LIMNOLOGY and OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2025, 1–16

doi: 10.1002/lno.70280

RESEARCH ARTICLE

Hierarchical modeling of Baltic Sea phytoplankton reveals increasing cyanobacteria dominance

James Andrew de Haast [1,2*], **Aleksandra M. Lewandowska** [2], **Janne Soininen** [1]

[1]Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland; [2]Tvärminne Zoological Station, University of Helsinki, Hanko, Finland

Abstract

Understanding how phytoplankton communities respond to environmental changes is critical for mitigating the impact of changing oceans. To identify the main drivers of changes in phytoplankton community composition and species richness, hierarchical modeling of species communities (HMSC) was used to model the summer phytoplankton communities from 29 sites, sampled between 1972 and 2017, in the Helsinki Archipelago, Finland. Models were fitted to both occurrence and abundance data. Spatial–temporal random effects accounted for most of the variance explained, followed by sea surface temperature (SST) and total phosphorus for both models. Statistically supported relationships between SST and occurrence emerged for most species. Two statistically supported trait–environment relationships were detected; however, species responses to environmental variables were strongly linked to taxonomic relatedness. A negative relationship between species richness and temperature was found. The results indicated that, independent of seasonal succession, the abundance of cyanobacteria was predicted to increase with increasing temperature, while the abundance of diatoms was predicted to decrease. This trend was most notable in the hurdle model, suggesting that even if species are not completely lost, there is still a shift in dominance from diatoms to cyanobacteria with increasing temperature. Additionally, higher total phosphorus levels also resulted in increased abundance of cyanobacteria. The primary environmental drivers of changes in the community composition of phytoplankton in the Helsinki Archipelago were SST and total phosphorus; however, the community is not temporally stable. The Baltic Sea is becoming warmer; therefore, summer phytoplankton communities are expected to be increasingly dominated by cyanobacteria.

Understanding how marine plankton communities respond to the rapidly changing oceans is critical. Rising global temperatures drive increases in sea surface temperature (SST), and over the last decade this rate of change has accelerated (Garcia-Soto et al. 2021; Venegas et al. 2023). Rising global temperatures further impact oceans by reducing Arctic ice coverage (Kumar et al. 2020; Meier and Stroeve 2022), rising sea levels (Nerem et al. 2018; Frederikse et al. 2020) and altering ocean circulation (Peng et al. 2022). Ocean chemistry is also impacted by climate change, an example of which is higher atmospheric CO_2 levels resulting in ocean acidification (Bates et al. 2014). While anthropogenic CO_2 impacts the oceans at large, nutrient runoff from coastal settlements and rivers leads to eutrophication, resulting in harmful algal blooms (HAB) (Glibert and Burford 2017; Devlin and Brodie 2023). Phytoplankton make up the base of the aquatic food web; thus, changes in their community composition can result in cascading effects that have lasting impacts on other species. Likewise, climate change has also been shown to result in cascading effects down the food web, leading to changes in phytoplankton community structure (Murphy et al. 2020). Species distributions, and by extension the community composition of phytoplankton, have changed as a result of changing oceans, such as changes in ocean currents (Oziel et al. 2020), and in general as a result of long-term alterations in environmental conditions (Barton et al. 2015).

Climate change affects all oceans and seas; however, local conditions can accelerate or buffer against global trends. The Baltic Sea is one of the planet's fastest-warming seas, with SST

*Correspondence: james.dehaast@helsinki.fi

Associate editor: Bingzhang Chen

having increased at a rate of 0.4°C decade^{-1} between 1950 and 2020 (Stockmayer and Lehmann 2023). In line with the global trend, the rate of warming in the Baltic Sea has increased in recent years (Meier et al. 2022). The Baltic Sea is relatively shallow, with a mean depth of 53 m (Jakobsson et al. 2019). The semi-enclosed Baltic Sea is naturally susceptible to eutrophication due to the long residence time (26–29 years) of water (Döös et al. 2004). Additionally, the Baltic Sea is bordered by nine countries, home to approximately 85 million people (Snoeijs-Leijonmalm and Andrén 2017). Anthropogenic nutrients are known to be the primary driver of eutrophication in the Baltic. Nutrient input peaked in the 1980s but has decreased in recent decades with the implementation of improved wastewater processing (Andersen et al. 2017). Phytoplankton summer community composition has changed in the Baltic Sea over time; however, these changes were not related to eutrophication patterns (Olli et al. 2011). Pigment analysis indicated a decrease in the abundances of all phytoplankton groups other than cyanobacteria in the southern Baltic between 1999 and 2018 (Stoń-Egiert and Ostrowska 2022). As a result of increasing sea surface temperature, cold-water phytoplankton species are at risk of disappearing from the spring bloom in the southern and central Baltic Sea (Paul et al. 2023).

Flexible statistical approaches are required to quantify community changes over time, identify the underlying drivers, and make predictions under multiple future change scenarios. As communities are made up of species, these methods need to account for different species' responses to abiotic drivers and biotic interactions between species. Joint species distribution models (JSDMs) are a relatively new method for modeling species communities (Ovaskainen and Soininen 2011). Single species distribution models (SDMs), which predate JSDMs, can be "stacked" to make inferences and predictions at a community level (Guisan and Rahbek 2011; Calabrese et al. 2013). The stacked SDM approach results in a community prediction based on each individual species relationship to the covariates considered (Ferrier and Guisan 2006; Guisan and Rahbek 2011); thus, it misses important community assembly processes (Guisan and Rahbek 2011). Joint species distribution models avoid this by modeling taxa jointly, rather than independently as stacked SDMs do (Ovaskainen and Soininen 2011).

Hierarchical modeling of species communities (HMSC) is a Bayesian hierarchical JSDM that is strongly linked to community assemblage theory (Ovaskainen and Abrego 2020). HMSC models the joint structure of environmental filtering by allowing for the optional inclusion of trait profiles and phylogenetic relationships (Ovaskainen et al. 2017; Ovaskainen and Abrego 2020). This hierarchical structure improves the model performance overall; however, it is particularly notable when making predictions of rare species (Ovaskainen and Soininen 2011; Poggiato et al. 2021). HMSC allows for the estimation of several ecologically relevant parameters. These include the β parameters, which represent species–environment responses and thus the realized niche of each species. The parameter ρ represents the phylogenetic signal between species (i.e., phylogenetic structured responses to the environmental variables), while γ indicates the relationship between traits and the environment. Finally, residual species–species co-occurrences are captured by the Ω parameters. Poggiato et al. (2021) caution against blindly interpreting the residual correlation matrix produced by JSDMs as biotic interactions. This applies to the HMSC's Ω parameters as well; these should always be interpreted with respect to the random effect that they are related to. For example, co-occurrences in 100 km^2 plots should not be attributed to direct competition (Ovaskainen and Abrego 2020), but rather other scale-appropriate shared responses to unmeasured variables. The HMSC model makes use of hidden variables, otherwise known as latent factors, to model residual co-occurrence between species. Thus, some species co-occurrences might not be biotic in nature but linked to different species responding differently to latent factors; this is likely the case with temporal random effects. For example, spring temperatures are warming in the Baltic Sea, and species A requires cooler springs while species B requires warmer springs; the resulting co-occurrence will be a negative correlation between species A and B based on year. However, in this case, the driver is an unmeasured environmental variable rather than biotic interactions. These cautions apply to the interpretation of parameters and their ecological links. When applied correctly, JSDMs are very powerful explanatory and predictive tools.

This study aims to identify the major drivers of changes in phytoplankton community composition and species richness over the period 1972–2017 in the Helsinki Archipelago, Finland, using HMSC. This study adds to Olli et al.'s (2022) study on phytoplankton communities in the Helsinki Archipelago, which utilized direct ordination, by investigating phytoplankton responses at a species level. Olli et al. (2022) found that the primary explanatory variable for community differences was the sampling year, followed by nutrient loading at sites nearest to nutrient runoff sources. Based on previous findings, it is hypothesized that the sampling year will be a major explanatory variable for community differences in Baltic Sea phytoplankton. The use of HMSC allows for the identification of trait-environment relationships and information about shared phylogenetic responses. Thus, HMSC allows for testing the hypothesis that species responses to environmental variables are taxonomically structured. The use of a JSDM allows for species-level predictions to be made and these can be aggregated. Thus, it allows for both community summary statistics (e.g., richness) and changes in group-level dynamics, such as shifts between diatoms, dinoflagellates, and cyanobacteria, to be identified as the net result of changes in their constituent species. Based on the results of previous studies (Hällfors et al. 2013; Andersson et al. 2015; Anderson et al. 2021; Benedetti et al. 2021), SST and nutrients are

hypothesized to influence community composition at a group level, specifically favoring cyanobacteria species.

Methods

Study area and data

Data obtained by Olli et al. (2022) from the City of Helsinki Urban Environment Division were utilized. These data consist of phytoplankton counts and associated environmental observations from the Helsinki Archipelago, located between 24.5° and 25.4° E at a latitude of 60° N (Fig. 1), over a 52-year period (1966–2018). The study area contained 29 stations, with a depth range of 2.5–51 m (median 18 m); all but one of these stations were located within 11 km of the mainland coastline. The furthest station was 23 km from the coastline. Nutrient levels in the region were relatively high, particularly at the stations nearest Helsinki, and peaked in the 1970s.

To focus on summer phytoplankton communities, only observations between 1 June and 30 September were utilized in this analysis. The data were filtered to retain samples with observations for water temperature, salinity, total nitrogen, and total phosphorus, known to be highly influential environmental variables for phytoplankton in the Baltic Sea (Olli et al. 2011; Wasmund et al. 2011; Berthold et al. 2025). All samples were taken at a depth of between 5 and 10 m (depending on station depth) and contained station-specific values for water depth, the distance to the mainland coastline, longitude and latitude. The filtered dataset contained 2703 unique phytoplankton and water chemistry samples, with a reduced temporal range (1972–2018) and southern spatial extent. The temporal range was reduced to exclude 2018, as only three offshore stations were sampled. The inclusion of this year would confound spatial and temporal effects in the model. The phytoplankton data contained 566 different taxa, with 410 of these identified to a species or subspecies level. These data included ciliates containing autotrophic endosymbionts (e.g., *Mesodinium rubrum*) and the heterotrophic *Telonema subtile*. The observations that were not resolved to at least the species level were excluded to maintain a consistent taxonomic level. To reduce the influence of rare species, only species present in at least 5% (135) of the samples were retained. Thus, the final dataset included 80 species and covered a temporal range of 45 years (1972–2017).

Trait data for the binary traits; nitrogen fixation, mobility, presence of silica, and nutrient source (auto-, hetero-, or mixotrophy), were obtained from Klais et al. (2016) as these are functional phytoplankton traits (Litchman and Klausmeier 2008). These traits were also well-defined for species in the existing database. The taxonomic IDs (Aphia) were verified against the World Register of Marine Species (WoRMS 2024) to account for taxonomic changes since 2015. Genus-level traits were used for three species, for which species-level trait information could not be obtained.

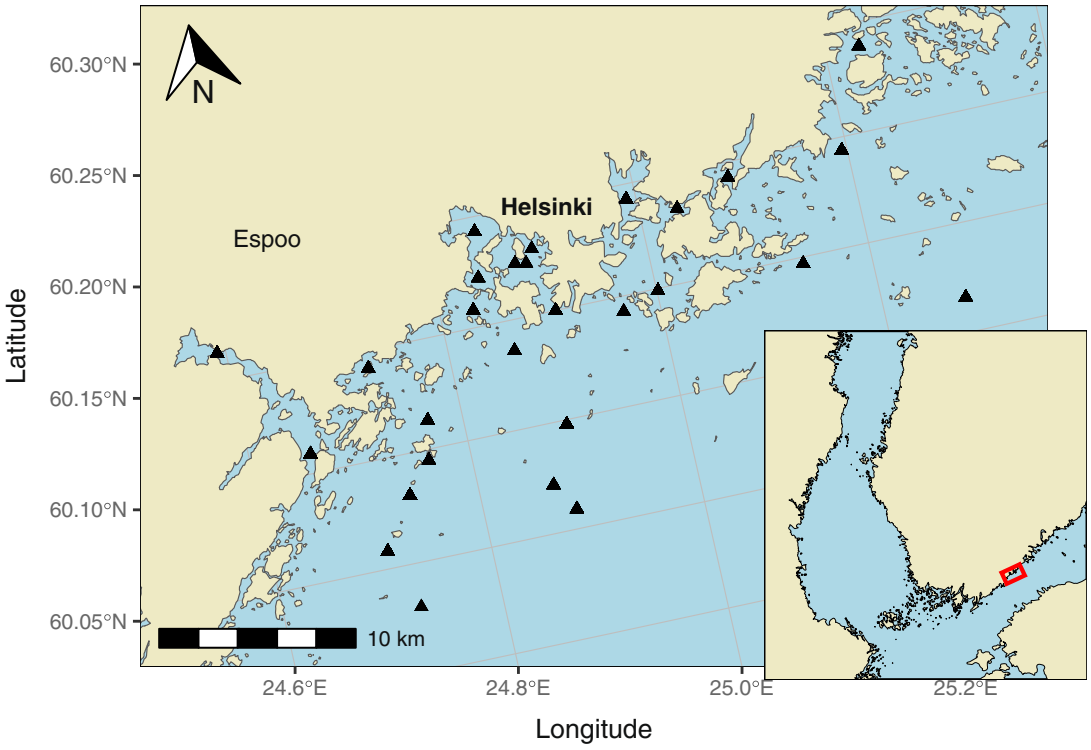

Fig. 1. Map of the Helsinki Archipelago showing the location of the sampling sites; the inlay indicates the location of the study area (red box) relative to Southern Finland.

Modeling

Prior to model construction, the pairwise correlations between environmental variables and sampling year were analyzed for strong correlation (> 0.75) to avoid multicollinearity. Depth and distance from the coast were highly correlated with each other. Depth was retained due to the fragmented nature of the coast. Nutrient loading is known to be linked to year and location; however, there was no strong linear correlation between year and total nitrogen or phosphorus over the full sampling period (Supporting Information Fig. S2). Note that at the start of the temporal range, a relationship between year and nutrient concentration was present at some of the sites closest to Helsinki. Total nitrogen and phosphorus appeared to be correlated at lower nutrient loads; however, the relationship displayed heteroscedasticity. Spearman's rank correlation coefficient indicated a strong correlation (> 0.75); thus, total nitrogen was excluded as it contains both dissolved inorganic nitrogen (DIN) and nitrogen produced by nitrogen fixation. Many cyanobacteria, which are present in the summer community, are nitrogen fixers, adding to the total nitrogen pool (Larsson et al. 2001; Wulff 2017). As a result, total phosphorus was considered a more reliable measurement of eutrophication.

Potential drivers of summer phytoplankton community composition were investigated using HMSC (Ovaskainen et al. 2017; Tikhonov et al. 2020). Sea surface temperature, salinity, total phosphorus, station depth, and day of the year were included as fixed effects in the model. Additionally, the inclusion of average temperature in April and year as fixed effects was tested using candidate models. All variables, except station depth and year, were included as second-order polynomials to account for species niche optima being present within the sampled ranges (Peltonen and Weigel 2022; Weigel et al. 2022). Site coordinates were included as an explicit spatial random effect. To account for annual stochasticity, unrelated to the fixed effect of year, sampling year was included as a categorical random effect (Weigel et al. 2022). Taxonomic relatedness was included as a proxy for phylogenetic differences (Tikhonov et al. 2024). The model requires all taxonomic units to be at the same level (i.e., species, genus, or other OTU). For the purpose of taxonomic relatedness, subspecies, forma, and varieties were treated as though they were species, thus one taxonomic level away from genus. The following taxonomic levels were used: Kingdom, Phylum, Order, Family, Genus, and Species, with a distance of one between each level.

Model comparison was performed on candidate models (Supporting Information Table S1), to determine whether model performance was improved by the inclusion of fixed effects relating to sampling year. Models were compared using the Widely Applicable Information Criterion (WAIC) as the primary information criterion (Watanabe 2010). All models were implemented using the R (R Core Team 2023) package Hmsc-R (Tikhonov et al. 2024) and the Python-based Hmsc-HPC (Rahman et al. 2024). Hmsc-HPC is a TensorFlow-based sampling routine which is executed in Python; this approach increases the sampling speed. High-performance computing (HPC) was used for model fitting; scripts were run on the University of Helsinki Ukko Cluster. The maximum number of latent variables related to year and location was set to 6 and 11, respectively. All models were fitted assuming default prior distributions (Ovaskainen and Abrego 2020).

Model convergence was evaluated using potential scale reduction factors (psrf) (Gelman and Rubin 1992), a target value of < 1.1 was set for convergence. However, convergence of the Ω parameter is known to be challenging for models that contain latent factors, especially in non-normal models (Ovaskainen and Abrego 2020). A median psrf value of < 1.15 was considered acceptable for the Ω parameters. To achieve acceptable convergence, models were fitted using 281,250 burn-in steps, followed by 562,500 sampling steps. Sampling was thinned by 750, resulting in 750 retained posterior samples. All models were fitted using 4 chains. Default priors were used for all parameters (Ovaskainen et al. 2017).

To account for zero inflation in the data, a hurdle model approach was used. Hurdle models consist of an occurrence model and an abundance conditional on presence model (Cragg 1971). The occurrence model was fitted to binary data calculated from the observed species abundances, recorded as biomass ($\mu g\, L^{-1}$). The abundance conditional on presence model was fitted to log-transformed abundance data. Prior to log transformation, zero observations were removed; thus, they were treated as missing observations, allowing the model to interpolate during fitting. The log-transformed abundance data were scaled using *z*-scoring during HMSC fitting; as a result, the parameter estimates from the conditional abundance are uninformative (Ovaskainen and Abrego 2020). Therefore, only the parameter estimations from the occurrence model were reported. Back-transformation of scaled community data was performed when making predictions. The log-transformed conditional abundance predictions were back-transformed. Community predictions were made by multiplying the predicted values from the occurrence and conditional abundance models.

The explanatory and predictive power of both models was evaluated. Explanatory power was evaluated by using the full dataset for both training the model and making predictions. Predictive power was evaluated based on the models' ability to make predictions from separate training data, using k-folding with 5 folds. The following metrics were used to evaluate the predictions: Tjur's R^2 and the Area Under the Curve (AUC) were used for the occurrence model (Pearce and Ferrier 2000; Tjur 2009), while R^2 values were used for the conditional abundance model (Ovaskainen and Abrego 2020). The model was considered over-fitted if the predictive power was less than 4/5 of the explanatory power. Final model selection was based on the combined performance of the occurrence and conditional models, since combining these models required them to be equivalent.

Results

The model selection metrics indicated that the removal of neither the fixed effect of year nor mean April temperature improved model performance. Thus, considering both the abundance and occurrence models, the best candidate model included random effects for year and spatial distance between sites, and fixed effects for temperature, salinity, total phosphorus, mean April temperature, day of the year and year (*see* Supporting Information Table S1).

Convergence and validation

Both the conditional abundance and occurrence models had good convergence for their respective β and γ parameters (mean < 1.02). However, both models had worse convergence for the Ω related to the random effect of year (mean: 1.03 and 1.15, Supporting Information Fig. S3).

Neither model displayed clear indicators of overfitting, with near equal predictive and explanatory power across 5 folds (Supporting Information Fig. S4). However, the explanatory power of the conditional model is expected to be higher than the predictive power since zeros are encoded as missing data.

Drivers of the phytoplankton community

The random effects of sampling year accounted for the highest proportion of the variance in both occurrence and conditional abundance models (mean: 15.8 and 13.4%, respectively), followed by the fixed effect of year (mean: 9.5 and 11.1%, respectively, Fig. 2). In both models, this was followed by the random spatial effect (mean: 3.4 and 10.3%, respectively, Fig. 2). For most species, environmental factors accounted for less of the total variance than the fixed effect of year and random effects combined. Overall, total phosphorus and SST were the most influential environmental factors for occurrence (mean: 1.9 and 1.6%) and conditional abundance (mean: 7.6 and 2.0%, Fig. 2). Compared to the random effects, their influences were small. Salinity, mean April temperature, and water depth each accounted for < 1% of the total variance for species occurrence; however, these variables were slightly more influential in explaining conditional abundance (mean: 1.9, 1.5, and 3.8%, respectively, Fig. 2). The amount of variance accounted for by seasonality (day of the year) differed between species in both models; however, the mean variance explained across species was similar between the occurrence and abundance models (mean: 3.1 and 4.8%, respectively, Fig. 2).

For several species, occurrence and conditional abundance were explained by different variables (Fig. 2). For example, while the presence of species such as *Borghiella pascheri*, *Plagioselmis prolonga*, and *Mesodinium rubrum* was primarily explained by both the random and fixed effects of sampling year, environmental factors influenced their conditional abundances. For all three species, the environmental variable that accounts for the most variance in their conditional abundances is total phosphorus. Note that the highest levels of total phosphorus were present at the start of the sampling period, and these levels decreased until the 90s, after which they stabilized (Supporting Information Fig. S1).

Differences in mean variance explained across species within common groupings were also detected (Fig. 3). The majority of species included in the model were part of the following groups: diatoms (22), green algae (21), cyanobacteria (15), or dinoflagellates (14). Variance partitioning differed for both models between these groups. Seasonality accounted for a larger amount of the total variance in the occurrences of dinoflagellates and diatoms, compared to cyanobacteria and green algae. Total phosphorus and SST accounted for a notable proportion of the variance in occurrences for dinoflagellates, diatoms, and cyanobacteria. Total phosphorus accounted for more variance in all these groups in the conditional abundance model. The single largest contributor to explained variance in the conditional abundances of dinoflagellates was total phosphorus. Additionally, station depth accounted for a notable proportion of the variance in the conditional abundances of green algae.

Species response to environmental factors

For the majority of species, occurrence was influenced by total phosphorus and/or SST with a non-zero posterior probability of $\geq 95\%(\Pr(\beta \neq 0) \geq 95\%)$ (Fig. 4). Additionally, there were $\geq 95\%$ posterior probabilities for non-zero responses to the day of the year and/or sampling year for nearly all species. Many species responded to salinity with non-zero posterior probabilities $\geq 95\%$; however, both overall and at a species level, these responses account for a very small proportion of the total variance in occurrences (Figs. 2 and 4). Only cyanobacteria and chlorophyta (green algae) species had $\geq 95\%$ posterior probabilities of non-zero responses to mean April temperature. The statistically supported beta values for SST, day of the year, and mean April temperature were most often positive for the linear term and negative for the squared term. The linear response to sampling year was more often negative than positive. The direction of the response to total phosphorus was more variable.

Several species showed linear responses to total phosphorus, indicated by 95% posterior support for a non-zero beta for the first polynomial term but not for the second (e.g., $y = \beta_1 x + 0x^2$). These associations accounted for a notable proportion of the variance explained by environmental factors, especially for species such as the dinoflagellates *Dinophysis norvegica* and *D. acuminata*, the diatoms *Skeletonema subsalsum*, *Chaetoceros holsaticus*, *C. wighamii*, and *C. danicus*, the silicoflagellate *Ebria tripartita*, the golden-brown algae *Dinobryon faculiferum*, the cyanobacteria *Pseudanabaena limnetica* and *Planktothrix agardhii*, and the green algae *Koliella spiculiformis*. In the case of *P. agardhii*, total phosphorus was the most important explanatory variable for species occurrence; however, it explained much less of the variance in its conditional

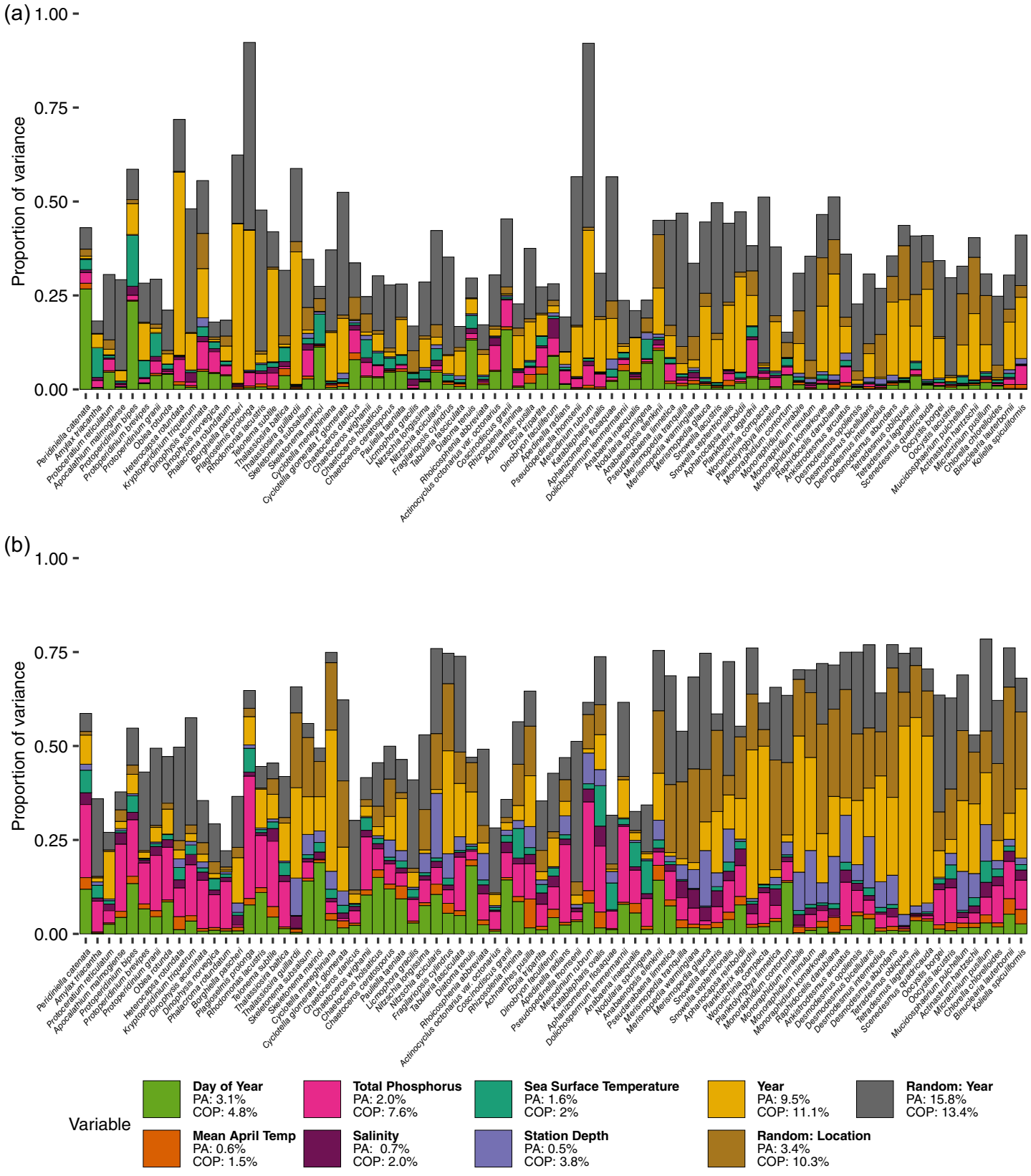

Fig. 2. Proportion of raw variance explained by each variable for the (**a**) occurrence and (**b**) conditional abundance model. The mean variance explained by each variable for the occurrence (PA) and conditional abundance (COP) models are shown in the key.

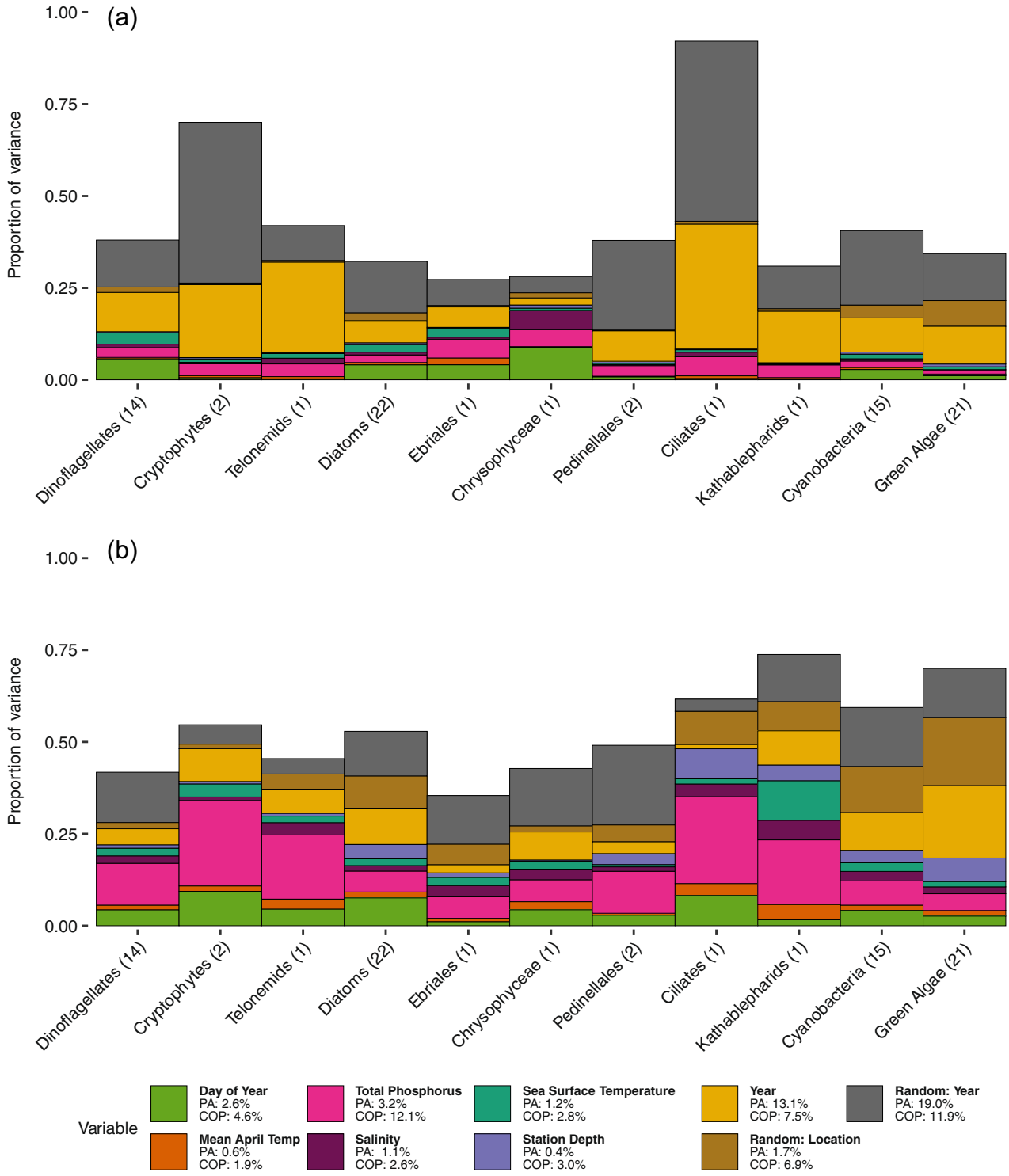

Fig. 3. The mean proportion of raw variance for common species groups, explained by each variable for the (**a**) occurrence and (**b**) conditional abundance model. The mean variance explained by each variable for the occurrence (PA) and conditional abundance (COP) models are shown in the key. Species are grouped at the finest taxonomic level associated with a common name, typically class. The number of species in each group is reported in parentheses. The order of groups matches the order of species in Fig. 2.

abundance. The difference in response between diatom species within the genera *Skeletonema* and *Chaetoceros* must be noted. Unlike *S. subsalsum*, *S. marinoi* did not respond to total phosphorus. Within the genus *Chaetoceros*, *C. holsaticus* and *C. danicus* had positive linear responses to total phosphorus, while *C. wighamii* had a negative linear

response, and *C. ceratosporus* did not respond to phosphorus (Fig. 4).

Species occurrence responses to environmental factors were strongly linked to taxonomic relatedness, as indicated by the phylogenetic correlation parameter (ρ: mean = 0.83, 95% CI: 0.70–0.94). Two statistically supported trait-environment relationships were found ($\Pr(\gamma \neq 0) \geq 95\%$, Fig. 5). The presence of a silica cell wall had a negative linear response to salinity, while the ability for nitrogen fixation had a negative linear response to mean April temperature (Fig. 5). The ρ parameter suggests the presence of additional taxonomically linked traits that account for the realized species niches. The taxonomic structure of species responses to the environment (Fig. 4) was particularly noticeable at the genus level across all three

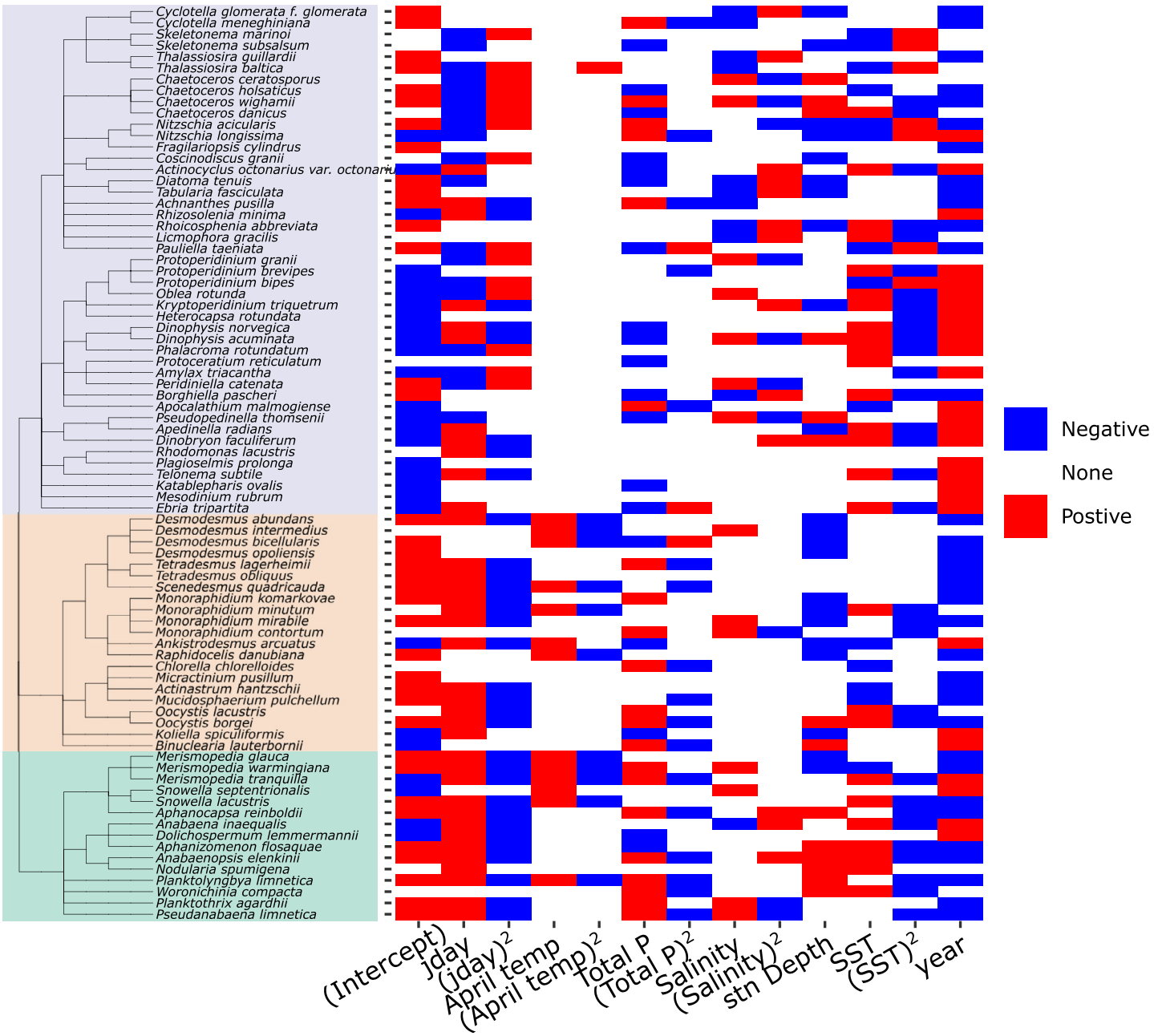

Fig. 4. Responses of species occurrences to environmental factors. Colors indicate > 95% posterior support for non-zero β values (blue negative, red positive). The tree represents the taxonomic relationship between species. The major divisions are indicated with color and from top to bottom are Protista (Blue), Plantae (Chlorophyta) (Orange), and Bacteria (cyanobacteria) (Cyan). SST refers to Sea Surface Temperature, jday is the day of the year, April temperature is the mean average temperature of the month of April for the sampling year, and total P is total phosphorus. Squared terms represent the β value associated with the second-order polynomial term.

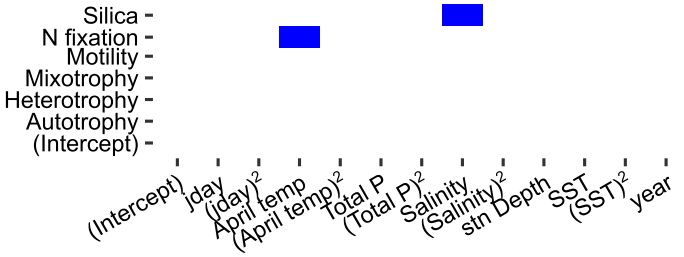

Fig. 5. Responses of trait occurrences to environmental factors. Colors indicate > 95% posterior support for non-zero γ values (blue negative, red positive). SST refers to Sea Surface Temperature, jday is the day of the year, April temperature is the mean average temperature of the month of April for the sampling year, and total P is total phosphorus. The silica trait represents the presence of silica in the cell walls, N fixation is the ability to fix nitrogen. Squared terms represent the γ value associated with the second-order polynomial term.

kingdoms present (Bacteria, Protista, and Plantae). Shared statistically supported responses based on genus appear less common among chlorophyta (green algae, Fig. 4). However, the occurrences of chlorophyta species were less responsive to environmental factors in general compared to the other major groups.

Community trends

The occurrence model predicted a negative relationship between SST and overall species richness, even when all other variables are held at their median values (Fig. 6). No notable trend between total community abundances and SST was predicted by the hurdle model. Although the median predicted value increased between 5 and 15°C, it decreased and leveled off across higher temperatures.

Predictions of community composition were made across different SSTs for the median sampling day (day 211, 30 July), with all environmental variables held at their median values. These predictions indicated changes in proportional community composition between different planktonic groups. The predicted proportion of cyanobacteria increased, while diatoms decreased with increasing temperature (Fig. 7). These patterns were more pronounced in terms of abundances modeled by the hurdle model (Fig. 7b), indicating that even in the absence of local extinctions there is a shift from diatom dominance to cyanobacterial dominance with increasing temperature. The predicted proportion of abundance made up of dinoflagellate species increased with increasing temperature, until 15°C, after which it decreased. The abundance of cyanobacteria was predicted to exceed that of dinoflagellates at temperatures above 8°C. Sea surface temperatures below 15°C are uncommon in the study area for late July. Above 15°C cyanobacteria and green algae species make up the majority of species in the community (Fig. 7a).

Total phosphorus concentrations of over 20 μg L^{-1} were only observed in six samples from before 1980. The predicted proportion of cyanobacteria, green algae, and diatom species in the community increased or remained relatively constant with increased phosphorus, at the expense of all other groups (Fig. 8a). For cyanobacteria species, this increase plateaued at total phosphorus values of around 20 μg L^{-1}. The hurdle model predicted different trends in the total abundances of groups. Cyanobacteria were predicted to dominate the community in terms of abundance. Despite an increase in the proportion of diatom species in the community, the predicted proportion of total abundance made up of diatoms decreased with increased phosphorus (Fig. 8a,c). Likewise, despite the constant decrease in the proportion of the total species in the community made up of dinoflagellate species, the predicted proportion of total abundance made up of dinoflagellate species increased with increased total phosphorus below 5 μg L^{-1}, decreasing after this point (Fig. 8a,c).

The predicted changes in community composition in response to seasonality (day of the year) were similar both in terms of proportional species richness and abundance (Fig. 8). The proportion of diatoms decreased, while the cyanobacteria increased during the first part of summer. This

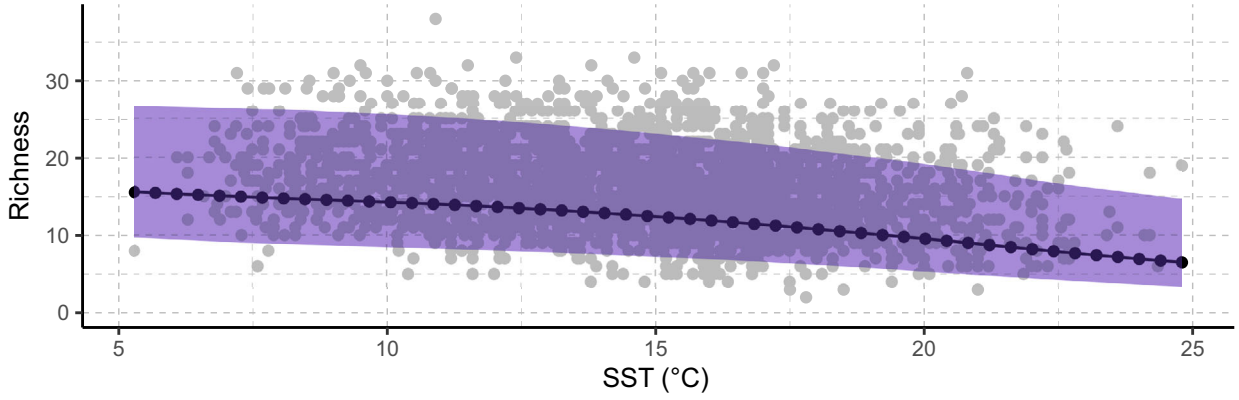

Fig. 6. The predicted relationship between species richness and Sea Surface Temperature (SST), when all other variables are held at their median value. Median posterior values are indicated by the black points with the 95% credibility interval indicated in blue; gray points indicate raw observations.

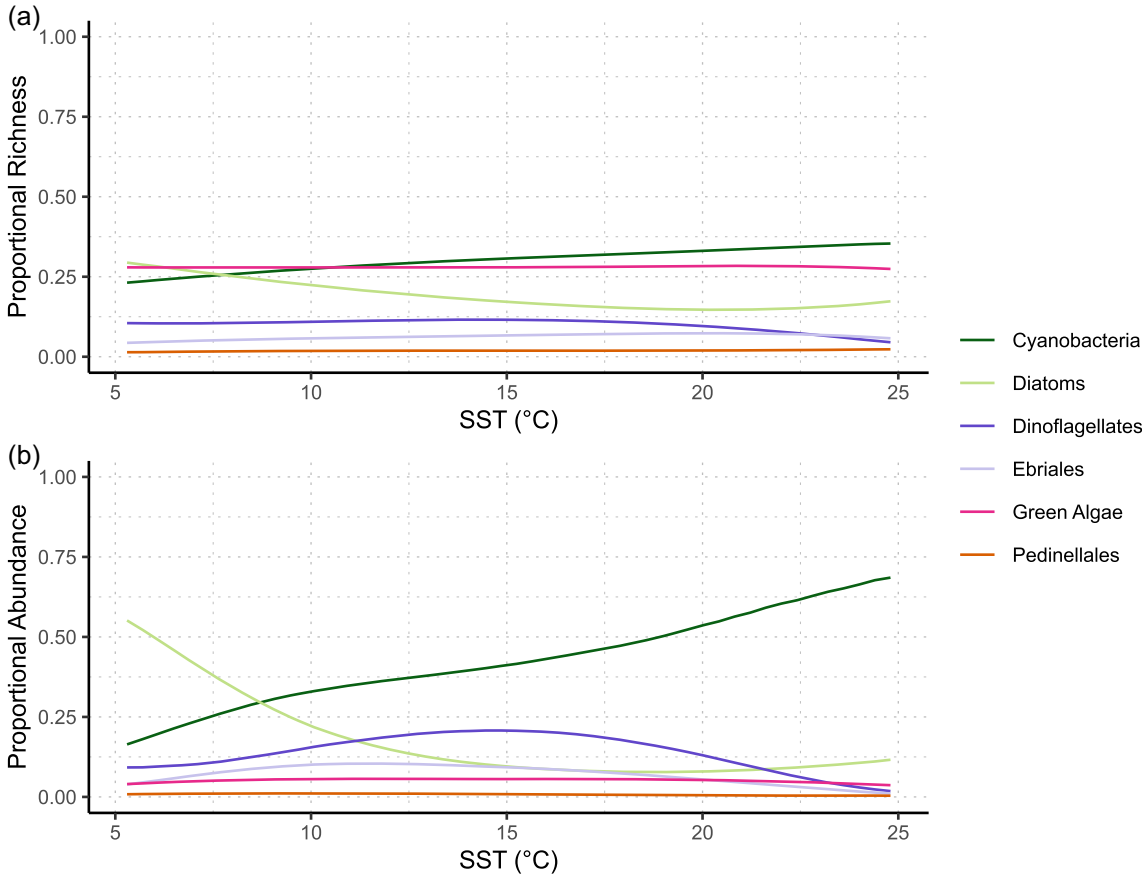

Fig. 7. Median proportional composition in terms of predicted (**a**) species richness and (**b**) abundance of common phytoplankton groups in response to Sea Surface Temperature (SST) change. Only groups that accounted for at least 1% of the proportional richness and abundance are included (excluded groups: Cryptophytes, Telonemids, Chrysophyceae, Ciliates, and Kathablepharids).

leveled off towards day 212 (31 July) for both groups, and the trend inverted after day 237 (26 August).

Discussion

The results indicated that the primary drivers of species occurrences, abundances, and community composition were sampling year, location, total phosphorus, and SST. Additionally, even within the summer months, seasonality influenced the phytoplankton community structure. The use of a hurdle model allowed for the detection of differences in the variance explained by each variable for species occurrences and abundances. Spatial–temporal variables (the fixed effect of year and the random effects) accounted for the vast majority of the variance explained for almost all species in the occurrence model. However, the ratio between the variance explained by spatial–temporal variables and environmental variables was more balanced for the conditional abundance model. This suggests a potential mismatch between the drivers of species occurrences and abundance in the region.

The results suggest that multiple variables act together in shaping phytoplankton community composition. These include the measured environmental variables as well as unmeasured variables and processes such as stochasticity, dispersal, underwater irradiance, biotic and trophic interactions. The relatively small amount of variance explained by total phosphorus and SST suggests that while they are the most important measured environmental variables, they alone were not the key determinants of species distributions in the Helsinki Archipelago over the past four decades.

Temporal and spatial effects

Random temporal and spatial effects accounted for the majority of the variance explained for both conditional abundance and occurrence models. The random effect of year likely captured environmental variables acting on an annual timescale, in addition to biotic factors, such as immigration, local extinctions, and interspecific competition. Temporally variable factors such as the timing and nature of the earlier blooms (Wasmund et al. 2011), rainfall (Thompson et al. 2015), winter temperatures (Evstigneev et al. 2023), wind intensity (Dickson and Reid 1983; Crawford et al. 2020; Mesman et al. 2022), and light intensity (Zhang et al. 2022a) are known to influence phytoplankton community dynamics.

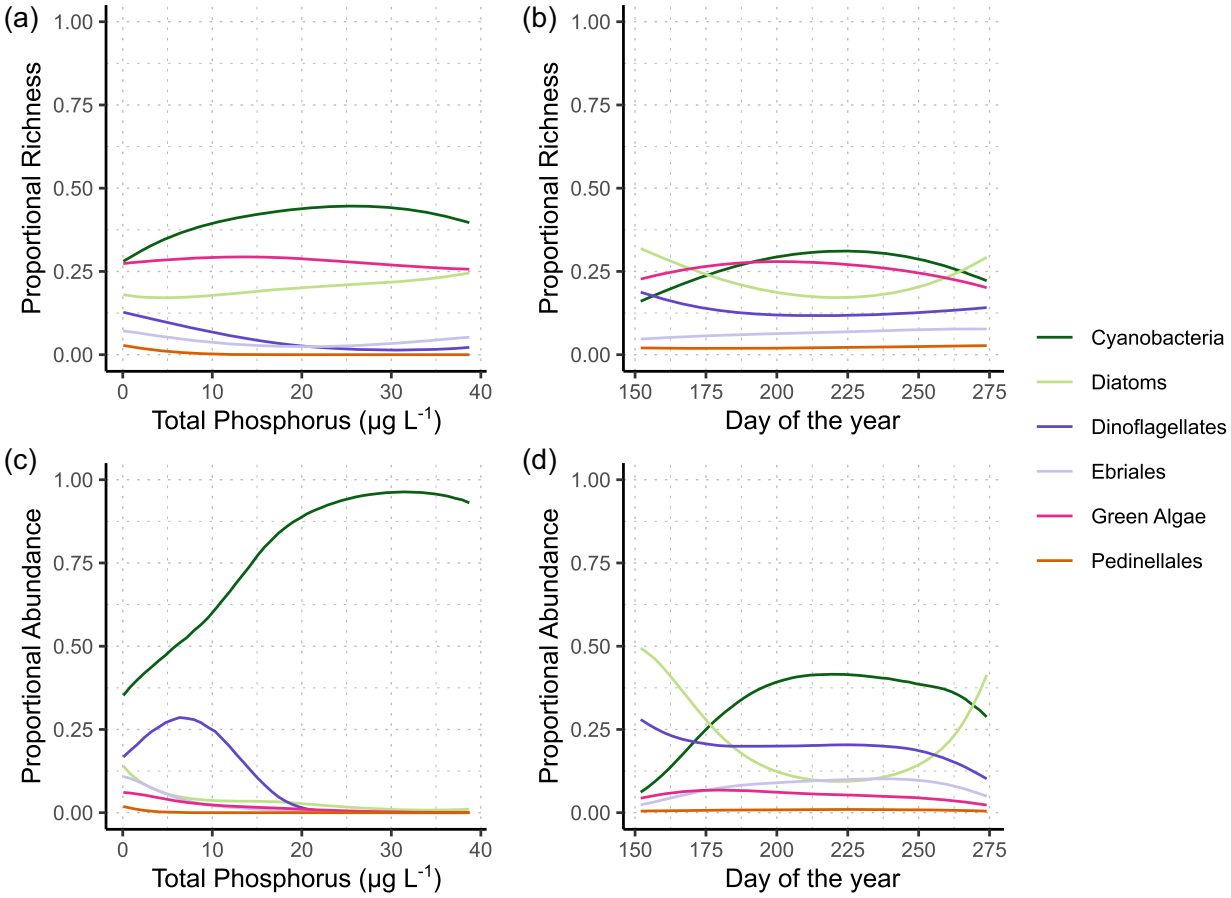

Fig. 8. Median proportional composition in terms of predicted species richness (top row) and abundance (bottom row) of common phytoplankton groups in response to changes in total phosphorus (**a** and **c**) and day of the year (**b** and **d**). Only groups that accounted for at least 1% of the proportional richness and abundance are included (excluded groups: Cryptophytes, Telonemids, Chrysophyceae, Ciliates, and Kathablepharids).

Additionally, the fixed effect of year captures species turnover, accounting for extinctions and emergences. The occurrences of several species were found to be almost entirely explained by year; these species typically emerged or disappeared partway through the sampling period. For example, the dinoflagellate species *Heterocapsa rotundata* and *Borghiella pascheri* disappeared from the summer community in 1985 and 1995, respectively. The model indicated that both species responded to changes in SST. However, fully untangling the drivers of these changes remains challenging, since the species did not re-emerge. The disappearance of the cyanobacteria species *Snowella lacustris* was followed by the emergence of its sister species *S. septentrionalis*, while the disappearance of the sister green algae species *Oocystis borgei* and *O. lacustris* was followed by the emergence of the ciliate *Mesodinium rubrum*.

These species turnover dynamics were captured by temporal effects (primarily the fixed effect of year); thus, explaining why the sampling year was the single most important explanatory variable. The HMSC results support previous findings that the phytoplankton community present in the Helsinki Archipelago is not temporally stable but rather exhibits constant species turnover (Olli et al. 2022). Species turnover can be induced by fluctuations in the rate of temperature change as temperature sensitivity differs between species (Pinsky et al. 2025).

Location may be a proxy for physical and biotic factors and is strongly linked to species dispersal patterns. The distributions of many phytoplankton species in the region were explained by location. Salinity accounted for less variance than expected; however, this was the result of the narrow salinity range (0–6.9 psu) covered by the study, which is expected to be tolerated by most of the brackish species (Olli et al. 2019). Freshwater species enter the system primarily via rivers, and this information was, in part, captured by the latent factors related to site location. Station depth did not explain species occurrences; however, it accounted for a notable proportion of variance in the conditional abundances of many species. Station depth was highly correlated to distance from the shore; thus, station depth might act as a proxy for the shore effect for some species. Additionally, location also captures environmental factors such as wave exposure (Stockwell et al. 2020), current (Font-Muñoz et al. 2017), and

wind patterns (Cyr 2017; Mesman et al. 2022), which are known to influence community dynamics in phytoplankton. Location was notably a better explanatory factor for conditional abundances, indicating that the latent variables related to location influenced co-abundance patterns more than co-occurrence. Dinoflagellate species occurrences and conditional abundances were poorly explained by both location and station depth, in contrast to Cyanobacteria and Green Algae (Fig. 3).

Richness and community responses

Species richness increased in the Helsinki Archipelago prior to 2000 and remained relatively stable until the end of the study period (2018) (Olli et al. 2022). The results showed a negative relationship between summer SST and species richness (Fig. 6). Temperature is known to be a major driver of changes in phytoplankton species richness, although this relationship is not monotonic (Righetti et al. 2019; Benedetti et al. 2021). A negative relationship is expected between phytoplankton species richness and mean annual temperatures below 10°C (Righetti et al. 2019). Thus, provided that the mean annual temperature of the Baltic Sea remains below 10°C, increased summer temperatures would be expected to reduce phytoplankton species richness. However, increases in SST have been linked to greater immigration of warm-adapted species and thus increased richness (Beaugrand et al. 2010). The high volume of international maritime traffic in the Baltic Sea (HELCOM 2018), provides a route for the introduction of warm-adapted species. Despite the undersaturated nature of the Baltic Sea phytoplankton species pool (Olenina et al. 2010), the presence of sea-ice and frigid SSTs in winter has likely hindered the establishment of sustained warm-water species populations.

Independent of the natural transition between spring and summer communities, increased SST favored a shift from diatom to cyanobacteria dominance in the Helsinki Archipelago (Fig. 7). Phytoplankton species composition is known to be influenced by SST (Hällfors et al. 2013; Anderson et al. 2021; Benedetti et al. 2021). An increase in SST over the past four decades was found to have resulted in increased biovolume of cyanobacteria in summer in the Baltic Sea, although this response was found to differ between basins (Olofsson et al. 2020). However, this increase has not been monotonic (Kahru and Elmgren 2014). Part of the inter-annual variation in the frequency and magnitude of cyanobacteria blooms can be explained by the availability of phosphorus (Tamminen and Andersen 2007; Vahtera et al. 2010). Total phosphorus peaked in the late 1970s and has constantly decreased since, which matches known patterns of nutrient inflow in the Helsinki Archipelago (Andersen et al. 2017). Despite this known temporal trend, total phosphorus was not correlated with sampling year in the dataset (Supporting Information Fig. S1). High phosphorus levels are associated with changes in the community composition within the cyanobacteria (Andersson et al. 2015), as well as with overall increased cyanobacteria biomass (Eilola et al. 2009). The results of the hurdle model support this. Additionally, the proportional abundance of dinoflagellate was shown to increase with total phosphorus at levels below 5 μg L^{-1} (Fig. 8c). This response is notable as total phosphorus levels above 5 μg L^{-1} have become extremely rare since 1995. This supports the hypothesis that both SST and phosphorus play a role in driving phytoplankton community structure in the region.

Riverine transport is the primary method by which silicate enters sea water (Tréguer and De La Rocha 2013). Freshwater inflow is associated with lower salinity. Thus, lower salinity values likely overlap with increased silicate levels due to increased river input or proximity to river mouths. The detected negative association between the presence of silicate cell walls and salinity is likely driven by silicate. The trait-environment relationship between nitrogen fixation and mean April temperature is likely more direct. While all nitrogen fixers observed in this study were cyanobacteria, many of the observed cyanobacteria species were not nitrogen fixers. Higher mean April temperatures are indicative of an early summer and therefore earlier peaks of cyanobacteria (Berner et al. 2018). At the species level, the observed nitrogen-fixing species did not respond to mean April temperature, while most of the other cyanobacteria species did. Thus, the negative relationship between the presence of nitrogen fixers and mean April temperature is likely driven by interspecific differences in thermal and seasonal responses of cyanobacteria species.

HMSC: Advantages and limitations

The HMSC model allows for many community ecology questions to be addressed simultaneously (Ovaskainen and Abrego 2020). The relationship between species occurrences, traits, and environmental conditions (the fourth-corner problem) forms the basis of the increasingly popular trait-based approach to functional ecology. HMSC inherently addresses this by allowing trait and phylogenetic information to be included in niche modeling. The results indicated two trait-environment relationships for the included traits. However, as hypothesized, there was a strong phylogenetic signal in species responses to environmental variables, suggesting the presence of one or more unaccounted-for phylogenetically structured traits that influence species' environmental responses. Additionally, utilizing HMSC allowed for species co-occurrences, their relationships to various environmental variables, and the impact of random spatio-temporal effects to be directly addressed using a single model. This would not have been possible with traditional single-species distribution models (SDMs) or multivariate statistical methods.

In the context of long-term datasets, the structure of HMSC supports many different study designs and allows for the use of community data that is binary, continuous, or a

combination of both; thus, making it applicable to datasets that were collected for various purposes. This is particularly useful for creating models based on long-term sampling, much of which was not conducted with such statistical methods in mind. As is common for long-term datasets, in the dataset analyzed in this study, many potential explanatory environmental variables were not measured consistently or at all over the sampling period. These were, in part, captured by random effects in the HMSC model, which capture unmeasured processes that represent both known unknowns and unknown unknowns. However, an over-reliance on latent variables accounting for unmeasured fixed effects limits the interpretation of the random effects. This represents a limitation in the current model for the Helsinki Archipelago, since both location and sampling year are believed to capture environmental variables for which data could not be obtained. The Bayesian nature of HMSC allows for the inclusion of informative priors, which allows prior knowledge to be included in new models. However, informative priors are currently rarely used in HMSC models. Finally, uncertainty is important in predictive modeling; HMSC allows the uncertainty in parameter values to be reflected in predictions.

The Baltic Sea has become warmer and fresher over time (Belkin 2009; Meier et al. 2022; Kankaanpää et al. 2023). Future predictions indicate spatial and temporal variation in these changes; however, the pervasive general trend is an increase in temperature. Additionally, growing populations and changing weather patterns may increase phosphorus input, further shifting the system towards increased cyanobacteria. Many cyanobacteria species form toxic blooms that negatively impact consumers and human health (Zhang et al. 2022b; Dos Reis et al. 2023). Previously, cyanobacteria were considered to be a poor food source for zooplankton; however, recent studies have shown this to be uncertain (Hogfors et al. 2014; Motwani et al. 2017; Suikkanen et al. 2021; Novotny et al. 2023). Additional methods are thus required to understand the wider implications of increasing cyanobacteria dominance in the summer phytoplankton community.

Author Contributions

James A. de Haast: Formal analysis (lead); writing – original draft (lead); writing – review and editing (equal). Aleksandra M. Lewandowska: Review and editing (supporting) and conceptualization (equal). Janne Soininen: Review and editing (equal) and conceptualization (equal).

Acknowledgments

This research was funded by the European Union's Horizon Europe project ACTNOW: Advancing understanding of Cumulative Impacts on European marine biodiversity, ecosystem functions and services for human wellbeing (No. 101060072). Open access publishing facilitated by Helsingin yliopisto, as part of the Wiley - FinELib agreement.

Data Availability Statement

That data and code that support the findings of this study are openly available on GitHub at https://github.com/Lord-Rivers/Helsinki_Bay_HMSC.

References

Andersen, J. H., J. Carstensen, D. J. Conley, et al. 2017. "Long-Term Temporal and Spatial Trends in Eutrophication Status of the Baltic Sea." *Biological Reviews* 92, no. 1: 135–149. https://doi.org/10.1111/brv.12221.

Anderson, S. I., A. D. Barton, S. Clayton, S. Dutkiewicz, and T. A. Rynearson. 2021. "Marine Phytoplankton Functional Types Exhibit Diverse Responses to Thermal Change." *Nature Communications* 12, no. 1: 6413. https://doi.org/10.1038/s41467-021-26651-8.

Andersson, A., H. Höglander, C. Karlsson, and S. Huseby. 2015. "Key Role of Phosphorus and Nitrogen in Regulating Cyanobacterial Community Composition in the Northern Baltic Sea." *Estuarine, Coastal and Shelf Science* 164: 161–171. https://doi.org/10.1016/j.ecss.2015.07.013.

Barton, A. D., A. J. Irwin, Z. V. Finkel, and C. A. Stock. 2015. "Anthropogenic Climate Change Drives Shift and Shuffle in North Atlantic Phytoplankton Communities." *Proceedings of the National Academy of Sciences of the United States of America* 113, no. 11: 2964–2969. https://doi.org/10.1073/pnas.1519080113.

Bates, N., Y. Astor, M. Church, et al. 2014. "A Time-Series View of Changing Ocean Chemistry Due to Ocean Uptake of Anthropogenic CO_2 and Ocean Acidification." *Oceanography* 27, no. 1: 126–141. https://doi.org/10.5670/oceanog.2014.16.

Beaugrand, G., M. Edwards, and L. Legendre. 2010. "Marine Biodiversity, Ecosystem Functioning, and Carbon Cycles." *Proceedings of the National Academy of Sciences of the United States of America* 107, no. 22: 10120–10124. https://doi.org/10.1073/pnas.0913855107.

Belkin, I. M. 2009. "Rapid Warming of Large Marine Ecosystems." *Progress in Oceanography* 81, no. 1–4: 207–213. https://doi.org/10.1016/j.pocean.2009.04.011.

Benedetti, F., M. Vogt, U. H. Elizondo, D. Righetti, N. E. Zimmermann, and N. Gruber. 2021. "Major Restructuring of Marine Plankton Assemblages under Global Warming." *Nature Communications* 12: 5226. https://doi.org/10.1038/s41467-021-25385-x.

Berner, C., M. Bertos-Fortis, J. Pinhassi, and C. Legrand. 2018. "Response of Microbial Communities to Changing Climate Conditions During Summer Cyanobacterial Blooms in the Baltic Sea." *Frontiers in Microbiology* 9: 1562. https://doi.org/10.3389/fmicb.2018.01562.

Berthold, M., P. Nieters, and R. Vortmeyer-Kley. 2025. "Machine Learning to Identify Environmental Drivers of Phytoplankton Blooms in the Southern Baltic Sea." *Scientific Reports* 15, no. 1: 3077. https://doi.org/10.1038/s41598-025-85605-y.

Calabrese, J. M., G. Certain, C. Kraan, and C. F. Dormann. 2013. "Stacking Species Distribution Models and Adjusting Bias by Linking them to Macroecological Models." *Global Ecology and Biogeography* 23, no. 1: 99–112. https://doi.org/10.1111/geb.12102.

Cragg, J. G. 1971. "Some Statistical Models for Limited Dependent Variables with Application to the Demand for Durable Goods." *Econometrica* 39, no. 5: 829–844. https://doi.org/10.2307/1909582.

Crawford, A. D., K. M. Krumhardt, N. S. Lovenduski, G. L. van Dijken, and K. R. Arrigo. 2020. "Summer High-Wind Events and Phytoplankton Productivity in the Arctic Ocean." *Journal of Geophysical Research: Oceans* 125, no. 9: e2020JC016565. https://doi.org/10.1029/2020jc016565.

Cyr, H. 2017. "Winds and the Distribution of Nearshore Phytoplankton in a Stratified Lake." *Water Research* 122: 114–127. https://doi.org/10.1016/j.watres.2017.05.066.

Devlin, M., and J. Brodie. 2023. "Nutrients and Eutrophication." In Marine Pollution – Monitoring, Management and Mitigation, edited by A. Reichelt-Brushett, 75–100. Springer Nature Switzerland. https://doi.org/10.1007/978-3-031-10127-4_4.

Dickson, R., and P. Reid. 1983. "Local Effects of Wind Speed and Direction on the Phytoplankton of the Southern Bight." *Journal of Plankton Research* 5, no. 4: 441–455. https://doi.org/10.1093/plankt/5.4.441.

Döös, K., H. E. M. Meier, and R. Döscher. 2004. "The Baltic Haline Conveyor Belt or the Over-Turning Circulation and Mixing in the Baltic." *Ambio* 33, no. 4/5: 261–266. https://doi.org/10.1579/0044-7447-33.4.261.

Dos Reis, G. C., G. H. A. de Carvalho, M. C. P. Vilar, S. M. F. Azevedo, and A. S. Ferrão-Filho. 2023. "Saxitoxin-Producing *Raphidiopsis raciborskii* (Cyanobacteria) Constrains Daphnia Fitness and Feeding Rate despite High Nutritious Food Availability." *Toxics* 11, no. 8: 693. https://doi.org/10.3390/toxics11080693.

Eilola, K., H. M. Meier, and E. Almroth. 2009. "On the Dynamics of Oxygen, Phosphorus and Cyanobacteria in the Baltic Sea; A Model Study." *Journal of Marine Systems* 75, no. 1–2: 163–184. https://doi.org/10.1016/j.jmarsys.2008.08.009.

Evstigneev, V., I. Serikova, S. Piontkovski, V. Zhuk, and I. Minsky. 2023. "Fall-Winter Sea Surface Temperature Anomalies Affect Subsequent Spring-Summer Phytoplankton Succession and Bioluminescence Patterns in the Black Sea Coastal Waters near Crimea." *Marine Environmental Research* 192: 106246. https://doi.org/10.1016/j.marenvres.2023.106246.

Ferrier, S., and A. Guisan. 2006. "Spatial Modelling of Biodiversity at the Community Level." *Journal of Applied Ecology* 43, no. 3: 393–404. https://doi.org/10.1111/j.1365-2664.2006.01149.x.

Font-Muñoz, J. S., A. Jordi, I. Tuval, J. Arrieta, S. Anglès, and G. Basterretxea. 2017. "Advection by Ocean Currents Modifies Phytoplankton Size Structure." *Journal of the Royal Society Interface* 14, no. 130: 20170046. https://doi.org/10.1098/rsif.2017.0046.

Frederikse, T., F. Landerer, L. Caron, et al. 2020. "The Causes of Sea-Level Rise since 1900." *Nature* 584, no. 7821: 393–397. https://doi.org/10.1038/s41586-020-2591-3.

Garcia-Soto, C., L. Cheng, L. Caesar, et al. 2021. "An Overview of Ocean Climate Change Indicators: Sea Surface Temperature, Ocean Heat Content, Ocean pH, Dissolved Oxygen Concentration, Arctic Sea Ice Extent, Thickness and Volume, Sea Level and Strength of the AMOC (Atlantic Meridional Overturning Circulation)." *Frontiers in Marine Science* 8: 642372. https://doi.org/10.3389/fmars.2021.642372.

Gelman, A., and D. B. Rubin. 1992. "Inference from Iterative Simulation Using Multiple Sequences." *Statistical Science* 7, no. 4: 457–472. https://doi.org/10.1214/ss/1177011136.

Glibert, P. M., and M. A. Burford. 2017. "Globally Changing Nutrient Loads and Harmful Algal Blooms: Recent Advances, New Paradigms, and Continuing Challenges." *Oceanography* 30, no. 1: 58–69. https://doi.org/10.5670/oceanog.2017.110.

Guisan, A., and C. Rahbek. 2011. "SESAM – A New Framework Integrating Macroecological and Species Distribution Models for Predicting Spatio-Temporal Patterns of Species Assemblages." *Journal of Biogeography* 38, no. 8: 1433–1444. https://doi.org/10.1111/j.1365-2699.2011.02550.x.

Hällfors, H., H. Backer, JM. Leppänen, S. Hällfors, G. Hällfors, and H. Kuosa. 2013. "The Northern Baltic Sea Phytoplankton Communities in 1903–1911 and 1993–2005: A Comparison of Historical and Modern Species Data." *Hydrobiologia* 707, no. 1: 109–133. https://doi.org/10.1007/s10750-012-1414-4.

HELCOM. 2018. HELCOM Assessment on Maritime Activities in the Baltic Sea 2018. Helsinki Commission.

Hogfors, H., N. H. Motwani, S. Hajdu, et al. 2014. "Bloom-Forming Cyanobacteria Support Copepod Reproduction and Development in the Baltic Sea." *PLoS One* 9, no. 11: e112692. https://doi.org/10.1371/journal.pone.0112692.

Jakobsson, M., C. Stranne, M. O'regan, et al. 2019. "Bathymetric Properties of the Baltic Sea." *Ocean Science* 15, no. 4: 905–924. https://doi.org/10.5194/os-15-905-2019.

Kahru, M., and R. Elmgren. 2014. "Multidecadal Time Series of Satellite-Detected Accumulations of Cyanobacteria in the Baltic Sea." *Biogeosciences* 11, no. 13: 3619–3633. https://doi.org/10.5194/bg-11-3619-2014.

Kankaanpää, H. T., P. Alenius, P. Kotilainen, and P. Roiha. 2023. "Decreased Surface and Bottom Salinity and Elevated Bottom Temperature in the Northern Baltic Sea Over the Past Six Decades." *Science of the Total Environment* 859, no. Pt 2: 160241. https://doi.org/10.1016/j.scitotenv.2022.160241.

Klais, R., K. Olli, and S. Lehtinen. 2016. "Phytoplankton Trait Compilation" [Unpublished]. https://www.researchgate.

net/publication/303549914_phytoplankton_trait_compilation.

Kumar, A., J. Yadav, and R. Mohan. 2020. "Global Warming Leading to Alarming Recession of the Arctic Sea-Ice Cover: Insights from Remote Sensing Observations and Model Reanalysis." *Heliyon* 6, no. 7: e04355. https://doi.org/10.1016/j.heliyon.2020.e04355.

Larsson, U., S. Hajdu, J. Walve, and R. Elmgren. 2001. "Baltic Sea Nitrogen Fixation Estimated from the Summer Increase in Upper Mixed Layer Total Nitrogen." *Limnology and Oceanography* 46, no. 4: 811–820. https://doi.org/10.4319/lo.2001.46.4.0811.

Litchman, E., and C. A. Klausmeier. 2008. "Trait-Based Community Ecology of Phytoplankton." *Annual Review of Ecology, Evolution, and Systematics* 39, no. 1: 615–639. https://doi.org/10.1146/annurev.ecolsys.39.110707.173549.

Meier, H. E. M., M. Kniebusch, C. Dieterich, et al. 2022. "Climate Change in the Baltic Sea Region: A Summary." *Earth System Dynamics* 13, no. 1: 457–593. https://doi.org/10.5194/esd-13-457-2022.

Meier, W. N., and J. Stroeve. 2022. "An Updated Assessment of the Changing Arctic Sea Ice Cover." *Oceanography* 35, no. 3/4: 10–19. https://doi.org/10.5670/oceanog.2022.114.

Mesman, J. P., A. I. Ayala, S. Goyette, et al. 2022. "Drivers of Phytoplankton Responses to Summer Wind Events in a Stratified Lake: A Modeling Study." *Limnology and Oceanography* 67, no. 4: 856–873. https://doi.org/10.1002/lno.12040.

Motwani, N. H., J. Duberg, J. B. Svedén, and E. Gorokhova. 2017. "Grazing on Cyanobacteria and Transfer of Diazotrophic Nitrogen to Zooplankton in the Baltic Sea." *Limnology and Oceanography* 63, no. 2: 672–686. https://doi.org/10.1002/lno.10659.

Murphy, G. E. P., T. N. Romanuk, and B. Worm. 2020. "Cascading Effects of Climate Change on Plankton Community Structure." *Ecology and Evolution* 10, no. 4: 2170–2181. https://doi.org/10.1002/ece3.6055.

Nerem, R. S., B. D. Beckley, J. T. Fasullo, B. D. Hamlington, D. Masters, and G. T. Mitchum. 2018. "Climate-Change–Driven Accelerated Sea-Level Rise Detected in the Altimeter Era." *Proceedings of the National Academy of Sciences of the United States of America* 115, no. 9: 2022–2025. https://doi.org/10.1073/pnas.1717312115.

Novotny, A., B. Serandour, S. Kortsch, B. Gauzens, K. M. G. Jan, and M. Winder. 2023. "DNA Metabarcoding Highlights Cyanobacteria as the Main Source of Primary Production in a Pelagic Food Web Model." *Science Advances* 9, no. 17: eadg1096. https://doi.org/10.1126/sciadv.adg1096.

Olenina, I., N. Wasmund, S. Hajdu, et al. 2010. "Assessing Impacts of Invasive Phytoplankton: The Baltic Sea Case." *Marine Pollution Bulletin* 60, no. 10: 1691–1700. https://doi.org/10.1016/j.marpolbul.2010.06.046.

Olli, K., E. Nyman, and T. Tamminen. 2022. "Half-Century Trends in Alpha and Beta Diversity of Phytoplankton Summer Communities in the Helsinki Archipelago, the Baltic Sea." *Journal of Plankton Research* 45, no. 1: 146–162. https://doi.org/10.1093/plankt/fbac029.

Olli, K., R. Klais, T. Tamminen, R. Ptacnik, and T. Andersen. 2011. "Long Term Changes in the Baltic Sea Phytoplankton Community." *Boreal Environment Research* 16: 3–14.

Olli, K., R. Ptacnik, R. Klais, and T. Tamminen. 2019. "Phytoplankton Species Richness along Coastal and Estuarine Salinity Continua." *The American Naturalist* 194, no. 2: E41–E51. https://doi.org/10.1086/703657.

Olofsson, M., S. Suikkanen, J. Kobos, N. Wasmund, and B. Karlson. 2020. "Basin-Specific Changes in Filamentous Cyanobacteria Community Composition across Four Decades in the Baltic Sea." *Harmful Algae* 91: 101685. https://doi.org/10.1016/j.hal.2019.101685.

Ovaskainen, O., and J. Soininen. 2011. "Making More out of Sparse Data: Hierarchical Modeling of Species Communities." *Ecology* 92, no. 2: 289–295. https://doi.org/10.1890/10-1251.1.

Ovaskainen, O., and N. Abrego. 2020. "Joint Species Distribution Modelling: With Applications in R." In Ecology, Biodiversity and Conservation, edited by N. Abrego. Cambridge, United Kingdom: Cambridge University Press. https://doi.org/10.1017/9781108591720.

Ovaskainen, O., G. Tikhonov, A. Norberg, et al. 2017. "How to Make More out of Community Data? A Conceptual Framework and its Implementation as Models and Software." *Ecology Letters* 20, no. 5: 561–576. https://doi.org/10.1111/ele.12757.

Oziel, L., A. Baudena, M. Ardyna, et al. 2020. "Faster Atlantic Currents Drive Poleward Expansion of Temperate Phytoplankton in the Arctic Ocean." *Nature Communications* 11, no. 1: 1705. https://doi.org/10.1038/s41467-020-15485-5.

Paul, C., U. Gräwe, and A. Kremp. 2023. "Long-Term Changes in Bloom Dynamics of Southern and Central Baltic Cold-Water Phytoplankton." *Frontiers in Marine Science* 10: 121412. https://doi.org/10.3389/fmars.2023.1212412.

Pearce, J., and S. Ferrier. 2000. "Evaluating the Predictive Performance of Habitat Models Developed Using Logistic Regression." *Ecological Modelling* 133, no. 3: 225–245. https://doi.org/10.1016/s0304-3800(00)00322-7.

Peltonen, H., and B. Weigel. 2022. "Responses of Coastal Fishery Resources to Rapid Environmental Changes." *Journal of Fish Biology* 101, no. 3: 686–698. https://doi.org/10.1111/jfb.15138.

Peng, Q., S.-P. Xie, D. Wang, et al. 2022. "Surface Warming–Induced Global Acceleration of Upper Ocean Currents." *Science Advances* 8, no. 16: eabj8394. https://doi.org/10.1126/sciadv.abj8394.

Pinsky, M. L., H. Hillebrand, J. M. Chase, et al. 2025. "Warming and Cooling Catalyse Widespread Temporal Turnover in Biodiversity." *Nature* 638, no. 8052: 995–999. https://doi.org/10.1038/s41586-024-08456-z.

Poggiato, G., T. Münkemüller, D. Bystrova, J. Arbel, J. S. Clark, and W. Thuiller. 2021. "On the Interpretations of Joint Modeling in Community Ecology." *Trends in Ecology & Evolution* 36, no. 5: 391–401. https://doi.org/10.1016/j.tree.2021.01.002.

R Core Team. 2023. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Rahman, A. U., G. Tikhonov, J. Oksanen, T. Rossi, and O. Ovaskainen. 2024. "Accelerating Joint Species Distribution Modelling with Hmsc-HPC by GPU Porting." *PLoS Computational Biology* 20, no. 9: e1011914. https://doi.org/10.1371/journal.pcbi.1011914.

Righetti, D., M. Vogt, N. Gruber, A. Psomas, and N. E. Zimmermann. 2019. "Global Pattern of Phytoplankton Diversity Driven by Temperature and Environmental Variability." *Science Advances* 5, no. 5: eaau6253. https://doi.org/10.1126/sciadv.aau6253.

Snoeijs-Leijonmalm, P., and E. Andrén. 2017. "Why is the Baltic Sea So Special to Live in?" In Biological Oceanography of the Baltic Sea, 23–84. Springer Netherlands. https://doi.org/10.1007/978-94-007-0668-2_2.

Stockmayer, V., and A. Lehmann. 2023. "Variations of Temperature, Salinity and Oxygen of the Baltic Sea for the Period 1950 to 2020." *Oceanologia* 65, no. 3: 466–483. https://doi.org/10.1016/j.oceano.2023.02.002.

Stockwell, J. D., J. P. Doubek, R. Adrian, et al. 2020. "Storm Impacts on Phytoplankton Community Dynamics in Lakes." *Global Change Biology* 26, no. 5: 2756–2784. https://doi.org/10.1111/gcb.15033.

Stoń-Egiert, J., and M. Ostrowska. 2022. "Long-Term Changes in Phytoplankton Pigment Contents in the Baltic Sea: Trends and Spatial Variability during 20 Years of Investigations." *Continental Shelf Research* 236: 104666. https://doi.org/10.1016/j.csr.2022.104666.

Suikkanen, S., L. Uusitalo, S. Lehtinen, et al. 2021. "Diazotrophic Cyanobacteria in Planktonic Food Webs." *Food Webs* 28: e00202. https://doi.org/10.1016/j.fooweb.2021.e00202.

Tamminen, T., and T. Andersen. 2007. "Seasonal Phytoplankton Nutrient Limitation Patterns as Revealed by Bioassays over Baltic Sea Gradients of Salinity and Eutrophication." *Marine Ecology Progress Series* 340: 121–138. https://doi.org/10.3354/meps340121.

Thompson, P. A., T. D. O'brien, H. W. Paerl, B. L. Peierls, P. J. Harrison, and M. Robb. 2015. "Precipitation as a Driver of Phytoplankton Ecology in Coastal Waters: A Climatic Perspective." *Estuarine, Coastal and Shelf Science* 162: 119–129. https://doi.org/10.1016/j.ecss.2015.04.004.

Tikhonov, G., Ø. H. Opedal, N. Abrego, et al. 2020. "Joint Species Distribution Modelling with the r-Package Hmsc." *Methods in Ecology and Evolution* 11, no. 3: 442–447. https://doi.org/10.1111/2041-210x.13345.

Tikhonov, G., O. Ovaskainen, J. Oksanen, M. de Jonge, O. Opedal, and T. Dallas. 2024. "Hmsc: Hierarchical Model of Species Communities." https://doi.org/10.32614/CRAN.package.Hmsc.

Tjur, T. 2009. "Coefficients of Determination in Logistic Regression Models—A New Proposal: The Coefficient of Discrimination." *The American Statistician* 63, no. 4: 366–372. https://doi.org/10.1198/tast.2009.08210.

Tréguer, P. J., and C. L. De La Rocha. 2013. "The World Ocean Silica Cycle." *Annual Review of Marine Science* 5, no. 1: 477–501. https://doi.org/10.1146/annurev-marine-121211-172346.

Vahtera, E., R. Autio, H. Kaartokallio, and M. Laamanen. 2010. "Phosphate Addition to Phosphorus-Deficient Baltic Sea Plankton Communities Benefits Nitrogen-Fixing Cyanobacteria." *Aquatic Microbial Ecology* 60, no. 1: 43–57. https://doi.org/10.3354/ame01408.

Venegas, R. M., J. Acevedo, and E. A. Treml. 2023. "Three Decades of Ocean Warming Impacts on Marine Ecosystems: A Review and Perspective." *Deep Sea Research Part II: Topical Studies in Oceanography* 212: 105318. https://doi.org/10.1016/j.dsr2.2023.105318.

Wasmund, N., J. Tuimala, S. Suikkanen, L. Vandepitte, and A. Kraberg. 2011. "Longterm Trends in Phytoplankton Composition in the Western and Central Baltic Sea." *Journal of Marine Systems* 87, no. 2: 145–159. https://doi.org/10.1016/j.jmarsys.2011.03.010.

Watanabe, S. 2010. "Asymptotic Equivalence of Bayes Cross Validation and Widely Applicable Information Criterion in Singular Learning Theory." *Journal of Machine Learning Research* 11, no. 116: 3571–3594. https://doi.org/10.48550/arXiv.1004.2316.

Weigel, B., N. Kotamäki, O. Malve, K. Vuorio, and O. Ovaskainen. 2022. "Macrosystem Community Change in Lake Phytoplankton and its Implications for Diversity and Function." *Global Ecology and Biogeography* 32, no. 2: 295–309. https://doi.org/10.1111/geb.13626.

Worms Editorial Board. 2024. "World Register of Marine Species (WoRMS)" [Online] https://doi.org/10.14284/170.

Wulff, F. 2017. "Impacts of Changed Nutrient Loads on the Baltic Sea." In Managing a Sea, 57–65. Routledge. https://doi.org/10.4324/9781315071367-5.

Zhang, M., Z. Yang, X. Shi, and Y. Yu. 2022*a*. "The Synergistic Effect of Rising Temperature and Declining Light Boosts the Dominance of Bloom-Forming Cyanobacteria in Spring." *Harmful Algae* 116: 102252. https://doi.org/10.1016/j.hal.2022.102252.

Zhang, W., J. Liu, Y. Xiao, et al. 2022*b*. "The Impact of Cyanobacteria Blooms on the Aquatic Environment and Human Health." *Toxins* 14, no. 10: 658. https://doi.org/10.3390/toxins14100658.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 26 March 2025
Revised 25 August 2025
Accepted 13 November 2025