To our knowledge, this is the first report of causal relationship between ecosystem variability and phytoplankton diversity using such a long-term and regularly sampled data set of a marine ecosystem. Our ability to solve this puzzle of phytoplankton diversity increase at Helgoland Roads will help to understand the role of long-term environmental heterogeneity and inherited complexity of community to maintain the biodiversity.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2018.02.002>.

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References

- Aebischer, N.J., Coulson, J.C., Colebrook, J.M., 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* 347, 753–755.
- Beaugrand, G., 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fish. Oceanogr.* 12, 270–283.
- Beaugrand, G., 2014. Theoretical basis for predicting climate-induced abrupt shifts in the oceans. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 370, 20130264.
- Beaugrand, G., Ibañez, F., 2002. Spatial dependence of calanoid copepod diversity in the North Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 232, 197–211.
- Beaugrand, G., Reid, P.C., 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Glob. Chang. Biol.* 9, 801–817.
- Beaugrand, G., Edwards, M., Brander, K., Luczak, C., Ibañez, F., 2008. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecol. Lett.* 11, 1157–1168.
- Beaugrand, G., Harley, X., Edwards, M., 2014. Detecting plankton shifts in the North Sea: a new abrupt ecosystem shift between 1996 and 2003. *Mar. Ecol. Prog. Ser.* 502, 85–104.
- Boersma, M., Wiltshire, K.H., Kong, S.M., Greve, W., Renz, J., 2015. Long-term change in the copepod community in the southern German Bight. *J. Sea Res.* 101, 41–50.
- Bonachela, J.A., Klausmeier, C.A., Edwards, K.F., Litchman, E., Levin, S.A., 2015. The role of phytoplankton diversity in the emergent oceanic stoichiometry. *J. Plankton Res.* (4), 1021–1035.
- Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.C., Watson, R., 2010. Global biodiversity: indicators of recent declines. *Science* 328, 1164–1168.
- Cadotte, M.W., 2007. Competition–colonization trade-offs and disturbance effects at multiple scales. *Ecology* 88, 823–829.
- Caswell, H., 1976. Community structure: a neutral model analysis. *Ecol. Monogr.* 46, 327–354.
- Collins, S.L., 1987. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology* 68, 1243–1250.
- Collins, S.L., Gibson, D.J., 1990. Effects of Fire on Community Structure in Tallgrass and Mixed-grass Prairie. Fire in North American Tallgrass Prairies. University of Oklahoma Press, Norman, pp. 81–98.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Conversi, A., Fonda Umani, S., Peluso, T., Molinero, J.C., Santojanni, A., Edwards, M., 2010. The Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallels with other European Basins. *PLoS One* 5, e10633.
- Craine, J.M., 2005. Reconciling plant strategy theories of Grime and Tilman. *J. Ecol.* 93, 1041–1052.
- D'Odorico, P., Laio, F., Ridolfi, L., Lerda, M.T., 2008. Biodiversity enhancement induced by environmental noise. *J. Theor. Biol.* 255, 332–337.
- Dornelas, M., 2010. Disturbance and change in biodiversity. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 365, 3719–3727.
- Duarte, P., Macedo, M.F., da Fonseca, L.C., 2006. The relationship between phytoplankton diversity and community function in a coastal lagoon. In: Martens, K., Queiroga, H., Cunha, M.R., Cunha, A., Moreira, M.H., Quintino, V., Rodrigues, A.M., Seroódio, J., Warwick, R.M. (Eds.), *Marine Biodiversity: Patterns and Processes, Assessment, Threats, Management and Conservation*. Springer Netherlands, Dordrecht, pp. 3–18.
- Edwards, M., Reid, P., Planque, B., 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). *ICES J. Mar. Sci.* 58, 39–49.
- Edwards, M., Gregory, B., Philip, C.R., Ashley, A.R., Malcolm, B.J., 2002. Ocean climate anomalies and the ecology of the North Sea. *Mar. Ecol. Prog. Ser.* 239, 1–10.
- Fager, E.W., 1972. Diversity: a sampling study. *Am. Nat.* 106, 293–310.
- Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281, 237–240.
- Flöder, S., Sommer, U., 1999. Diversity in planktonic communities: an experimental test of the intermediate disturbance hypothesis. *Limnol. Oceanogr.* 44, 1114–1119.
- Fox, J.W., 2013. The intermediate disturbance hypothesis should be abandoned. *Trends Ecol. Evol.* 28, 86–92.
- Gaedeke, A., Sommer, U., 1986. The influence of the frequency of periodic disturbances on the maintenance of phytoplankton diversity. *Oecologia* 71, 25–28.
- Gilks, W.R., Richardson, S., Spiegelhalter, D., 1995. *Markov Chain Monte Carlo in Practice*. Taylor & Francis, Chapman & Hall/CRC, London, UK.
- Grasshoff, K., 1976. *Methods of Seawater Analysis*. Verlag Chemie, Weinheim and New York.
- Greve, W., Prina, S., Zidowitz, H., Nast, J., Reiners, F., 2005. On the phenology of North Sea ichthyoplankton. *ICES J. Mar. Sci.* 62, 1216–1223.
- Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242, 344–347.
- Grime, J.P., 2007. Plant strategy theories: a comment on Craine (2005). *J. Ecol.* 95, 227–230.
- Hughes, R.A., Byrnes, J.E., Kimbro, D.L., Stachowicz, J.J., 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecol. Lett.* 10, 849–864.
- IPCC, 2007. *Climate Change 2007: the physical science basis*. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Kraberg, A.C., Rodriguez, N., Salewski, C.R., 2015. Historical phytoplankton data from Helgoland Roads: can they be linked to modern time series data? *J. Sea Res.* 101, 51–58.
- Mackey, R.L., Currie, D.J., 2001. The diversity–disturbance relationship: is it generally strong and peaked? *Ecology* 82, 3479–3492.
- Mutshinda, C.M., Finkel, Z.V., Irwin, A.J., 2013. Which environmental factors control phytoplankton populations? A Bayesian variable selection approach. *Ecol. Model.* 269, 1–8.
- Padisák, J., Reynolds, C.S., Sommer, U., 2013. Intermediate Disturbance Hypothesis in Phytoplankton Ecology: Proceedings of the 8th Workshop of the International Association of Phytoplankton Taxonomy and Ecology Held in Baja (Hungary), 5–15 July 1991. Springer Netherlands.
- Pereira, H.M., Navarro, L.M., Martins, I.S., 2012. Global biodiversity change: the bad, the good, and the unknown. In: Gadgil, A., Liverman, D.M. (Eds.), *Annu. Rev. Environ. Resour.* 37, pp. 25–50.
- Petratits, P.S., Latham, R.E., Niesenbaum, R.A., 1989. The maintenance of species diversity by disturbance. *Q. Rev. Biol.* 64, 393–418.
- Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13, 131–144.
- Pounds, J.A., Fogden, M.P.L., Campbell, J.H., 1999. Biological response to climate change on a tropical mountain. *Nature* 398, 611–615.
- R Development Core Team, 2010. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Raabe, T., Wiltshire, K.H., 2009. Quality control and analyses of the long-term nutrient data from Helgoland Roads, North Sea. *J. Sea Res.* 61, 3–16.
- Reid, P.C., Edwards, M., Hunt, H.G., Warner, A.J., 1998. Phytoplankton change in the North Atlantic. *Nature* 391, 546.
- Reid, P.C., Hari, R.E., Beaugrand, G., Livingstone, D.M., Marty, C., Straile, D., Barichivich, J., Goberville, E., Adrian, R., Aono, Y., Brown, R., Foster, J., Groisman, P., Hélaoui, P., Hsu, H.-H., Kirby, R., Knight, J., Kraberg, A., Li, J., Lo, T.-T., Myneni, R.B., North, R.P., Pounds, J.A., Sparks, T., Stübi, R., Tian, Y., Wiltshire, K.H., Xiao, D., Zhu, Z., 2016. Global impacts of the 1980s regime shift. *Glob. Chang. Biol.* 22, 682–703.
- Robinson, C.T., Minshall, G.W., 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. *J. N. Amer. Benthol. Soc.* 5, 237–248.
- Robinson, J.V., Sandgren, C.D., 1984. An experimental evaluation of diversity indices as environmental discriminators. *Hydrobiologia* 108, 187–196.
- Rockström, J., Klum, M., Miller, P., 2015. *Big World, Small Planet*. Yale University Press.
- Sanders, H.L., 1968. Marine benthic diversity: a comparative study. *Am. Nat.* 102, 243–282.
- Scharfe, M., 2013. Analyse biologischer Langzeitveränderungen auf Basis hydro-klimatischer Parameter in der südlichen Nordsee (Helgoland) Hamburg. (Hamburg).
- Şen, Z., 1998. Point cumulative semivariogram for identification of heterogeneities in regional seismicity of Turkey. *Math. Geol.* 30, 767–787.
- Şen, Z., Habib, Z.Z., 1998. Point cumulative semivariogram of areal precipitation in mountainous regions. *J. Hydrol.* 205, 81–91.
- Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communication*. University of Illinois Press.
- Siegmund, F., Schrum, C., 2001. Decadal changes in the wind forcing over the North Sea. *Clim. Res.* 18, 39–45.
- Sommer, U., 1995. An experimental test of the intermediate disturbance hypothesis using cultures of marine phytoplankton. *Limnol. Oceanogr.* 40, 1271–1277.
- Steele, J.H., 1970. *Marine Food Chains*. University of California Press.
- Stirling, G., Wilsey, B., 2001. Empirical relationships between species richness, evenness, and proportional diversity. *Am. Nat.* 158, 286–299.
- Sturtz, S., Ligges, U., Gelman, A., 2005. R2WinBUGS: a package for running WinBUGS from R. *J. Stat. Softw.* 12, 1–16.
- Thomas, A., O'Hara, B., Ligges, U., Sturtz, S., 2006. Making BUGS open. *R News* 6, 12–17.
- Wiltshire, K.H., Boersma, M., 2016. Meeting in the middle: on the interactions between microalgae and their predators or zooplankton and their food. In: Gilbert, M.P., Kana, M.T. (Eds.), *Aquatic Microbial Ecology and Biogeochemistry: A Dual Perspective*. Springer International Publishing, Cham, pp. 215–223.
- Wiltshire, K.H., Dürselen, C.D., 2004. Revision and quality analyses of the Helgoland Reede long-term phytoplankton data archive. *Helgol. Mar. Res.* 58, 252–268.
- Wiltshire, K.H., Manly, B.F.J., 2004. The warming trend at Helgoland Roads, North Sea: phytoplankton response. *Helgol. Mar. Res.* 58, 269–273.
- Wiltshire, K.H., Malzahn, A.M., Wirtz, K., Greve, W., Janisch, S., Mangelsdorf, P., Manly, B.F.J., Boersma, M., 2008. Resilience of North Sea phytoplankton spring bloom dynamics: an analysis of long-term data at Helgoland Roads. *Limnol. Oceanogr.* 53, 1294–1302.
- Wiltshire, K.H., Kraberg, A., Bartsch, I., Boersma, M., Franke, H.D., Freund, J., Gebuhr, C., Gerdt, G., Stockmann, K., Wichels, A., 2010. Helgoland Roads, North Sea: 45 years of change. *Estuar. Coasts* 33, 295–310.
- Wiltshire, K.H., Boersma, M., Carstens, K., Kraberg, A.C., Peters, S., Scharfe, M., 2015. Control of phytoplankton in a shelf sea: determination of the main drivers based on the Helgoland Roads time series. *J. Sea Res.* 105, 42–52.
- Wootton, J.T., 2001. Causes of species diversity differences: a comparative analysis of Markov models. *Ecol. Lett.* 4, 46–56.