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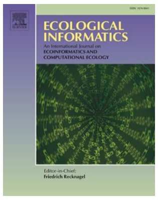

Future increase of filamentous cyanobacteria in coastal Baltic Sea predicted by multiple realm models of marine, terrestrial, and climate change scenarios

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ABSTRACT

Blooms of filamentous cyanobacteria regularly occur in the Baltic Sea during warm summer months. These blooms can be toxic and interfere with recreational activities. However, the underlying drivers of these events and how their distribution might change in response to future climate conditions remain poorly understood. To investigate this, we applied a multi-realm modeling approach that integrates environmental data from both marine and terrestrial systems, combined with climate projections, to predict future filamentous and nitrogen-fixing cyanobacterial distribution along Sweden's Baltic Sea coast. Our models identified several key factors significantly influencing bloom distribution: terrestrial temperature, precipitation during the wettest quarter, sea surface temperature, nitrate levels, and interactions between land-based and marine environmental variables. Our projections suggest an expansion of filamentous cyanobacteria in the northern Baltic Proper, Bothnian Sea, Bothnian Bay, and Arkona Basin driven by rising land temperatures by 2070, increasing sea surface temperatures by 2100, and declining salinity in specific basins. Overall, the results demonstrate that incorporating environmental data from both land and sea improves predictions of cyanobacterial distribution in coastal Baltic Sea regions. This multi-realm modeling strategy may also prove valuable for forecasting and managing harmful cyanobacterial blooms in other coastal areas experiencing similar environmental challenges.

1. Introduction

Areas of dense accumulation of filamentous nitrogen-fixing cyanobacteria, so-called blooms, regularly occur during the summertime at the water surface of the Baltic Sea (Kahru et al., 2020). These blooms may influence biogeochemical dynamics, and the cyanotoxins they produce may negatively affect some aquatic organisms and human recreational activities (Munkes et al., 2021; Paerl et al., 2018). The ongoing and predicted future warming (Meier et al., 2022), along with increased occurrences of these filamentous cyanobacteria, have therefore raised both scientific and societal concerns (Deutsch et al., 2007; Helcom, 2018; Kownacka et al., 2022; Munkes et al., 2021; Viitasalo and Bonsdorff, 2022; Wasmund et al., 2013). However, the extent to which environmental and climate changes may influence the future occurrence and abundance of filamentous nitrogen-fixing cyanobacteria in the coastal Baltic Sea is not entirely understood.

Three key taxa of filamentous diazotrophic cyanobacteria in the Baltic Sea; *Nodularia spumigena, Aphanizomenon* sp., and *Dolichospermum* spp., are known to occupy distinct ecological niches (Klawonn et al., 2016; Olofsson et al., 2020b). *N. spumigena* dominates the Baltic Proper, but salinity levels in the Bothnian Sea are below its preferred range (Cegłowska et al., 2018; Olofsson et al., 2020b; Wasmund et al., 2013). *Dolichospermum* spp. is less common but occurs throughout the Baltic Sea (Fewer et al., 2009; Halinen et al., 2008). *Aphanizomenon* sp. has the broadest niche, appearing early in the summer and extending deeper into the water column (Klawonn et al., 2016). There has been a recent increase in the Bothnian Sea observed using 40 years of monitoring data (Olofsson et al., 2020b). Cyanobacteria can produce a wide array of toxins, with some genera releasing numerous toxins during a single bloom (Rastogi et al., 2015). For example, *N. spumigena* and

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Dolichospermum spp. have the potential to produce the hepatotoxins nodularin and microcystin, respectively (Kaiser et al., 2020), while *Aphanizomenon* sp. is not considered to be toxic in the Baltic Sea (Luckas et al., 2005; Wasmund, 2002). Filamentous cyanobacteria have a competitive advantage over other phytoplankton in the Baltic Sea due to their ability to fix dissolved nitrogen during the nitrate-depleted summers (Klawonn et al., 2016; Stal et al., 2003).

Earlier studies showed that there are several factors that influence the occurrence of cyanobacterial blooms in the Baltic Sea. For example, sea surface temperature, salinity, solar irradiance, wind speed at sea, biogeochemical stratification, and dissolved inorganic nitrogen concentrations relative to phosphate concentrations have been shown to influence the abundance and distribution of the filamentous cyanobacteria (Karlson et al., 2010; Lips and Lips, 2008; Löptien and Dietze, 2022; Unger et al., 2013; Wang et al., 2022; Wurtsbaugh et al., 2019; Yang et al., 2008). Solar irradiance significantly affects their growth, photosynthetic performance, (Gao et al., 2007; Wang et al., 2022), while salinity limits their habitat (Lehtimäki et al., 1994; Moisander et al., 2002; Olofsson et al., 2020a; Olofsson et al., 2020b; Silveira and Odebrecht, 2019). Based on monitoring data from the past four decades (Olofsson et al., 2020b), the impact of temperature and salinity change due to climate warming has also been shown to affect filamentous cyanobacteria. However, little is known on whether their abundance and distribution are driven by single or multi-interacting variables.

Several modeling approaches have been tested to understand what drives cyanobacterial blooms (Hense et al., 2013; Hieronymus et al., 2021; Löptien and Dietze, 2022; Munkes et al., 2021). Earlier modeling studies have mainly focused on environmental variables from the marine realm (MAR) (Kahru et al., 2020; Viitasalo and Bonsdorff, 2022; Wåhlström et al., 2024; Wasmund, 1997; Wasmund et al., 2013), whereas coastal areas are also directly exposed to environmental variables originating from the terrestrial realm (TERR), such as air temperature and land runoff of organic matter associated with increased precipitation (Andersson et al., 2015b). Coastal areas have a crucial role in regulating nutrient availability (Almroth-Rosell et al., 2016) and may therefore influence future bloom predictions (Wåhlström et al., 2024). Consequently, there is a lack of comprehensive understanding of how interactions between environmental conditions from both the marine and the terrestrial realms may affect the distribution of filamentous cyanobacteria. Models that rely on environmental data from only one biogeographic realm tend to yield lower prediction accuracy and reliability.

Species distribution models (SDMs) and machine-learning (ML) algorithms (Elith et al., 2010; Elith and Leathwick, 2009) have improved the ability to integrate multiple environmental variables, handle missing data, and reveal hidden relationships (Abdelgadir et al., 2023; Ghannam and Techtmann, 2021; Janßen et al., 2021; Lembrechts et al., 2020; Mod et al., 2021). SDMs have been applied to estimate cyanobacterial blooms in various freshwater ecosystems (Guimarães et al., 2020; Meriggi et al., 2022, 2023). However, current SDM approaches do not efficiently integrate multi-realm environmental variables (Bentlage et al., 2013; Dambach and Rödder, 2011; Robinson et al., 2011). This methodological gap may stem from the lack of an efficient method for stacking environmental data from both realms and extracting relevant information needed for modeling, as well as the uncertainty in potential species distribution due to omission rates, i.e., the percentage of test localities falling outside predicted suitable areas.

This study aimed to: I) assess how the spatial distribution of filamentous nitrogen-fixing cyanobacteria along the Swedish coast of the Baltic Sea is influenced by multi-realm environmental variables from both marine and terrestrial domains, and II) evaluate the effect of projected climate change scenarios for the years 2050, 2070, and 2100. To address these aims, occurrence records of three key filamentous cyanobacteria, *Nodularia spumigena, Aphanizomenon* sp., and *Dolichospermum* spp., along the Swedish coastal areas of the Baltic Sea were compiled and analyzed alongside data layers representing MAR and TERR environmental variables and projected climate scenarios. Modeling was performed using six different machine-learning (ML) algorithms embedded within SDM-based approaches, including ensemble species distribution modeling (ESDM) and stacked species distribution modeling (SSDM). Interaction effects between MAR and TERR variables, as well as the importance of predicted variables, were statistically evaluated in stacked multi-realm models. Final model forecasts were subsequently analyzed for accuracy, performance, and omission rates.

2. Material and methods

2.1. Data preparation

2.1.1. Environmental variables

To predict the future distribution of filamentous cyanobacteria and investigate the effects of different abiotic conditions of terrestrial and marine realms, we used a total of 62 environmental raster layers (Table S1). The raster layers contained data from either the sea surface, the water column of MAR, or the mainland (TERR) and included various statistical measures (range, minimum, maximum, mean) calculated monthly and annually. MAR raster layers included variables such as sea surface temperature (°C), bathymetry (m), sea surface nitrate concentration (mol m^{-3}), primary production of carbon (g m^{-3}day), phosphate concentration (mol m^{-3}), dissolved oxygen concentration (mol m^{-3}), sea surface salinity (PSS) and photosynthetically available radiation (E m^{-2} day^{-1}). These downscaled data at 2.5 arc-minute spatial resolution were sourced from the Bio-ORACLE project v.2.2 (https://www.bio-oracle.org/) (Assis et al., 2018; Tyberghein et al., 2012), the MARSPEC project: Ocean climate layers for the Marine Spatial Ecology (Sbrocco and Barber, 2013), and the ENVIREM (https://envirem.github.io/): Environmental Rasters For Ecological Modeling (Title and Bemmels, 2018). Monthly data for sea surface temperature were obtained from the 'Aqua-MODIS': Moderate Resolution Imaging Spectroradiometer database (Aqua-MODIS; http://oceancolor.gsfc.nasa.gov/), and from the high-resolution bathymetry product (SRTM30_PLUS V6.0; http://topex.ucsd.edu/WWW_html/srtm30_plus.html) (Becker et al., 2009). The Marine layer for distance to shore (kilometer) was downloaded from 'GSHHS': Global Self-consistent, Hierarchical, High-resolution Geography Database v. 2.3.7 (http://www.soest.hawaii.edu/pwessel/gshhg/). TERR variables included temperature (°C), monthly precipitation (mm), altitude (m) and monthly solar radiation (kJ m^{-2} day^{-1}) and were sourced from the WorldClim v. 2.1 (https://www.worldclim.org/): the Global Climate and Weather database (Booth et al., 2014; Fick and Hijmans, 2017).

The future biogeographic distribution of filamentous cyanobacteria in response to projected temperature increases in the Baltic Sea was modeled using climate change trajectories for the years 2050, 2070, and 2100, respectively. These projections were derived from the IPCC Sixth Assessment Report (AR6) of global warming increase (°C) projections (Calvin et al., 2023; IPCC, 2023). We used the Representative Concentration Pathway 8.5 (RCP8.5) greenhouse gas concentration trajectory, which represents a worse-case climate scenario with a mean global temperature increase ranging from 2.0 to 5.0 °C. The RCPs used are representing three periods of time: RCP85–2050 (warming increase of ≈ 2.00 °C), RCP85–2070 (warming increase of ≈ 2.60 °C) and RCP85–2100 (warming increase of ≈ 3.0–4.8 °C). Climate trajectories were obtained from Coupled Model Intercomparison Project -phase 6 CMIP6 (Eyring et al., 2016). All environmental raster layers for MAR ($n = 40$), TERR ($n = 18$), and trajectories of future climate change ($n = 4$) were downloaded as ESRI raster grids at a spatial resolution of 2.5 arc-minute, corresponding to approximately 4 km^2 grid cell size at the equator. For subsequent analysis of habitat suitability, all raster layers in tag image file (.tif) were converted to the ESRI ASCII (.asc) format using the raster conversion function in QGIS v. 3.28.3 (QGIS Development Team, 2022).

2.1.2. *Occurrence records of filamentous cyanobacteria*

Occurrence records of *Nodularia spumigena, Aphanizomenon* sp., and *Dolichospermum* spp. (Data S1, DOI: https://doi.org/10.15468/dd.zc83q5) with 'present' status in the Global Biodiversity Information Facility GBIF (GBIF, 2023) were downloaded on 2023-05-22 using the package 'rgbif" (Chamberlain et al., 2023) in RStudio (RStudio Team, 2020) with R v.4.2.2 (R Core Team, 2021). Occurrence records were restricted to coastal areas, where data on MAR and TERR variables are available, and allowing for the assessment of interaction effects between environmental variables. The search for records was limited to 10,000 records per taxon and constrained to the spatial extent of the Baltic Sea (latitude: 53–66°N; longitude: 10–30°E). Here we limit searching for records to 10,000 per query for each taxon due to the strict spatial extent of the study area that lies only along the coastal area of the Baltic Sea. Occurrence records with spatial duplicates, invalid format, or missing longitude, latitude, or taxon names were removed from the dataset using the package "scrubr" (Chamberlain, 2016).

2.2. *Data processing*

2.2.1. *Environmental data layers*

Environmental layers were loaded into RStudio using the packages 'ENVIREM v2.3' (Title and Bemmels, 2018), 'sdmpredictors' (Bosch and Fernandez, 2022), 'bioclim' (Booth et al., 2014), 'sdm' (Naimi and Araújo, 2016), and 'SSDM' (Schmitt et al., 2017). Collinearity among environmental layers (predictors) can destabilize the performance of regression-based models (Dormann et al., 2013). Therefore, detection and removal of predictors based on multicollinearity was performed using the variance inflation factor functions of 'vif', 'vifcor', and 'vifstep' provided in package 'usdm' v1.1–18 (Naimi et al., 2014). Multicollinear environmental layers with a Pearson correlation coefficient ≥ 0.7 were detected and removed.

2.2.2. *Extraction of environmental data linked to the occurrence records*

Environmental variables associated with occurrence records were extracted by generating a spatial data frame plotted over a vector layer composed of all stacked environmental predictors. All MAR and TERR environmental data were extracted using the packages 'raster" (van Etten, 2012), 'sp' (Bivand et al., 2013; Pebesma and Bivand, 2005), 'dismo' (Hijmans et al., 2015), 'sdmpredictors' (Bosch and Fernandez, 2022) and the extraction function implemented in 'tidyvers' package (Wickham et al., 2019). In total, 496 occurrence records located between 1 km and 10 km from the shore were used to retrieve environmental data from both MAR and TERR realms (Fig. 1).

2.3. *Modeling workflow*

Modeling codes and data are available at the public repository on

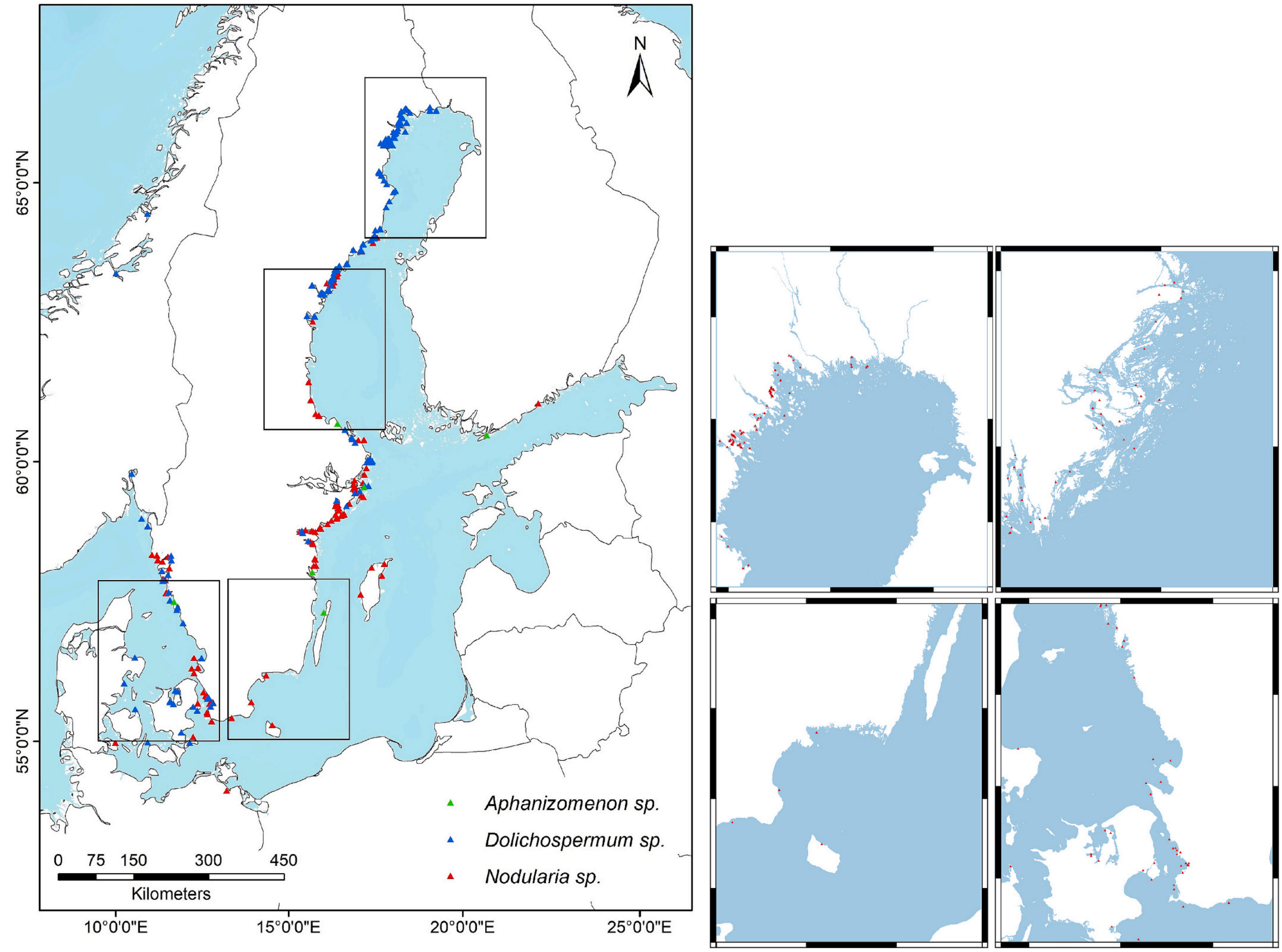

Fig. 1. A map showing the geographic locations of the 496 present occurrence records of the three filamentous cyanobacteria *Aphanizomenon* sp., *Dolichospermum* spp., and *Nodularia spumigena* along the Swedish coastline and the Baltic Sea. Occurrence records were retrieved from the Global Biodiversity Information Facility (GBIF) database accessed on 2023-05-22. Occurrence records 1 to10 km from the shore.

GitHub. SDMs, hereafter referred to as base estimator models, were built using Classification Tree Analysis (CTA) (Steinberg, 2009), Maximum-Entropy learning (MAXENT) (Phillips et al., 2006), Multivariate Adaptive Regression Spline (MARS) (Friedman, 1991), Random Forest (RF) (Breiman, 2001), Generalized Boosting regression Model (GBM) (Friedman, 2002), and Generalized Linear Model (GLM) (Guisan et al., 2002).

The modeling workflow (Fig. S1) was conducted at three different levels. To create the base estimator models, individual SDMs were generated by fitting the environmental predictors to the occurrences of each cyanobacterial taxon using each algorithm. Data objects were created with the 'sdmData' function from the "sdm" package, containing all occurrence records and stacked predictors. A background of 10,000 pseudoabsence data points (Barbet-Massin et al., 2012) was randomly generated within the spatial extent of the study area and added to the data object. Model fitting was performed by adding base estimator algorithms tested with 10-fold bootstrapping (Harrell et al., 2005; Lima et al., 2019) as the replication technique. Models were validated using a repeated split-samples procedure, where 70 % of the occurrence dataset was used for model training and the remaining 30 % for testing, repeated over 10-fold cross validation (Roberts et al., 2017).

The modeling workflow continued with an ensemble approach 'ESDM' (Araújo and New, 2007), where all base-estimator models were combined into a single forecast model. Using all stacked layers, six different ESDMs were generated. The ESDM approach was implemented using the ensemble functions from the 'sdm' package and the ensemble platform package "biomod2" (Thuiller et al., 2009; Thuiller, 2014). Lastly, the base estimator models and ESDMs were combined into a stacked species distribution model, SSDM (Fig. S1). All models were assessed for prediction success, omission rate, accuracy, and performance using the functions from the "SSDM" package (Schmitt et al., 2017).

Since the environmental predictors differed in origin, cell grid size, and resolution, a resampling operation was implemented by transferring values between the non-matching raster layers and by stacking the predictors from both biogeographic realms into a single raster stack. Resampling computation was performed using the nearest neighbor 'ngb' function from the "raster" package (Hijmans and Etten, 2012). Final resampled raster layers had a spatial resolution of 2.5 arc-minutes, approximately 4 km^2 grid cell size at the equator. Two different raster stacks were created: MAR over TERR (MAR/TERR), and TERR over MAR (TERR/MAR). For single-realm modeling, four additional models were developed using single predictors created from MAR (Only-MAR), TERR (Only-TERR), Future-MAR and Future-TERR. These single models were used to evaluate prediction capabilities and to determine whether the distributions of filamentous cyanobacteria were more influenced by single or multi-realm predictors. In total, six different stacked environmental layers (i.e. four single and two multi-realms) were used in the modeling. Multicollinear predictors in each raster stack with a Pearson correlation coefficient ≥ 0.7 were identified and removed. After excluding multicollinear variables from each raster stack, 17 predictors in MAR/TERR and 15 predictors in TERR/MAR, with correlation coefficients ranging from -0.0003 to 0.6991, were included in the modeling. Additionally, 13, 5, 3, and 6 predictors with correlation coefficients ranging from -0.3061 to 0.6071 in Only-MAR, Only-TERR, Future-MAR, and Future-TERR, respectively, were used for single-realm future distribution modeling and for suitable habitats. All stacked and single raster layers were constrained and aligned to the spatial extent of the Baltic Sea using coordinate reference system (CRS) EPSG: 5845-SWEREF99 TM.

2.4. Variable importance and model assessment

The variable importance of each model was estimated using the function 'getVarImp' from the "sdm" and "SSDM" packages. Variable of importance was assessed using Pearson Correlation (Benesty et al., 2009) that implemented in 'usdm' v1.1–18 package, and Area Under the Curve AUC (Hanley and McNeil, 1982) as metrics. Base estimator algorithms, individual SDMs, ESDMs, and SSDMs were assessed for accuracy and performance using the True Skill Statistics (TSS) (Monserud and Leemans, 1992), Cohen's KAPPA coefficient (Allouche et al., 2006), Area Under the Curve (AUC), and the Jaccard coefficient (Jaccard, 1912). Model TSS, KAPPA, and AUC values were extracted and visualized using the "shiny" package platform (Chang et al., 2023).

Models were further assessed for accuracy and performance using model thresholds, omission rates (Franklin, 2010; Phillips et al., 2006), proportion of correctly predicted occurrences, and model prediction success estimated with the "SSDM" package. Habitat suitability predictions were combined with the Jackknife test (Efron, 1982) for variable importance and contribution, performed in MaxEnt v.3.4.1 java-based software (Phillips et al., 2006, 2017).

2.5. Statistical analysis

Variable contributions and mean differences of filamentous cyanobacteria responses to predicted variable importance were assessed using analysis of variance (ANOVA). Strengths of the relationships were quantified using omega squared (ω^2). Differences among cyanobacterial taxa in response to stacked variables were tested with non-parametric analysis of similarities (ANOSIM) and permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations, using the Bray-Curtis dissimilarity index. Generalized linear models were used to assess interaction effects between predictors in all stacked layers. Linear discriminant analysis (LDA) and Wilk's lambda (λ) were used to evaluate the strength and contribution of each set of predictors to the model. Variable contributions to SSDMs were visualized in the linear two-dimensional space of principle component analysis (PCA). ANOVA was conducted in jamovi v.23.21 (The Jamovi Project, 2023), while ANOSIM, PERMANOVA, LDA, and pairwise comparisons were performed in PAST v.4.09 (Hammer et al., 2001). Ordination and visualization were performed using the "FactoMinR" package (Lê et al., 2008) in RStudio (RStudio Team, 2020). Graphical representations for habitat suitability were visualized in QGIS Desktop v3.28.3 (QGIS Development Team, 2022).

3. Results

3.1. Model robustness and performance

The analysis of base estimator algorithms indicated high prediction performances, with AUC between 0.90 and 0.96 (mean ± SD, 0.92 ± 0.04) and TSS between 0.66 and 0.80 (mean ± SD, 0.75 ± 0.08), where AUC and TSS values close to one indicate excellent performance. The generalized boosted regression model (GBM) and random forest (RF) among tested algorithms indicated excellent model performances with high AUC, TSS, and lower omission rates (Fig. 2 & Table S2).

3.2. Significant environmental variables predicted by SDM

Pearson correlation analysis for variable importance indicated that mean annual sea surface temperature 'Biogeo13' (MAR/TERR = 0.39, TERR/MAR = 0.43, Only-MAR = 0.34, *ANOVA*, $F = 61.9, p < 0.001, \omega^2 = 0.197$), nitrate concentration (MAR/TERR = 0.19, TERR/MAR = 0.22; *ANOVA*, $F = 71.3, p < 0.001, \omega^2 = 0.221$), phosphate (MAR/TERR = 0.11, TERR/MAR = 0.10; *ANOVA*, $F = 108, p < 0.001, \omega^2 = 0.301$) long term phosphate concentration (MAR/TERR = 0.10, TERR/MAR = 0.10; *ANOVA*, $F = 60.9, p < 0.001, \omega^2 = 0.195$), primary production of carbon (Only-MAR = 0.13, *ANOVA*, $F = 51.4, p < 0.001, \omega^2 = 0.0.169$), mean annual temperature 'bio1' (Only-TERR = 0.165, *ANOVA*, $F = 112, p < 0.001, \omega^2 = 0.309$), bathymetry (Only-MAR = 0.237, *ANOVA*, $F = 2.73, p = 0.066, \omega^2 = 0.007$), and altitude (Only-TERR = 0.548, *ANOVA*, $F = 0.937, p = 0.392, \omega^2 = 0.00$), all had high contribution to the base

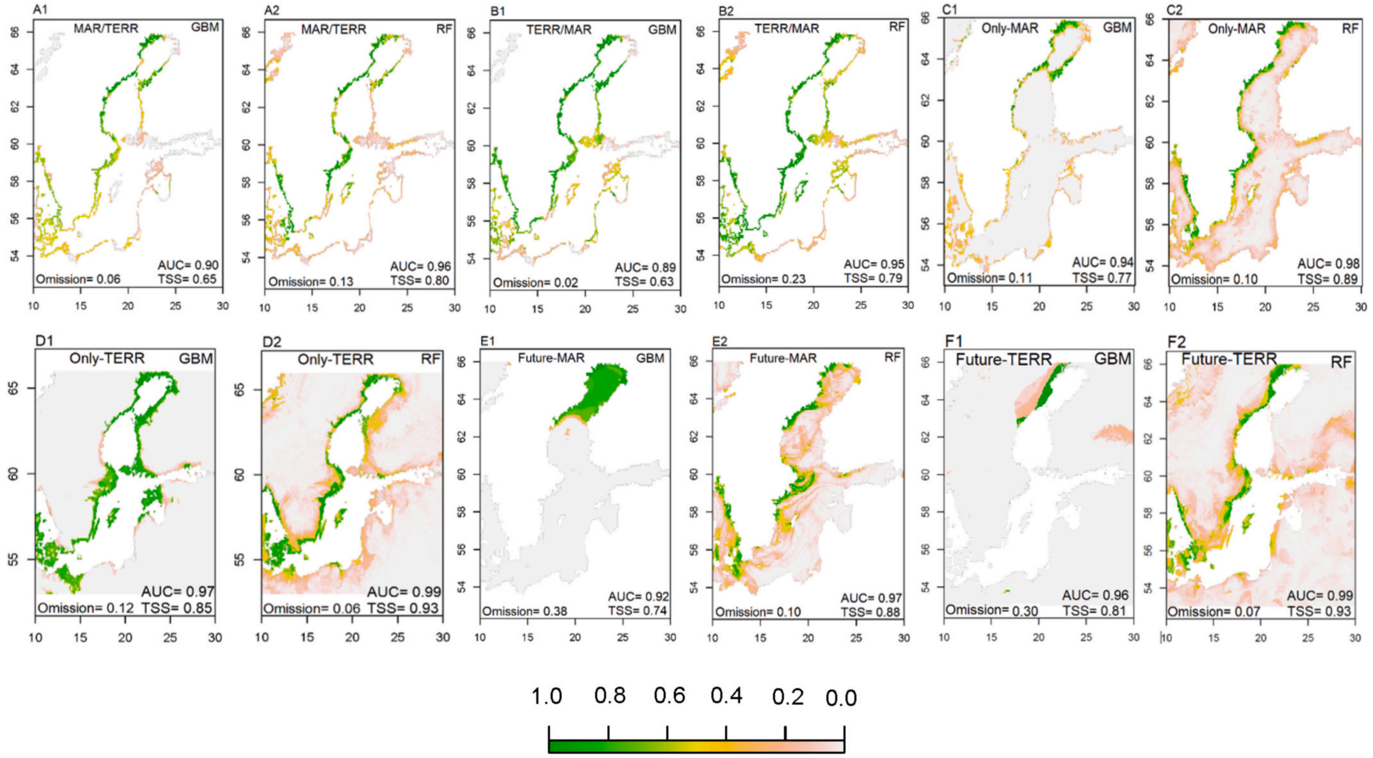

Fig. 2. Model prediction performance and habitat suitability as revealed by base algorithms (1) generalized boosted regression model GBM and (2) random forest RF for stacked multi-realms (A) MAR/TERR, (B) TERR/MAR, and single realms (C) Only-MAR, (D) Only-TERR, (E) Future-MAR, and (F) Future-TERR. Each model was built using all occurrence records and 10,000 pseudoabsence data points as a background. Model performances were assessed by AUC, TSS, and omission rate. Model values (AUC and TSS) close to 1.00 and lower omission rates indicate excellent performance. The scale bar from 0.0 to 1.0 unit represents the grading of sites predicted to be suitable for filamentous nitrogen-fixing cyanobacterial distribution, where dark green colour corresponds to the best suitability for their distribution in Swedish coastal areas of the Baltic Sea. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

model prediction (Fig. S2 &Table S3).

There were 3 and 6 variables of importance predicted among the MAR and TERR future scenarios, respectively. Among the MAR future variables with high contributions to model prediction were the long-term sea surface temperature for the year 2100 (RCP85–2100_templtmax: 0.623, *ANOVA*, $F = 95$, $p < 0.001$, $\omega^2 = 0.275$) and the mean temperature for the year 2050 (RCP85–2050_tempmean: 0.356, *ANOVA*, $F = 94$, $p < 0.001$, $\omega^2 = 0.276$). In the TERR future climate change scenarios, the future mean temperature of the wettest quarter for the year 2070 (RCP85BIO08–2070: 0.516, *ANOVA*, $F = 77.9$, $p < 0.001$, $\omega^2 = 0.276$), and the future annual temperature range for the year 2070 (RCP85BIO07–2070: 0.213, *ANOVA*, $F = 67.4$, $p < 0.001$, $\omega^2 = 0.247$) had high contributions to the model prediction (Fig. S3 &Table S4).

Cyanobacterial taxa showed dissimilar responses to the Future-MAR scenario (*ANOSIM*, $R = 0.33$, $p<0.0001$), Only-MAR (*ANOSIM, permutation* $= 9999$, $R = 0.22$, $p<0.0001$), and the Future-TERR scenario (*ANOSIM, permutation* $= 9999$, $R = 0.20$, $p<0.0001$), respectively, as shown in Table S5 and S6. Moreover, significant differences were observed among the three cyanobacterial taxa in response to both single and stacked multi-realms scenarios (*PERMANOVA, permutation* $= 9999$, $F = 16.2$, $p<0.01$), as well as across all climate scenarios (*PERMANOVA, permutation* $= 9999$, $F = 57.1$, $p<0.001$), Table S7.

3.3. ESDM and SSDM performance

Analysis of ESDMs revealed good model performance *(AUC: (mean ± SD), 0.84 ± 0.06; kappa: 0.56 ± 0.13).* Omission rate analysis showed that Only-TERR, Only-MAR, and Future-TERR models had the lowest omission rates (*Only-TERR = 0.10; Only-MAR = 0.12; Future-TERR = 0.16*), along with higher proportions of correct prediction compared to other stacked realms *(Only-TERR = 0.90, AUC = 0.90; Only-MAR = 0.88, AUC = 0.89; Future-TERR = 0.87, AUC = 0.87),* indicating excellent performance for each model, respectively (Fig. 3.1 &Table S8).

Predictions of SSDMs, based on the kappa coefficient, revealed excellent model performance across both single and stacked multi-realm models *(MAR/TERR: kappa (mean ± SD), 0.75 ± 0.54; TERR/MAR 1.08 ± 0.5; Only-MAR 0.99 ± 0.23; Only-TERR 1.00 ± 0.17)*. Future scenario models also performed well, with Future-MAR (kappa (mean ± SD), 0.94 ± 0.3) and Future-TERR (kappa, 0.99 ± 0.22), showing high accuracy (Fig. 3.2). SSDM predictions identified 17, 15, 13, and 4 important variables in MAR/TERR, TERR/MAR, Only-MAR, and Only-TERR models, respectively, along with 3 and 5 variables in Future-MAR and Future-TERR models, respectively, for cyanobacterial distribution (Table S9 & Fig. S4).

Variables contributing most to model performance included the range of nitrate concentration (*MAR/TERR (mean ± SD), 18.84 ± 2.03; TERR/MAR 19.53 ± 2.19*), mean temperature of wettest quarter ‘bio8’ (*MAR/TERR 15.36 ± 1.27; TERR/MAR 14.72 ± 4.02*), and mean annual sea surface temperature ‘Biogeo13’ (*MAR/TERR 8.65 ± 1.44; TERR/MAR 6.82 ± 1.07*). Other influential variables included Maximum and minimum photosynthetically available radiation (PAR), minimum primary productivity of carbon, bathymetry, altitude, and precipitation of the warmest quarter ‘bio18’, all of which had significant contributions to the model performance of TERR/MAR and MAR/TERR stacked realms.

Interestingly, the predicted distributions of the studied cyanobacteria were more strongly influenced by TERR environmental variables than by MAR variables. TERR variables, such as mean temperature of wettest quarter ‘bio8’ (°C), precipitation of warmest quarter ‘bio18’(mm) and temperature of driest quarter ‘bio9’(°C), had higher mean contributions than MAR variables in both stacked realms *(bio8 (mean ± SD), 15.04 ± 0.44; bio18 5.28 ± 1.58; bio9 4.83 ± 0.99).* Additionally, the stacked TERR/MAR model outperformed the MAR/

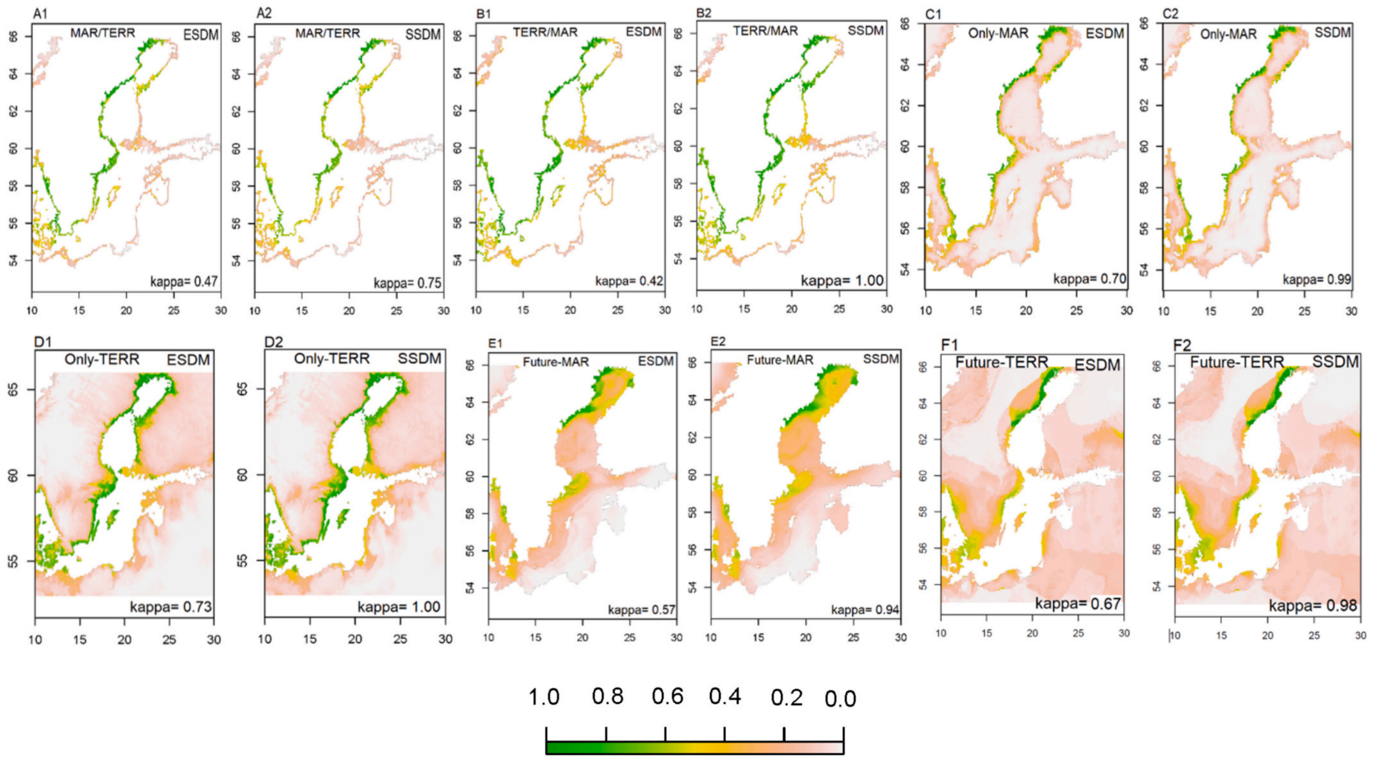

Fig. 3. Model prediction performances and habitat suitability as revealed by (1) ESDM and (2) SSDM for multi-realms (A) MAR/TERR, (B) TERR/MAR, and single realms (C) Only-MAR and (D) Only-TERR, (E) Future-MAR and (F) Future-TERR. Model performances were assessed using the kappa coefficient, where values close to 1.00 indicate excellent performances. The scale bar from 0.0 to 1.0 unit represents the grading of suitable predicted sites, where the dark green colour corresponds to the best predicted sites for filamentous cyanobacteria distribution in Swedish coastal areas of the Baltic Sea. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

TERR model *(TERR/MAR: kappa (mean ± SD),1.08 ± 0.50; MAR/TERR 0.75 ± 0.54)* (Fig. S5). Among all environmental variables in the SSDM, the MAR variables annual sea surface temperature 'Bioge13', sea surface nitrate concentration, sea surface phosphorus concentration, salinity range, along with the TERR variables of temperature of wettest quarter 'bio8', precipitation of warmest quarter 'bio18', temperature of driest quarter 'bio9', maximum temperature of warmest month 'bio5', and altitude had the highest contributions to overall model prediction.

We observed pairwise interaction effects between MAR and TERR variables in both stacked realms on predicted distributions, with significant interaction effects more frequently occurring among MAR variables between MAR and TERR variables (Data S2). General linear models indicated significant interaction effects between sea surface nitrate range and sea surface temperature (MAR/TEER: *ANOVA,* $F = 5.36$, $p < 0.05$), and between phosphate range and temperature of wettest quarter (TERR/MAR: *ANOVA,* $F = 3.97$, $p < 0.05$) on the predicted distributions of cyanobacteria. Further analysis using SSDM indicated high prediction success for Only-TERR (mean ± SD): 0.72 ± 0.13), Future-TERR: 0.70 ± 0.17; and Only-MAR: 0.69 ± 0.18, with high Jaccard coefficients for Only-TERR (mean ± SD): 0.97 ± 0.18, Future-TERR: 0.94 ± 0.22, and Only-MAR: 0.93 ± 0.24). Model performances, as measured by the kappa coefficient, were excellent for Only-TERR, (mean ± SD): 1.00 ± 0.17, Future-TERR: 0.99 ± 0.22, and Only-MAR: 0.99 ± 0.23 (Table S9).

Monthly TERR precipitation and solar radiation together contributed more to the model prediction performance than any other environmental variables in the TERR and MAR domains. The MAXENT model predicted high habitat suitability (AUC = 0.98) with a very low omission rate (omission rate = 0.01), indicating superior model performance (Fig. 4). Variables with the highest contribution to the model included monthly precipitation in May, June, July, and August, as assessed by Jackknife regularized training gain and Jackknife evaluation of AUC (Fig. S4).

3.4. Predicted future spatial distribution of filamentous cyanobacteria

Scenarios with high contributions to the model included long-term sea surface temperature for the year 2100 *(RCP85–2100_templtmax (mean ± SD), 45.19 ± 0.41)* and future annual TERR temperature for the year 2070 *(RCP85BIO08–2070 (mean ± SD), 39.26 ± 1.05)*, see Table 1 and Fig. S5 E&F. Model predictions for the future distribution of filamentous cyanobacteria based on the TERR RCP85-2070 trajectory showed better performance than those based on the MAR RCP85-2100 trajectory (TERR RCP85-2070: AUC= 0.92, Omission rate= 0.07; MAR RCP85-2100: AUC = 0.84, Omission rate = 0.16), Fig. 5.

Linear discriminant analysis (LDA) showed that stacked MAR/TERR and TERR/MAR environmental variables had significantly greater discriminatory ability than variables in single-realm models, as indicated by lower Wilks' lambda (λ) values across all tested models (*MAR/TERR:* $F(34{,}954) = 11.89$, $p < 0.0001$, *Wilks' lambda* $= 0.49$; *TERR/MAR:* $F(30{,}958) = 12.67$, $p < 0.0001$, *Wilks' lambda* $= 0.51$), Table 2 & Fig. S6 & S7.

4. Discussion

In recent decades, summer blooms of filamentous cyanobacteria have emerged at new areas of the Baltic Sea (Olofsson et al., 2020b), highlighting the increasing need to understand factors governing their current and future distribution. For this purpose, we used multi-realm modeling to assess the predictive power and relative influence of terrestrial (TERR) and marine (MAR) environmental variables, as well as projected climate change scenarios, on the future distribution of three taxa of filamentous cyanobacteria along the Swedish coast. The results demonstrate that multi-realm models of stacked TERR and MAR

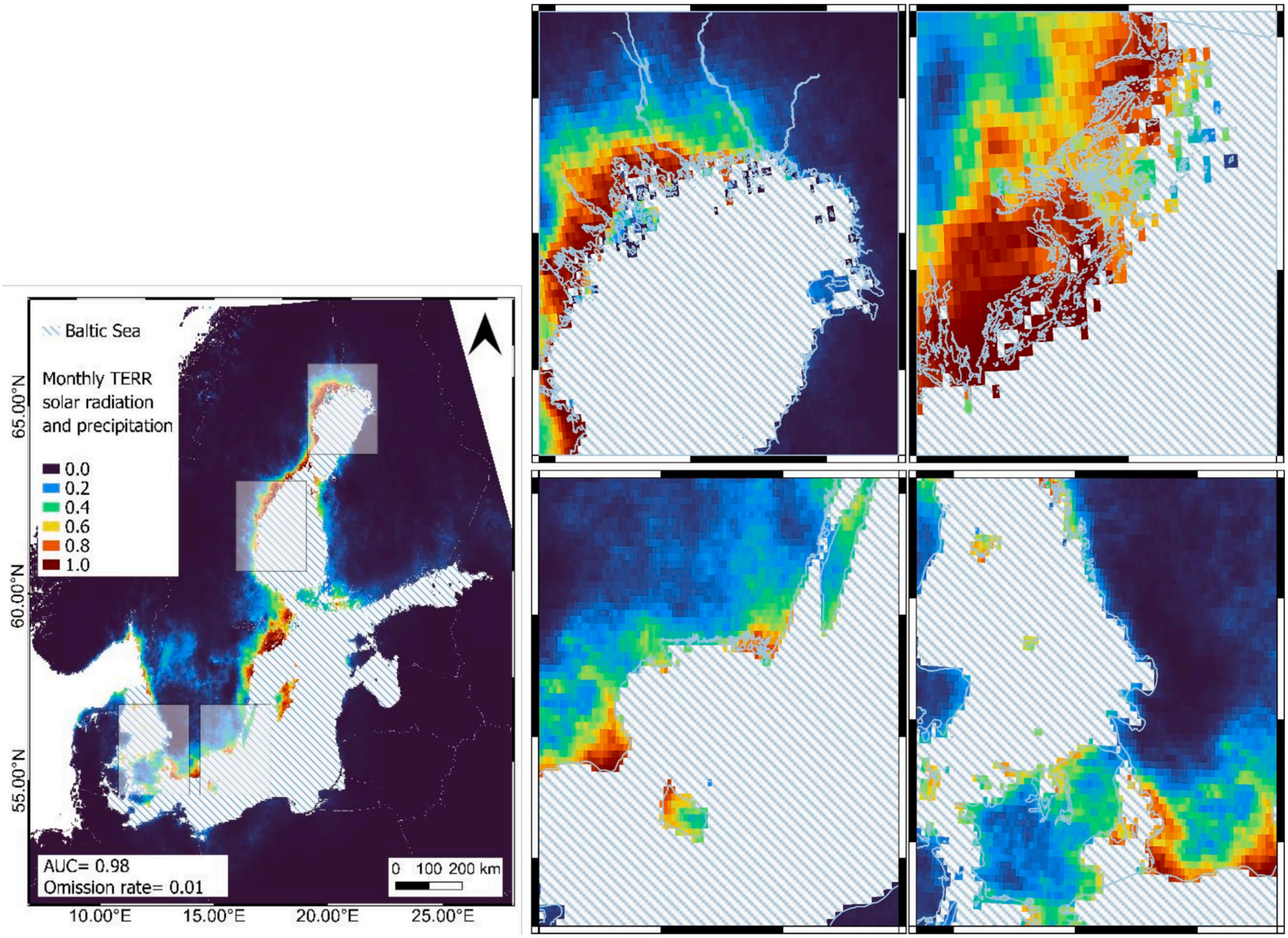

Fig. 4. Representation of the Maximum-Entropy algorithm (MAXENT) showing model prediction performance and habitat suitability based on the terrestrial variables ‘TERR’ monthly solar radiation (kJ m^{-2} day^{-1}) and monthly precipitation (mm). Model performance was assessed by area under the curve AUC and omission rate. Models with an AUC value close to 1.00 and lower omission rates indicate excellent performance. The scale bar from 0.0 to 1.0 unit represents the grading of suitability, where the dark blue, blue, and green colors (0.0 to 0.4) are predicted as areas with no or less suitability while yellow, red, and dark red colors (0.6 to 1.0) correspond to predicted as highly suitable areas for filamentous cyanobacteria in Swedish coastal areas of the Baltic Sea. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

environmental variables significantly enhance predictive performance. This finding suggests the importance of integrating data from both realms when predicting the distribution of filamentous cyanobacteria in coastal regions. The prediction models showed high accuracy and performance, according to AUC, TSS values, and kappa coefficients. The overall omission rates for the stacked models further confirmed the complementary contributions of predictors from both realms, suggesting strong discriminatory power across variables. However, models based solely on MAR variables exhibited lower omission rates than those based on TERR variables. This emphasizes the importance of stacking MAR variables in modeling coastal distribution of filamentous cyanobacteria and the ecological role of both marine and land based environmental conditions in shaping coastal filamentous cyanobacterial distributions.

Several studies have highlighted the methodological challenges of combining marine and terrestrial variables in species distribution models, primarily due to the heterogeneity and inherent differences in how these variables influence the species distribution (Fournier et al., 2017; Häkkinen et al., 2021; Klaassen et al., 2025; Robinson et al., 2011). For example, environmental variables from the MAR realm tend to be less variable (Robinson et al., 2011), while variables from the TERR realm are more heterogeneous due to variations in topography, altitude, and atmospheric conditions (Hijmans et al., 2005). Although multi-realm modeling has been tested for seabirds (Häkkinen et al., 2021) and multi-state modeling for mammals (Frans et al., 2018), their application to cyanobacterial communities is not straightforward (see Abdelgadir et al., 2023). This can be attributed to dynamic and complex environmental characteristics of the coastal zone as a land-sea interface that receives nutrient inputs from various sources, including rivers, runoff, atmospheric deposition, and internal load, factors that collectively influence the growth of cyanobacteria. It is worth mentioning that the accuracy of capturing river input into the Baltic Sea using current datasets or modeling framework is challenging due to the complexity of modeling the diverse and dynamic nature of river systems and quantifying the impact of human activities on water flow. Despite these challenges, our results demonstrate that multi-realm modeling can capture the drivers of spatial distribution of filamentous cyanobacteria along the Baltic Sea coast.

Among the environmental predictors, “Biogeo13” - annual sea surface temperature (°C) and sea surface nitrate concentration (mol m^{-3}) showed strong correlations with predicted occurrences and made substantial contributions to overall model performances across multi-realms (MAR/TERR, TERR/MAR) and single-realm (Only-MAR) models, as confirmed by Pearson’s r analysis. The significant influence of predictors from one realm over another on the predicted distribution

Table 1
Variables of importance predicted by SSDM (as Mean ± SD). Differences in predicted occurrence of filamentous cyanobacteria were assessed using analysis of variance ANOVA (at $p < 0.05$), and the strength of the relations was assessed by omega squared (ω^2).

Variable	SSDM		ANOVA			Realm
	Mean	SD	F	p	ω^2	
RCP85-2050-Sea surface minimum temperature	25.61	0.42	76.7	< 0.001	0.234	MAR
RCP85-2050- Sea surface mean temperature	29.20	0.03	94	< 0.001	0.273	
RCP85-2100- Sea surface long-term temperature	45.20	0.42	95	< 0.001	0.275	
RCP85-2050_BIO08 Mean Temperature of Wettest Quarter	5.71	0.64	5.59	0.004	0.022	TERR
RCP85-2050_BIO09 Mean Temperature of Driest Quarter	7.57	1.42	19.6	< 0.001	0.084	
RCP85-2070_BIO07 Temperature Annual Range	18.90	0.73	67.4	< 0.001	0.247	
RCP85-2070_BIO08 Mean Temperature of Wettest Quarter	39.27	1.06	77.9	< 0.001	0.275	
RCP85-2070_BIO09 Mean Temperature of Driest Quarter	19.08	2.10	43.5	< 0.001	0.173	
RCP85-2070_BIO14 Precipitation of Driest Month	9.46	2.07	4.42	0.013	0.017	

of filamentous cyanobacteria further supports the importance of including both MAR and TERR variables in modeling efforts of cyanobacterial distribution in the coastal Baltic Sea.

The predicted distribution of filamentous cyanobacteria was significantly affected by the interaction effects between sea surface nitrate and temperature, as well as between sea surface phosphate and TERR

Table 2
Significant contributions of different environmental variables to the predicted coastal distribution of the three studied filamentous cyanobacteria in the Baltic Sea, assessed by linear discriminant analysis (LDA). The discriminatory ability and significance of all environmental variables in current single, multi-realm, and future models, were assessed using Wilks' lambda (λ) and *p*-value ($p < 0.05$). Smaller λ values indicate greater discriminatory power of the respective variable(s).

	Current				Future (RCP85)	
	MAR/ TERR	TERR/ MAR	Only-MAR	Only-TERR	MAR	TERR
Wilks' Lambda (λ)	0.494	0.512	0.519	0.674	0.685	0.683
F (Observed value)	11.86	12.677	14.361	21.302	34.045	17.059
F (Critical value)	1.442	1.471	1.507	1.840	2.108	1.762
df1	34	30	26	10	6	12
df2	954	958	962	978	982	976
p-value	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

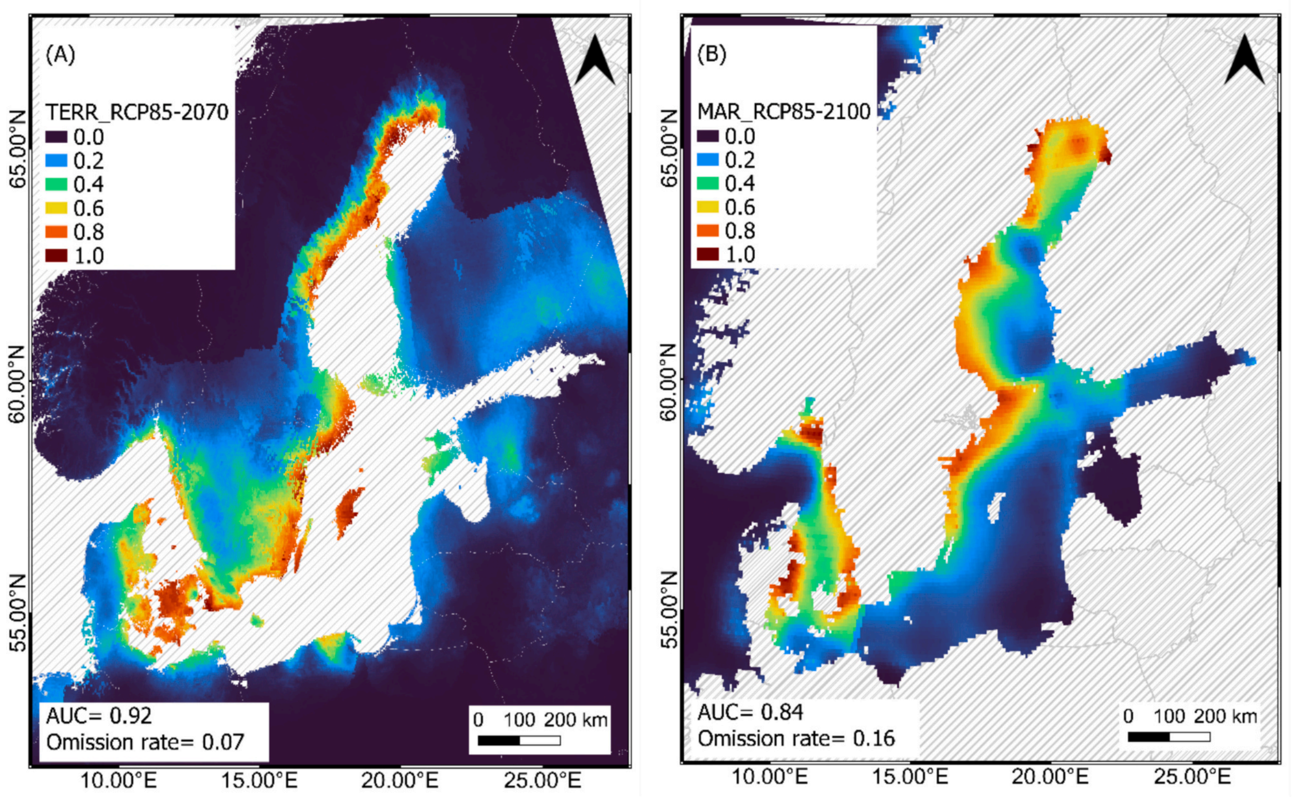

Fig. 5. Predicted future distribution and habitat suitability of filamentous cyanobacteria in Swedish coastal areas of the Baltic Sea based on the best overall model performances of the'RCP85' future scenario for the years (A) TERR 2070 and (B) MAR 2100. RCP85 for the year TERR 2070 corresponds to a projected global warming increase in land surface temperature of approximately 2.6 °C, while RCP85 for the year MAR 2100 corresponds to a projected global warming increase in sea surface temperature of approximately 3.0–4.8 °C. The scale bar from 0.0 to 1.0 unit represents estimated habitat suitability, where dark blue to green colors (0.0 to 0.4) indicate areas with no or low suitability, and yellow to dark red colors (0.6 to 1.0) indicate highly suitable areas, according to model predictions. Model performance was assessed by area under the curve 'AUC' and omission rate. Models with an AUC value close to 1.00 and a lower omission rate indicate excellent performance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temperature of the wettest quarter. Rising water temperatures may enhance nutrient availability and phosphate release from oxygen depleted bottom sediments, influencing the relative nitrogen and phosphate content of the sea water, with a positive effect on the growth of nitrogen-fixing filamentous cyanobacteria as described in Deng et al. (2022), Lürling et al. (2017) and Olofsson et al. (2016). Since filamentous cyanobacteria can fix atmospheric nitrogen, phosphate availability relative to nitrate becomes a key factor in their competitive advantage over other cyanobacterial and phytoplankton groups (Stal et al., 2003). Furthermore, our results indicate a significant effect of decreased salinity and an interaction between salinity and temperature of the warmest month (bio5) on the predicted distributions. These findings align with what has been described by Olofsson et al. (2020b), who reported that declining salinity, and to some extent, rising sea water temperatures have increased the abundance of filamentous cyanobacteria across the Baltic Sea according to data from four decades of environmental monitoring, but with basin-specific differences. Our study also predicts a regional heterogeneity in habitat suitability for filamentous cyanobacteria along the Swedish coastline.

Interaction effects among MAR variables may also explain the increased omission rates, reduced prediction accuracy, and consequently the overall low model performance observed in MAR/TERR, Only-MAR, and Future-MAR. Moreover, the absence of MAR variables and their interactions could explain the higher AUC values, stronger kappa coefficients, and the low omission rates observed in the 'Only-TERR' and 'Future-TERR' models. These interaction effects are likely to contribute to the robust predictive success of 'Only-TERR', 'Future-TERR' and 'Only-MAR' models, in comparison to TERR/MAR and MAR/TERR stacked models. Therefore, we recommend that interaction effects between predictors and changes in omission rates be carefully considered when interpreting the distribution patterns of filamentous cyanobacteria in predictive modeling.

Our models also predict an increased area distribution of filamentous cyanobacteria into northern parts of the Baltic Sea, driven by current TERR monthly solar radiation and precipitation, according to the stacked model of TERR. Model performance was high (AUC = 0.98), with monthly precipitation contributing more to overall model performance and accuracy than monthly solar radiation, as indicated by the Jackknife test and AUC values. These results indicate that increased precipitation may enhance the distribution of filamentous cyanobacteria. This may be explained by increased phosphorus availability and terrestrial dissolved organic matter resulting from greater riverine runoff in the north, driven by rising precipitation, as described in Andersson et al. (2015a, b), Kahru et al. (2020) and Kahru and Elmgren (2014). These model findings further support the inclusion of TERR variables in predicting the spatial distribution of filamentous cyanobacteria in the coastal zone.

Earlier studies have shown that the current nutrient regime in northern parts of the Baltic Sea is less suitable for the proliferation of filamentous cyanobacteria (Alasaarela, 1979; Niemi, 1979). In addition, currently, the Bothnian Bay does not experience dense blooms of filamentous cyanobacteria (Olofsson et al., 2020b) partly due to high organic matter content that darkens the water (Andersson et al., 2015b), a factor not included in our model. Yet, with climate change, as predicted in the ESDMs and SSDMs in our study, the coastal parts of the Bothnian Sea and Bothnian Bay in the northern Baltic Sea may become increasingly suitable habitats for these organisms. This may be explained by a gradual environmental shift driven by inorganic phosphorus from terrestrial riverine runoff and internal load making these regions more conducive to cyanobacterial growth (Andersson et al., 2015a; Kahru et al., 2020; Meier et al., 2022; Zhao et al., 2023). Earlier studies highlighted several factors behind thriving of cyanobacteria in the Baltic Sea such as nutrient availability (Munkes et al., 2021), water stratification (Huisman et al., 2018), level of photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) (Mohlin, 2010), and the low ratio of dissolved inorganic nitrogen to dissolved inorganic phosphorus, the N:P ratio (Stal et al., 2003). Our SSDM and ESDM findings in light of previous studies could also be attributed to increased water stratification in response to increased air–sea heat fluxes, which influence the sea surface temperature (Andersson et al., 2015b; Carey et al., 2012; Dutheil et al., 2023; Gröger et al., 2019; Paerl and Huisman, 2009; Placke et al., 2021) and the delivery of inorganic nutrients to surface waters via land runoff (Meier et al., 2022). Together, these environmental changes may provide favorable biogeochemical conditions for filamentous cyanobacteria at the coast (Kahru et al., 2020). In addition, the three dominant bloom-forming taxa, *Nodularia spumigena*, *Aphanizomenon* sp., and *Dolichospermum* spp., are known to compete with faster-growing phytoplankton for nutrients (see Löptien and Dietze, 2022; Munkes et al., 2021). Yet, this competition over nutrients is not possibly captured by our model setup.

Our models show that both solar radiation and precipitation contribute to the predicted increase in cyanobacterial occurrence, particularly in the northern Baltic Proper and the Bothnian Bay. While this may hold true for coastal areas, our models do not capture the offshore regions, which may still be experiencing light limitation due to colored dissolved organic matter which strongly absorbs light (Kratzer et al., 2020; Munkes et al., 2021; Śliwińska-Wilczewska et al., 2019). The prediction of cyanobacterial presence in coastal sites beyond present occurrences, based on stacked multi-realms, supports the inclusion of TERR environmental variables. Models incorporating TERR variables demonstrated higher predictive capability than those using MAR variables alone. Our results show that relying solely on MAR variables omit critical information from the terrestrial domain, thereby reducing the overall model accuracy, performance, and prediction.

Our model predicted an increased distribution of filamentous cyanobacteria into the northern Baltic Proper, northern parts of the Bothnian Sea, the Bothnian Bay, and southward to the Arkona basin. These increases are associated with increasing temperature of land surface along the coastal interface of the Baltic Sea for year 2070 'RCP85-2070' and long-term sea surface temperature increase for year 2100 'RCP85-2100'.These higher latitudes of the Earth are considered particularly exposed to climate change, known as the 'polar amplification' (Meier et al., 2022). Global and regional climate projections for the northern Baltic Sea, predict a sea surface temperature rise by 4 °C, and a ∼ 30 % rise in precipitation (Andersson et al., 2015b; Meier et al., 2022). These changes are expected to enhance terrestrial runoff of organic matter and reduce salinity in the northern Baltic Proper, northern parts of the Bothnian Sea, Bothnian Bay, and the Arkona basin (Andersson et al., 2013; Andersson et al., 2015b). Increased water temperature, reduced salinity, and elevated inorganic nutrient availability as a result of riverine runoff have all been linked to enhanced filamentous cyanobacterial abundance in the northern Baltic Sea (Andersson et al., 2015a; Jaanus et al., 2011; Kahru and Elmgren, 2014). Basin-specific reductions in salinity have also been associated with increases in cyanobacterial blooms (Kuosa et al., 2017; Olofsson et al., 2020b; Suikkanen et al., 2007), which may explain our predicted future increase of filamentous cyanobacteria in both northern and southern parts of the Baltic Sea. Our model projections indicate that future increases in TERR temperature along coastal areas will have a greater influence on predicted distribution than future MAR variables. Future TERR-based predictions showed a low omission rate and high model performance compared to future MAR-based predictions. Therefore, warming trends in the terrestrial domain should be considered when forecasting predictions of coastal distribution of filamentous cyanobacteria in the Baltic Sea.

To sum up, the discriminatory power of predictors in the stacked MAR/TERR and TERR/MAR models was higher than in single-realm models, indicating robust model performance of multi-realm approaches. Caution, however, is advised when interpreting these predictions, as other environmental variables not included in the present study may also influence filamentous cyanobacterial distribution. Additionally, adjacency effects in satellite imagery, particularly within 1–10 km of the shore (see Bulgarelli and Zibordi, 2018; Wu et al., 2024), can lead to misinterpretations of species distributions, particularly in coastal zones. The availability of occurrence records in the database, and that were limited to within 1 km to 10 km of the Swedish coastline, could lead to misinterpretations of species distributions in coastal zones. Furthermore, limited data, such as the unexpectedly low occurrence records from the southern parts Sweden's eastern Baltic Sea coastline, an area known for dense summer blooms (Karlson et al., 2022), likely influenced the predictions of the filamentous cyanobacterial distributions. Despite the above limitations, there are two advantages in our modeling approach: its ability to combine terrestrial and marine information for coastal filamentous cyanobacteria in a single modeling forecast, and the ability to consider and assess the interactions between variables of multiple ecological realms. If carefully used, this modeling approach can improve predictions of future expansion of filamentous cyanobacteria in the coastal Baltic Sea.

5. Conclusion

Using a multi-realm modeling approach that integrates environmental variables from both marine and terrestrial domains resulted in robust model performance and reliable predictions of filamentous cyanobacteria distribution along Sweden's Baltic Sea coast. Compared to single-realm models, this approach highlighted the importance of cross-realm interactions, showing that the combined influence of land and sea factors significantly shapes the predicted coastal distribution patterns. Notably, terrestrial variables had a stronger influence on the model outcomes than marine ones. The projections identified the northern Baltic Sea, including the Bothnian Bay and Bothnian Sea, as regions of concern, where future occurrences of filamentous cyanobacteria may intensify due to changing climate conditions. This modeling approach offers valuable insights into how climate change may affect cyanobacterial blooms in coastal ecosystems such as the Baltic Sea region. It can support decision-making and improve monitoring strategies by identifying priority areas likely to experience increased bloom activity.

CRediT authorship contribution statement

Mohanad Abdelgadir: Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Elias Broman:** Writing – review & editing, Investigation, Conceptualization. **Patrik Dinnétz:** Writing – review & editing, Supervision, Formal analysis. **Malin Olofsson:** Writing – review & editing. **Sara Sjöling:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2025.103439.

Data availability statement

The data and R codes that support the findings of this study are available at the public repository on GitHub, and supplementary tables and figures of this article.

References

Abdelgadir, M., Alharbi, R., AlRashidi, M., Alatawi, A.S., Sjöling, S., Dinnétz, P., 2023. Distribution of denitrifiers predicted by correlative niche modeling of changing environmental conditions and future climatic scenarios across the Baltic Sea. Eco. Inform. 78, 102346. https://doi.org/10.1016/j.ecoinf.2023.102346.

Alasaarela, E., 1979. Phytoplankton and environmental conditions in central and coastal areas of the Bothnian Bay. Ann. Bot. Fenn. 16 (3), 241–274. JSTOR. http://www.jstor.org/stable/23725161.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS): assessing the accuracy of distribution models. J. Appl. Ecol. 43 (6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Almroth-Rosell, E., Edman, M., Eilola, K., Meier, H.E.M., Sahlberg, J., 2016. Modelling nutrient retention in the coastal zone of an eutrophic sea. Biogeosciences 13 (20), 5753–5769. https://doi.org/10.5194/bg-13-5753-2016.

Andersson, A., Jurgensone, I., Rowe, O.F., Simonelli, P., Bignert, A., Lundberg, E., Karlsson, J., 2013. Can humic water discharge counteract eutrophication in coastal waters? PloS One 8 (4), e61293. https://doi.org/10.1371/journal.pone.0061293.

Andersson, A., Höglander, H., Karlsson, C., Huseby, S., 2015a. Key role of phosphorus and nitrogen in regulating cyanobacterial community composition in the northern Baltic Sea. Estuar. Coast. Shelf Sci. 164, 161–171. https://doi.org/10.1016/j.ecss.2015.07.013.

Andersson, A., Meier, H.E.M., Ripszam, M., Rowe, O., Wikner, J., Haglund, P., Eilola, K., Legrand, C., Figueroa, D., Paczkowska, J., Lindehoff, E., Tysklind, M., Elmgren, R., 2015b. Projected future climate change and Baltic Sea ecosystem management. AMBIO 44 (S3), 345–356. https://doi.org/10.1007/s13280-015-0654-8.

Araújo, M., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22 (1), 1. https://doi.org/10.1016/j.tree.2006.09.010.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., Tittensor, D., 2018. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. Glob. Ecol. Biogeogr. 27 (3), 277–284. https://doi.org/10.1111/geb.12693.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many?: how to use pseudo-absences in niche modelling? Methods Ecol. Evol. 3 (2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Becker, J., Sandwell, D., Smith, W., Braud, J., Binder, B., Depner, J., Fabre, D., Factor, J., Ingalls, S., Kim, S.H., Ladner, R., Marks, K., 2009. Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. Mar. Geodesy 32, 355–371. https://doi.org/10.1080/01490410903297766.

Benesty, J., Chen, J., Huang, Y., Cohen, I., 2009. Pearson correlation coefficient. In: Cohen, In I., Huang, Y., Chen, J., Benesty, J. (Eds.), Noise Reduction in Speech Processing, vol. 2. Springer, Berlin Heidelberg, pp. 1–4. https://doi.org/10.1007/978-3-642-00296-0_5.

Bentlage, B., Peterson, A.T., Barve, N., Cartwright, P., 2013. Plumbing the depths: extending ecological niche modelling and species distribution modelling in three dimensions: 3D ENM and SDM. Glob. Ecol. Biogeogr. 22 (8), 952–961. https://doi.org/10.1111/geb.12049.

Bivand, R.S., Pebesma, E., Gomez-Rubio, V., 2013. Applied Spatial Data Analysis with R, Second edition. Springer, NY. https://asdar-book.org/.

Booth, T.H., Nix, H.A., Busby, J.R., Hutchinson, M.F., 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. Divers. Distrib. 20 (1), 1–9. https://doi.org/10.1111/ddi.12144.

Bosch, S., Fernandez, S., 2022. sdmpredictors: Species Distribution Modelling Predictor Datasets. http://lifewatch.github.io/sdmpredictors/.

Breiman, L., 2001. Random forests. Mach. Learn. 45 (1), 5–32. https://doi.org/10.1023/A:1010933404324.

Bulgarelli, B., Zibordi, G., 2018. On the detectability of adjacency effects in ocean color remote sensing of mid-latitude coastal environments by SeaWiFS, MODIS-A, MERIS, OLCI, OLI and MSI. Remote Sens. Environ. 209, 423–438. https://doi.org/10.1016/j.rse.2017.12.021.

Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P.W., Trisos, C., Romero, J., Aldunce, P., Barrett, K., Blanco, G., Cheung, W.W.L., Connors, S., Denton, F., Diongue-Niang, A., Dodman, D., Garschagen, M., Geden, O., Hayward, B., Jones, C., Péan, C., 2023. In: Core Writing Team, Lee, H., Romero, J. (Eds.), IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change (IPCC), Geneva, Switzerland. https://doi.org/10.59327/IPCC/AR6-9789291691647.

Carey, C.C., Ibelings, B.W., Hoffmann, E.P., Hamilton, D.P., Brookes, J.D., 2012. Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. Water Res. 46 (5), 1394–1407. https://doi.org/10.1016/j.watres.2011.12.016.

Cegłowska, M., Toruńska-Sitarz, A., Kowalewska, G., Mazur-Marzec, H., 2018. Specific chemical and genetic markers revealed a thousands-year presence of toxic Nodularia spumigena in the Baltic Sea. Mar. Drugs 16 (4), 116. https://doi.org/10.3390/md16040116.

Chamberlain, S., 2016. scrubr: Clean Biological Occurrence Records. R Package Version 0.1, 1, p. 162.

Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L., Ram, K., 2023. rgbif: Interface to the Global Biodiversity Information Facility API. https://CRAN.R-project.org/package=rgbif.

Chang, W., Cheng, J., Allaire, J.J., Sievert, C., Schloerke, B., Xie, Y., Allen, J., McPherson, J., Dipert, A., Borges, B., 2023. shiny: Web Application Framework for R. https://shiny.rstudio.com/.

Dambach, J., Rödder, D., 2011. Applications and future challenges in marine species distribution modeling. Aquat. Conserv. Mar. Freshwat. Ecosyst. 21. https://doi.org/10.1002/aqc.1160.

Deng, L., Cheung, S., Kang, C., Liu, K., Xia, X., Liu, H., 2022. Elevated temperature relieves phosphorus limitation of marine unicellular diazotrophic cyanobacteria. Limnol. Oceanogr. 67 (1), 122–134. https://doi.org/10.1002/lno.11980.

Deutsch, C., Sarmiento, J.L., Sigman, D.M., Gruber, N., Dunne, J.P., 2007. Spatial coupling of nitrogen inputs and losses in the ocean. Nature 445 (7124), 163–167. https://doi.org/10.1038/nature05392.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Dutheil, C., Meier, H.E.M., Gröger, M., Börgel, F., 2023. Warming of Baltic Sea water masses since 1850. Climate Dynam. 61 (3–4), 1311–1331. https://doi.org/10.1007/s00382-022-06628-z.

Efron, B., 1982. The Jackknife, the Bootstrap and Other Resampling Plans. Society for Industrial and Applied Mathematics. https://doi.org/10.1137/1.9781611970319.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40 (1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species: the art of modelling range-shifting species. Methods Ecol. Evol. 1 (4), 4. https://doi.org/10.1111/j.2041-210X.2010.00036.x.

Eyring, V., Bony, S., Meehl, G.A., Senior, C.A., Stevens, B., Stouffer, R.J., Taylor, K.E., 2016. Overview of the coupled model Intercomparison project phase 6 (CMIP6) experimental design and organization. Geosci. Model Dev. 9 (5), 1937–1958. https://doi.org/10.5194/gmd-9-1937-2016.

Fewer, D.P., Köykkä, M., Halinen, K., Jokela, J., Lyra, C., Sivonen, K., 2009. Culture-independent evidence for the persistent presence and genetic diversity of microcystin-producing Anabaena (Cyanobacteria) in the Gulf of Finland. Environ. Microbiol. 11 (4), 855–866. https://doi.org/10.1111/j.1462-2920.2008.01806.x.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/joc.5086.

Fournier, A., Barbet-Massin, M., Rome, Q., Courchamp, F., 2017. Predicting species distribution combining multi-scale drivers. Glob. Ecol. Conserv. 12, 215–226. https://doi.org/10.1016/j.gecco.2017.11.002.

Franklin, J., 2010. Mapping Species Distributions: Spatial Inference and Prediction, 1st ed. Cambridge University Press. https://doi.org/10.1017/CBO9780511810602.

Frans, V.F., Augé, A.A., Edelhoff, H., Erasmi, S., Balkenhol, N., Engler, J.O., 2018. Quantifying apart what belongs together: a multi-state species distribution modelling framework for species using distinct habitats. Methods Ecol. Evol. 9 (1), 98–108. https://doi.org/10.1111/2041-210X.12847.

Friedman, J.H., 1991. Multivariate adaptive regression splines. Ann. Stat. 19 (1), 1. https://doi.org/10.1214/aos/1176347963.

Friedman, J.H., 2002. Stochastic gradient boosting. Comput. Stat. Data Anal. 38 (4), 4. https://doi.org/10.1016/S0167-9473(01)00065-2.

Gao, K., Yu, H., Brown, M.T., 2007. Solar PAR and UV radiation affects the physiology and morphology of the cyanobacterium Anabaena sp. PCC 7120. J. Photochem. Photobiol. B Biol. 89 (2–3), 117–124. https://doi.org/10.1016/j.jphotobiol.2007.09.006.

GBIF, 2023. GBIF.org. In GBIF. https://www.gbif.org/.

Ghannam, R.B., Techtmann, S.M., 2021. Machine learning applications in microbial ecology, human microbiome studies, and environmental monitoring. Comput. Struct. Biotechnol. J. 19, 1092–1107. https://doi.org/10.1016/j.csbj.2021.01.028.

Gröger, M., Arneborg, L., Dieterich, C., Höglund, A., Meier, H.E.M., 2019. Summer hydrographic changes in the Baltic Sea, Kattegat and Skagerrak projected in an ensemble of climate scenarios downscaled with a coupled regional ocean–sea ice–atmosphere model. Climate Dynam. 53 (9–10), 5945–5966. https://doi.org/10.1007/s00382-019-04908-9.

Guimarães, A., Silva, P.H.D., Carneiro, F.M., Silva, D.P., 2020. Using distribution models to estimate blooms of phytosanitary cyanobacteria in Brazil. Biota Neotrop. 20 (2), e20190756. https://doi.org/10.1590/1676-0611-bn-2019-0756.

Guisan, A., Edwards, T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. 157 (2–3), 2–3. https://doi.org/10.1016/S0304-3800(02)00204-1.

Häkkinen, H., Petrovan, S.O., Sutherland, W.J., Pettorelli, N., 2021. Terrestrial or marine species distribution model: why not both? A case study with seabirds. Ecol. Evol. 11 (23), 16634–16646. https://doi.org/10.1002/ece3.8272.

Halinen, K., Fewer, D.P., Sihvonen, L.M., Lyra, C., Eronen, E., Sivonen, K., 2008. Genetic diversity in strains of the genus Anabaena isolated from planktonic and benthic habitats of the Gulf of Finland (Baltic Sea): the phylogeny of the Baltic Sea Anabaena. FEMS Microbiol. Ecol. 64 (2), 199–208. https://doi.org/10.1111/j.1574-6941.2008.00461.x.

Hammer, O., Harper, D., Ryan, P., 2001. Paleontological statistics software package for education and data analsis. Palaeontol. Electron. 4, 9–18.

Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143 (1), 1. https://doi.org/10.1148/radiology.143.1.7063747.

Harrell, F.E., Lee, K.L., Mark, D.B., 2005. Prognostic/clinical prediction models: Multivariable prognostic models: Issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. In: D'Agostino, R.B. (Ed.), Tutorials in Biostatistics. John Wiley & Sons, Ltd., pp. 223–249. https://doi.org/10.1002/0470023678.ch2b(i)

Helcom, D., 2018. HELCOM Pre-Core indicator Report, Online.[Web Link]. ISSN, pp. 2343–2543.

Hense, I., Meier, H.E.M., Sonntag, S., 2013. Projected climate change impact on Baltic Sea cyanobacteria: climate change impact on cyanobacteria. Clim. Change 119 (2), 391–406. https://doi.org/10.1007/s10584-013-0702-y.

Hieronymus, J., Eilola, K., Olofsson, M., Hense, I., Meier, H.E.M., Almroth-Rosell, E., 2021. Modeling cyanobacteria life cycle dynamics and historical nitrogen fixation in the Baltic Proper. Biogeosciences 18 (23), 6213–6227. https://doi.org/10.5194/bg-18-6213-2021.

Hijmans, Etten, 2012. raster: Geographic Analysis and Modeling With Raster Data. http://CRAN.R-project.org/package=raster.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25 (15), 1965–1978. https://doi.org/10.1002/joc.1276.

Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2015. Package "dismo." Circles, p. 9.

Huisman, J., Codd, G.A., Paerl, H.W., Ibelings, B.W., Verspagen, J.M.H., Visser, P.M., 2018. Cyanobacterial blooms. Nat. Rev. Microbiol. 16 (8), 471–483. https://doi.org/10.1038/s41579-018-0040-1.

IPCC, 2023. Climate change 2022 – Impacts, adaptation and vulnerability. In: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, 1st ed. Cambridge University Press. https://doi.org/10.1017/9781009325844.

Jaanus, A., Andersson, A., Olenina, I., Toming, K., Kaljurand, K., 2011. Changes in Phytoplankton Communities along a North–South Gradient in the Baltic Sea between 1990 and 2008.

Jaccard, P., 1912. The distribution of the flora in the alpine zone. New Phytol. 11 (2), 37–50. https://doi.org/10.1111/j.1469-8137.1912.tb05611.x.

Janßen, R., Beck, A.J., Werner, J., Dellwig, O., Alneberg, J., Kreikemeyer, B., Maser, E., Böttcher, C., Achterberg, E.P., Andersson, A.F., Labrenz, M., 2021. Machine learning predicts the presence of 2,4,6-trinitrotoluene in sediments of a Baltic Sea munitions dumpsite using microbial community compositions. Front. Microbiol. 12, 626048. https://doi.org/10.3389/fmicb.2021.626048.

Kahru, M., Elmgren, R., 2014. Multidecadal time series of satellite-detected accumulations of cyanobacteria in the Baltic Sea. Biogeosciences 11 (13), 3619–3633. https://doi.org/10.5194/bg-11-3619-2014.

Kahru, M., Elmgren, R., Kaiser, J., Wasmund, N., Savchuk, O., 2020. Cyanobacterial blooms in the Baltic Sea: correlations with environmental factors. Harmful Algae 92, 101739. https://doi.org/10.1016/j.hal.2019.101739.

Kaiser, J., Wasmund, N., Kahru, M., Wittenborn, A.K., Hansen, R., Häusler, K., Moros, M., Schulz-Bull, D., Arz, H.W., 2020. Reconstructing N₂-fixing cyanobacterial blooms in the Baltic Sea beyond observations using 6- and 7-methylheptadecane in sediments as specific biomarkers. Biogeosciences 17 (9), 2579–2591. https://doi.org/10.5194/bg-17-2579-2020.

Karlson, B., Eilola, K., Hansson, M., 2010. Cyanobacterial blooms in the Baltic Sea: Correlating bloom observations with environmental conditions. Proc. In: 13th Int Conf on Harmful Algae, pp. 247–252.

Karlson, B., Arneborg, L., Johansson, J., Linders, J., Liu, Y., Olofsson, M., 2022. A suggested climate service for cyanobacteria blooms in the Baltic Sea – comparing three monitoring methods. Harmful Algae 118, 102291. https://doi.org/10.1016/j.hal.2022.102291.

Klaassen, M., Marques, T.A., Alves, F., Fernandez, M., 2025. Trends in marine species distribution models: a review of methodological advances and future challenges. Ecography, e07702. https://doi.org/10.1002/ecog.07702.

Klawonn, I., Nahar, N., Walve, J., Andersson, B., Olofsson, M., Svedén, J.B., Littmann, S., Whitehouse, M.J., Kuypers, M.M.M., Ploug, H., 2016. Cell-specific nitrogen- and carbon-fixation of cyanobacteria in a temperate marine system (Baltic Sea). Environ. Microbiol. 18 (12), 4596–4609. https://doi.org/10.1111/1462-2920.13557.

Kownacka, J., Busch, S., Göbel, J., Gromisz, S., Hällfors, H., Huseby, S., Jaanus, A., Jakobsen, H.H., Johansen, M., Johansson, M., Liebeke, N., Kobos, J., Kraśniewski, W., Kremp, A., Lehtinen, S., 2022. Cyanobacteria biomass, 1990-2021. HELCOM Baltic Sea Environment Fact Sheets 2021. Online. [Date Viewed]. http://www.helcom.fi/baltic-sea-trends/environment-fact-sheets/eutrophication/cyanobacteria-biomass/.

Kratzer, S., Kyryliuk, D., Brockmann, C., 2020. Inorganic suspended matter as an indicator of terrestrial influence in Baltic Sea coastal areas—algorithm development and validation, and ecological relevance. Remote Sens. Environ. 237, 111609. https://doi.org/10.1016/j.rse.2019.111609.

Kuosa, H., Fleming-Lehtinen, V., Lehtinen, S., Lehtiniemi, M., Nygård, H., Raateoja, M., Raitaniemi, J., Tuimala, J., Uusitalo, L., Suikkanen, S., 2017. A retrospective view of the development of the Gulf of Bothnia ecosystem. J. Mar. Syst. 167, 78–92. https://doi.org/10.1016/j.jmarsys.2016.11.020.

Lê, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. J. Stat. Softw. 25 (1). https://doi.org/10.18637/jss.v025.i01.

Lehtimäki, J., Sivonen, K., Luukkainen, R., Niemelä, S.I., 1994. The effects of incubation time, temperature, light, salinity, and phosphorus on growth and hepatotoxin production by Nodularia strains. Arch. Hydrobiol. 130 (3), 269–282. https://doi.org/10.1127/archiv-hydrobiol/130/1994/269.

Lembrechts, J.J., Broeders, L., De Gruyter, J., Radujković, D., Ramirez-Rojas, I., Lenoir, J., Verbruggen, E., 2020. A framework to bridge scales in distribution modeling of soil microbiota. FEMS Microbiol. Ecol. 96 (5), fiaa051. https://doi.org/10.1093/femsec/fiaa051.

Lima, T.A., Beuchle, R., Langner, A., Grecchi, R.C., Griess, V.C., Achard, F., 2019. Comparing Sentinel-2 MSI and Landsat 8 OLI imagery for monitoring selective logging in the Brazilian Amazon. Remote Sens 11 (8), 8. https://doi.org/10.3390/rs11080961.

Lips, I., Lips, U., 2008. Abiotic factors influencing cyanobacterial bloom development in the Gulf of Finland (Baltic Sea). Hydrobiologia 614 (1), 133–140. https://doi.org/10.1007/s10750-008-9449-2.

Löptien, U., Dietze, H., 2022. Retracing cyanobacteria blooms in the Baltic Sea. Sci. Rep. 12 (1), 10873. https://doi.org/10.1038/s41598-022-14880-w.

Luckas, B., Dahlmann, J., Erler, K., Gerdts, G., Wasmund, N., Hummert, C., Hansen, P.D., 2005. Overview of key phytoplankton toxins and their recent occurrence in the north and Baltic seas. Environ. Toxicol. 20 (1), 1–17. https://doi.org/10.1002/tox.20072.

Lürling, M., Van Oosterhout, F., Faassen, E., 2017. Eutrophication and warming boost cyanobacterial biomass and microcystins. Toxins 9 (2), 64. https://doi.org/10.3390/toxins9020064.

Meier, H.E.M., Kniebusch, M., Dieterich, C., Gröger, M., Zorita, E., Elmgren, R., Myrberg, K., Ahola, M.P., Bartosova, A., Bonsdorff, E., Börgel, F., Capell, R., Carlén, I., Carlund, T., Carstensen, J., Christensen, O.B., Dierschke, V., Frauen, C., Frederiksen, M., Zhang, W., 2022. Climate change in the Baltic Sea region: a summary. Earth Syst. Dynam. 13 (1), 457–593. https://doi.org/10.5194/esd-13-457-2022.

Meriggi, C., Drakare, S., Polaina Lacambra, E., Johnson, R.K., Laugen, A.T., 2022. Species distribution models as a tool for early detection of the invasive Raphidiopsis raciborskii in European lakes. Harmful Algae 113, 102202. https://doi.org/10.1016/j.hal.2022.102202.

Meriggi, C., Mehrshad, M., Johnson, R.K., Laugen, A.T., Drakare, S., 2023. Challenges in supplying empirical proof for predictions derived from Species Distribution Models (SDMs): the case of an invasive cyanobacterium. ISME Commun. 3 (1), 56. https://doi.org/10.1038/s43705-023-00264-2.

Mod, H.K., Buri, A., Yashiro, E., Guex, N., Malard, L., Pinto-Figueroa, E., Pagni, M., Niculita-Hirzel, H., van der Meer, J.R., Guisan, A., 2021. Predicting spatial patterns of soil bacteria under current and future environmental conditions. ISME J. 15 (9), 9. https://doi.org/10.1038/s41396-021-00947-5.

Mohlin, M., 2010. On the Ecophysiology of Baltic cyanobacteria, Focusing on Bottom-up Factors [Elektronisk Resurs]. Faculty of Science, University of Gothenburg, Department of Marine Biology.

Moisander, P.H., McClinton, E., Paerl, H.W., 2002. Salinity effects on growth, photosynthetic parameters, and nitrogenase activity in estuarine planktonic cyanobacteria. Microb. Ecol. 43 (4), 432–442. https://doi.org/10.1007/s00248-001-1044-2.

Monserud, R.A., Leemans, R., 1992. Comparing global vegetation maps with the kappa statistic. Ecol. Model. 62 (4), 4. https://doi.org/10.1016/0304-3800(92)90003-W.

Munkes, B., Löptien, U., Dietze, H., 2021. Cyanobacteria blooms in the Baltic Sea: a review of models and facts. Biogeosciences 18 (7), 2347–2378. https://doi.org/10.5194/bg-18-2347-2021.

Naimi, B., Araújo, M.B., 2016. sdm: a reproducible and extensible R platform for species distribution modelling. Ecography 39 (4), 4. https://doi.org/10.1111/ecog.01881.

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? Ecography 37 (2), 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x.

Niemi, A., 1979. Blue-Green Algal Blooms and N: P Ratio in the Baltic Sea.

Olofsson, M., Egardt, J., Singh, A., Ploug, H., 2016. Inorganic phosphorus enrichments in Baltic Sea water have large effects on growth, carbon fixation, and N2 fixation by Nodularia spumigena. Aquat. Microb. Ecol. 77 (2), 111–123. https://doi.org/10.3354/ame01795.

Olofsson, M., Hagan, J.G., Karlson, B., Gamfeldt, L., 2020a. Large seasonal and spatial variation in nano- and microphytoplankton diversity along a Baltic Sea—North Sea salinity gradient. Sci. Rep. 10 (1), 17666. https://doi.org/10.1038/s41598-020-74428-8.

Olofsson, M., Suikkanen, S., Kobos, J., Wasmund, N., Karlson, B., 2020b. 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.

Paerl, H.W., Huisman, J., 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. Environ. Microbiol. Rep. 1 (1), 27–37. https://doi.org/10.1111/j.1758-2229.2008.00004.x.

Paerl, H.W., Otten, T.G., Kudela, R., 2018. Mitigating the Expansion of Harmful Algal Blooms Across the Freshwater-to-Marine Continuum. Environ. Sci. Technol. 52 (10), 5519–5529. https://doi.org/10.1021/acs.est.7b05950.

Pebesma, E.J., Bivand, R., 2005. Classes and methods for spatial data in R. R News 5 (2), 9–13. https://CRAN.R-project.org/doc/Rnews/.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190 (3–4), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. Ecography 40 (7), 7. https://doi.org/10.1111/ecog.03049.

Placke, M., Meier, H.E.M., Neumann, T., 2021. Sensitivity of the Baltic Sea overturning circulation to long-term atmospheric and hydrological changes. J. Geophys. Res. Oceans 126 (3), e2020JC016079. https://doi.org/10.1029/2020JC016079.

QGIS Development Team, 2022. QGIS Geographic Information System. Open Source Geospatial Foundation. http://qgis.osgeo.org.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/.

Rastogi, R.P., Madamwar, D., Incharoensakdi, A., 2015. Bloom dynamics of cyanobacteria and their toxins: environmental health impacts and mitigation strategies. Front. Microbiol. 6. https://doi.org/10.3389/fmicb.2015.01254.

Roberts, D.R., Bahn, V., Ciuti, S., Boyce, M.S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J.J., Schröder, B., Thuiller, W., Warton, D.I., Wintle, B.A., Hartig, F., Dormann, C.F., 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40 (8), 913–929. https://doi.org/10.1111/ecog.02881.

Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P., Richardson, A.J., 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities: marine species distribution models. Glob. Ecol. Biogeogr. 20 (6), 789–802. https://doi.org/10.1111/j.1466-8238.2010.00636.x.

RStudio Team, 2020. RStudio: Integrated Development Environment for R. RStudio, PBC. http://www.rstudio.com/.

Sbrocco, E.J., Barber, P.H., 2013. MARSPEC: ocean climate layers for marine spatial ecology: ecological archives E094-086. Ecology 94 (4), 4. https://doi.org/10.1890/12-1358.1.

Schmitt, S., Pouteau, R., Justeau, D., Boissieu, F., Birnbaum, P., 2017. ssdm: an r package to predict distribution of species richness and composition based on stacked species distribution models. Methods Ecol. Evol. 8 (12), 1795–1803. https://doi.org/10.1111/2041-210X.12841.

Silveira, S.B., Odebrecht, C., 2019. Effects of salinity and temperature on the growth, toxin production, and akinete germination of the cyanobacterium Nodularia spumigena. Front. Mar. Sci. 6, 339. https://doi.org/10.3389/fmars.2019.00339.

Śliwińska-Wilczewska, S., Cieszyńska, A., Konik, M., Maculewicz, J., Latała, A., 2019. Environmental drivers of bloom-forming cyanobacteria in the Baltic Sea: effects of salinity, temperature, and irradiance. Estuar. Coast. Shelf Sci. 219, 139–150. https://doi.org/10.1016/j.ecss.2019.01.016.

Stal, L.J., Albertano, P., Bergman, B., Bröckel, K.V., Gallon, J.R., Hayes, P.K., Sivonen, K., Walsby, A.E., 2003. BASIC: Baltic Sea cyanobacteria. An investigation of the structure and dynamics of water blooms of cyanobacteria in the Baltic Sea—responses to a changing environment. Cont. Shelf Res. 23 (17–19), 1695–1714. https://doi.org/10.1016/j.csr.2003.06.001.

Steinberg, D., 2009. Chapter 10 CART: Classification and Regression Trees.

Suikkanen, S., Laamanen, M., Huttunen, M., 2007. Long-term changes in summer phytoplankton communities of the open northern Baltic Sea. Estuar. Coast. Shelf Sci. 71 (3–4), 580–592. https://doi.org/10.1016/j.ecss.2006.09.004.

The Jamovi Project, 2023. The Jamovi Project (2023). Jamovi (Version 2.3) [Computer Software]. Retrieved from. https://www.jamovi.org [Computer software].

Thuiller, W., 2014. Editorial commentary on ‘ BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. Glob. Chang. Biol. 20 (12), 3591–3592. https://doi.org/10.1111/gcb.12728.

Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD - a platform for ensemble forecasting of species distributions. Ecography 32 (3), 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x.

Title, P.O., Bemmels, J.B., 2018. ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. Ecography 41 (2), 291–307. https://doi.org/10.1111/ecog.02880.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., De Clerck, O., 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling: Bio-ORACLE marine environmental data rasters. Glob. Ecol. Biogeogr. 21 (2), 272–281. https://doi.org/10.1111/j.1466-8238.2011.00656.x.

Unger, J., Endres, S., Wannicke, N., Engel, A., Voss, M., Nausch, G., Nausch, M., 2013. Response of Nodularia spumigena to pCO_2 – part 3: turnover of phosphorus compounds. Biogeosciences 10 (3), 1483–1499. https://doi.org/10.5194/bg-10-1483-2013.

van Etten, R.J.H., 2012. raster: Geographic Analysis and Modeling With Raster Data. http://CRAN.R-project.org/package=raster.

Viitasalo, M., Bonsdorff, E., 2022. Global climate change and the Baltic Sea ecosystem: direct and indirect effects on species, communities and ecosystem functioning. Earth Syst. Dynam. 13 (2), 711–747. https://doi.org/10.5194/esd-13-711-2022.

Wåhlström, I., Almroth-Rosell, E., Edman, M., Olofsson, M., Eilola, K., Fleming, V., Gröger, M., Arneborg, L., Meier, H.E.M., 2024. Increased nutrient retention and cyanobacterial blooms in a future coastal zone. Estuar. Coast. Shelf Sci. 301, 108728. https://doi.org/10.1016/j.ecss.2024.108728.

Wang, Z., Li, G., Huang, H., Zhang, W., Wang, J., Huang, S., Zheng, Z., 2022. Effects of solar radiation on the Cyanobacteria: diversity, molecular phylogeny, and metabolic activity. Front. Ecol. Evol. 10, 928816. https://doi.org/10.3389/fevo.2022.928816.

Wasmund, N., 1997. Occurrence of cyanobacterial blooms in the Baltic Sea in relation to environmental conditions. Int. Rev. Gesamten Hydrobiol. Hydrogr. 82 (2), 169–184. https://doi.org/10.1002/iroh.19970820205.

Wasmund, N., 2002. Harmful algal blooms in coastal waters of the south-eastern Baltic Sea. In: Schernewski, G., Schiewer, U. (Eds.), Baltic Coastal Ecosystems. Springer, Berlin Heidelberg, pp. 93–116. https://doi.org/10.1007/978-3-662-04769-9_8.

Wasmund, N., Busch, S., Gromisz, S., Höglander, H., Jaanus, A., Johansen, M., Jurgensone, I., Karlsson, C., Kownacka, J., Kraśniewski, W., et al., 2013. Cyanobacteria Biomass. HELCOM Baltic Sea Environment Fact Sheet.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Yutani, H., 2019. Welcome to the tidyverse. J.Open Source Softw. 4 (43), 43. https://doi.org/10.21105/joss.01686.

Wu, Y., Knudby, A., Pahlevan, N., Lapen, D., Zeng, C., 2024. Sensor-generic adjacency-effect correction for remote sensing of coastal and inland waters. Remote Sens. Environ. 315, 114433. https://doi.org/10.1016/j.rse.2024.114433.

Wurtsbaugh, W.A., Paerl, H.W., Dodds, W.K., 2019. Nutrients, eutrophication and harmful algal blooms along the freshwater to marine continuum. WIREs Water 6 (5). https://doi.org/10.1002/wat2.1373.

Yang, X., Wu, X., Hao, H., He, Z., 2008. Mechanisms and assessment of water eutrophication. J. Zhejiang Univ. Sci. B 9 (3), 197–209. https://doi.org/10.1631/jzus.B0710626.

Zhao, L., Brugel, S., Ramasamy, K.P., Andersson, A., 2023. Bacterial community responses to planktonic and terrestrial substrates in coastal northern Baltic Sea. Front. Mar. Sci. 10, 1130855. https://doi.org/10.3389/fmars.2023.1130855.