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Using Long-Term Ecological Datasets to Unravel the Impacts of Short-Term Meteorological Disturbances on Phytoplankton Communities

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ABSTRACT

1. Extreme meteorological events such as storms are increasing in frequency and intensity, but our knowledge of their impacts on aquatic ecosystems and emergent system properties is limited. Understanding the ecological impacts of storms on the dynamics of primary producers remains a challenge that needs to be addressed to assess the vulnerability of freshwater ecosystems to extreme weather conditions and climate change.
2. One promising approach to gain insights into storm impacts on phytoplankton community dynamics is to analyse long-term monitoring datasets. However, such an approach requires disentangling the impacts of short-term meteorological disturbances from the effects of the seasonal trajectories of meteorological conditions. To this end, we applied boosted regression tree models to phytoplankton time series from eight relatively large lakes on four continents, coupled with a procedure adapted to detect and quantify rare events.
3. Overall, the patterns and potential drivers we identified provide important insights into the responses of lakes to short-term meteorological events and highlight differences in the response of phytoplankton communities according to lake morphological characteristics. Our results indicated that deepened thermoclines and lake-specific combinations of drivers describing altered thermal structures caused deviations from the typical trajectories of seasonal phytoplankton succession. For shallow polymictic lakes, shifts in phytoplankton succession also depended on changes in light availability.
4. Overall, our study highlights the value of long-term monitoring to improve our understanding of phytoplankton sensitivity to short-term meteorological disturbances.

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1 | Introduction

Extreme meteorological events are rare. They can strongly affect the dynamics of phytoplankton communities with consequences for ecosystem functioning and services (Stockwell et al. 2020). The urgency to assess the magnitude of such impacts is underpinned by the projected increase in the frequency, intensity, and spatial extent of extreme events under climate change (Trapp et al. 2007; Coumou and Rahmstorf 2012, IPCC 2021). Storms are among the extreme meteorological events that are of particular interest because they directly affect the hydrodynamics of lakes (e.g., Robarts et al. 1998; Kasprzak et al. 2017; Perga et al. 2018) with subsequent effects on biogeochemistry and the composition and seasonal succession of plankton communities (Padisák et al. 1988; Pannard et al. 2007). Therefore, an evaluation as to whether meteorologically induced disturbances in lake physics systematically affect phytoplankton successions is important, particularly in relatively large lakes, which play critical roles for society (Jenny et al. 2020).

Assessing the ecological impacts of episodic meteorological events such as storms is not straightforward (Jennings et al. 2012; Ummenhofer and Meehl 2017; Van de Pol et al. 2017), especially for phytoplankton communities that are characterised by rapid intrinsic dynamics (Reynolds 1997). One possible approach is to analyse existing long-term monitoring data on lake physics and phytoplankton succession from lakes that have been affected by storms in the past. Because the impact of meteorological events on lake physics may vary seasonally (Stockwell et al. 2020), assessments need to consider seasonality in both phytoplankton communities and lake physical structure, particularly thermal stratification dynamics. In temperate climates, stratification commences in spring (Wetzel 2001), corresponding to autogenic succession among species (Amblard 1992), where biotic factors become the dominant drivers, resulting in predictable directional dynamics (Sommer et al. 2012). Specifically, phytoplankton communities enter a phase of maturation (Price 1984), where community composition gradually shifts from small species, which allocate resources predominately to growth, to competitive species, which are efficient at securing resources in nutrient deficient conditions (Sommer et al. 2012; Ehrlich et al. 2020). Storm-induced physical disturbance can disrupt this standard trajectory (Figure 1) and potentially revert the community to an earlier seasonal successional stage (Amblard 1992; Reynolds 1993; Mancuso et al. 2021).

Our objectives were to test whether the occurrence of reversions in the seasonal successional trajectories of lake phytoplankton communities could be predicted based on storm-driven changes in lake physical characteristics and to identify the physical conditions involved, by analysing long-term monitoring datasets collected from relatively large lakes around the world. The basic

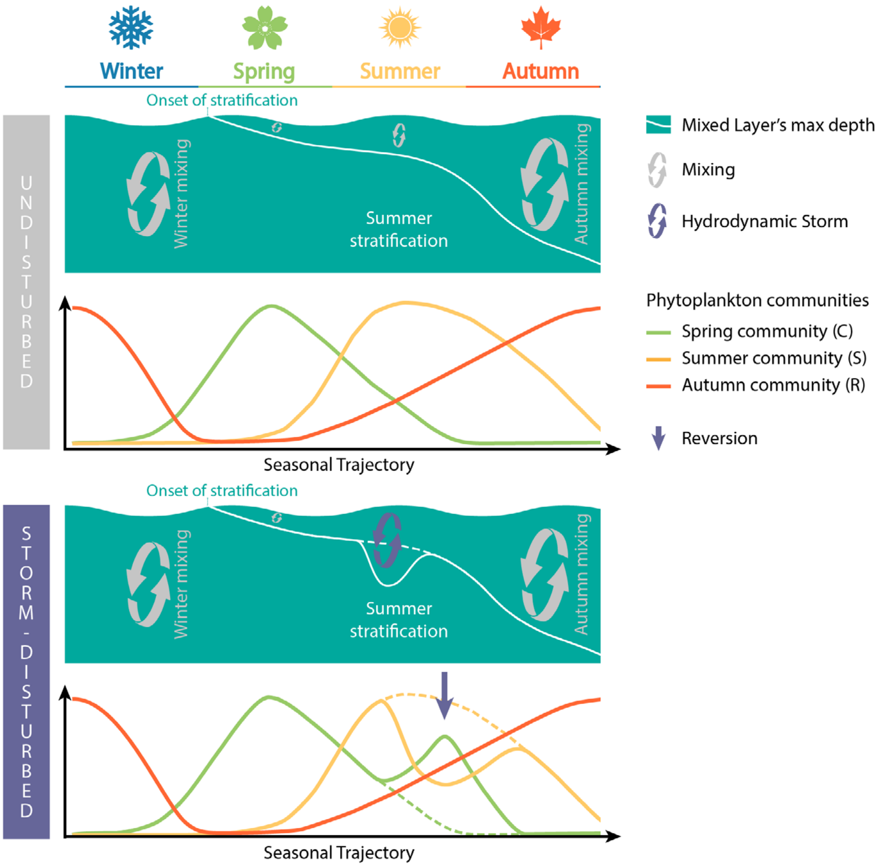

FIGURE 1 | Conceptual model of seasonal trajectories of lake physics and phytoplankton succession after a mid-summer meteorological disturbance resulting in a hydrodynamic storm and a temporary reset of a summer community to an early successional spring community.

premise underlying the analysis was that storms affect phytoplankton through changes in lake physical conditions. We focused on changes in thermal stratification (disrupted or weakened thermal stratification and deepened thermocline) that are usually associated with storms during the stratified period (Jennings et al. 2012). On a fortnightly time scale of observation, which was the most common sampling frequency in our lake monitoring programs, deviations from stratified conditions can be induced by meteorological forcing sufficient to modify the vertical thermal structure of lakes (Jennings et al. 2012). Thus, a disruption of the ordinary seasonal trajectory of stratification would indicate meteorological forcing resulting in a “Hydrodynamic storm” (HS), characterised by an increased mixing depth (Figure 1), reduced average light exposure experienced by phytoplankton (Reynolds 1980), and sometimes enhanced nutrient supply from deep mixing (Stockwell et al. 2020). HSs are hereafter considered as hydrodynamic signals of meteorological storms (Figure S1).

According to the conceptual model (Figure 1), changes in environmental conditions would result in a phytoplankton community characterised by low-light adapted and/or fast-growing species that dominate through the progression from mixed to strongly stratified conditions (Reynolds 1980). We thus predicted that reversions of phytoplankton communities would be associated with HSs (Figure 1). Specifically, we predicted that (i) storm-induced disturbances detected in the thermal structure of lakes could be related to concurrent or delayed deviations from the ordinary seasonal trajectory of phytoplankton succession, and (ii) the physical variables potentially associated with such reversions could be identified. Furthermore, if the impacts of meteorological disturbances on lake physics and phytoplankton can be systematically matched in long-term time series, then we should be able to (iii) identify a common set of physical, storm-associated drivers of phytoplankton community reversions that would be applicable across a broad range of lakes.

2 | Materials and Methods

2.1 | Study Sites and Data Collection

Time-series data were compiled for eight lakes distributed in Europe, Asia, North America, and Oceania (Table 1). The lakes range from 15 to 616 km^2 in surface area and from 3 to 153 m in average depth. They cover a range of mixing regimes and trophic states (Table 1). Water levels of the lakes varied little over the years, except in lakes Võrtsjärv and Kinneret, where stochastic dry periods and flooding after snowmelt or during heavy rain events caused water levels to fluctuate from year to year (Gophen 2023; Nõges et al. 2003). All lakes were periodically sampled throughout the year for at least five consecutive years. The exact years varied among lakes. Sampling frequency was usually once every two to three weeks, but monthly during winter. Data were collected during daylight hours at the deepest location of each lake, except for lakes Kasumigaura and Oneida, which had multiple sampling stations. For these two lakes, the sampling sites examined were selected based on the duration of data collection and the completeness of the dataset. No sampling occurred during storm events. Consequently, all hydrodynamic disturbances and any resultant reversions were assumed to be induced by a meteorological event between sampling events. Thermal profiles were measured throughout the water column in each lake, and water transparency was measured with a Secchi disk. Temperature profiles and water transparency were used to derive a suite of physical variables (Table S1) characterising the epilimnion temperature, the depth of the upper mixed layer and thermocline (depth of maximum buoyancy frequency, mixing depth, thermocline depth), light availability (Secchi depth, ratio of euphotic zone to mixing depth), and variables indicative of stratification strength (Brunt-Vaïsalä frequency and Schmidt stability; Read et al. 2011). The derived variables were computed using the *rLake-Analyser* package in R (version 1.11.4.1; Read et al. 2011) and are available in an online data

TABLE 1 | Lake characteristics and the number of time-series observations (Obs) and of hydrodynamic storms associated with a reversion of phytoplankton communities (HSR).

Lake	Location	Area (km^2)	Average depth (m)	Maximum depth (m)	Number of HSR/Obs	Trophic state	Mixing type	Residence time (year)	Winter ice cover
Windermere	UK	15	21.3	64	4/128	Mesotrophic	Monomictic	0.2–1.0	No
Bourget	France	44	80	147	9/116	Mesotrophic	Monomictic	11	No
Kinneret	Israel	169	25.6	41.7	7/127	Mesotrophic	Monomictic	7.0–10.0	No
Oneida	United States	207	6.8	16.8	16/230	Mesotrophic	Polymictic	0.5	Yes
Kasumigaura	Japan	220	4	7	7/141	Eutrophic	Polymictic	0.5	No
Võrtsjärv	Estonia	270	2.8	6	03/62	Eutrophic	Polymictic	1	Yes
Geneva	France/ Switzerland	580	152.7	309.7	34/337	Mesotrophic	Monomictic	11.3	No
Taupo	New Zealand	616	110	186	01/72	Oligotrophic	Monomictic	10	No

repository (Stockwell et al. 2021). Variable abbreviations are listed in Table S1.

Phytoplankton were collected from several discrete depths or with integrated water samplers or tubes within the upper water column (Stockwell et al. 2021), and preserved with Lugol's solution or glutaraldehyde. Phytoplankton were identified to species or genus. Although changes in taxonomists have occurred during the analysis of samples from most of the lakes, the basic protocols have remained constant over time. Phytoplankton and lake physical datasets were harmonised among datasets using standard data templates and data dictionaries (Stockwell et al. 2021). Phytoplankton taxa were counted under an inverted microscope following methods in Utermöhl (1958) and Lund et al. (1958). Biomass was computed for each species based on cell counts multiplied by the respective biovolume per cell, assuming a specific gravity of 1 g/cm^3. Species biovolumes were derived from mean cell volumes using geometrical models (Hillebrand et al. 1999; Kremer et al. 2014). Mean cell dimensions were estimated from size measurements on some individuals of identified species; they were lake-specific and were kept constant through time in some lakes, occasionally updated in other lakes when cell size changes were apparent, or routinely measured on each sampling date (e.g., Lake Kinneret). Biovolumes for species from Windermere were not available, so cell densities (cells/L) were used instead for this lake.

2.2 | Data Analysis

The time-series data from each lake were analysed in three steps (Figure 2A). First, phytoplankton species composition was analysed to determine average seasonal succession trajectories (AvST). From these patterns, the seasonal maturation period (see below) was identified in each lake (Analysis 1). Second, deviations from the AvST during the phytoplankton-maturation period were evaluated (Figure 2B) in relation to changes in physical conditions (Analysis 2). Finally, a binary classification model was developed to predict the occurrence of such deviations from the AvST, based only on data on physical conditions (Analysis 3). All statistical analyses were performed in the R Statistical Programming Language (version 3.6.1; R Core Team 2020) using the packages ADE4 (Dray and Dufour 2007; Analysis 1 and 2), caret (Kuhn et al. 2020; Analysis 3) and xgboost (Chen and Guestrin 2016; Chen et al. 2019; Analysis 3).

2.2.1 | Analysis 1: Seasonal Trajectories and Their Driving Factors

The AvST of phytoplankton communities was separately characterised for each lake using within-group Principal Component Analysis (within-PCA, Abdi and Williams 2010). We created matrices of phytoplankton abundance (biomass by species and sampling date) for each lake, except for Windermere where cell density was used instead of biomass. Within-PCA ordination allowed us to efficiently summarise the information in these matrices and test for changes in community composition over time. Phytoplankton communities vary seasonally as well as among years (Nõges et al. 2010; Anneville et al. 2019; Verburg and Albert 2020). The within-PCA allowed us to focus on the seasonal variability that was captured by the axes of the within-PCA at each lake, with the first axis accounting for most of the variability (Table 2) and describing the maturation of the community. Consequently, the AvST was calculated as the monthly average of scores on axis 1 defined by the within-PCA (Figure 2B). We determined statistical associations between seasonal changes in the phytoplankton community throughout the year and a range of physical factors such as lake mixing and light regimes. To this end, we calculated Pearson correlations separately for each lake between monthly coordinates on axis 1 and monthly averages of each of the derived physical variables (Table S1).

2.2.2 | Analysis 2: Occurrence of Phytoplankton Community Reversions and HS

The impact of meteorological disturbances such as storms on lake physics varies with season (Doubek et al. 2021). Therefore, our second analysis focused on the phytoplankton-maturation period when phytoplankton and the physical structure of the water column typically show a regular and well-defined seasonal pattern (Sommer et al. 2012). The maturation period typically begins at the onset of stratification and encompasses a progressive change from small species towards species adapted to competing for depleted nutrients and to resisting grazing pressure (Sommer et al. 2012). We identified the months that represented the maturation period for each lake based on a steady directional shift in average monthly ordination scores (Figure 2B), and restricted our analysis of phytoplankton community reversions to data collected during those months.

The successional trajectories described by axis 1 of the within-PCA reflect the seasonal maturation of the community (Figure 2B). Accordingly, we identified reversions as events when a community shifts to an earlier successional stage by moving backwards along the average seasonal trajectory of axis 1 (Figures 1 and 2B). We used a binary classification that ignored the extent of the reversions. Dates of all reversions were listed as the sampling dates when a reversion was observed. Those dates were identified for each lake and used in Analysis 3 (Figure 2A).

Meteorological storms most often decrease water-column stability and deepen the thermocline (Jennings et al. 2012; Kasprzak et al. 2017; Woolway et al. 2018). Accordingly, dates of a HS were inferred based on changes in hydrodynamic conditions relative to those observed in the preceding field campaign (Figure 2A), specifically in situations characterised by a decrease in the maximal Brunt-Väisälä frequency (max_bv) and an increased depth of the maximal Brunt-Väisälä frequency (Zbv) (Jennings et al. 2012). Because we focused on the period of normally stable lake stratification, those changes in hydrodynamic conditions were likely induced by strong meteorological perturbations directly to the lake and/or indirectly through storm impacts on inflowing rivers. River flow data were not available, but meteorological conditions (i.e., air temperature, rain, solar radiation and daily average wind speed) were available for a subset of in situ sampling data. Meteorological parameters were collected daily over periods ranging from 3 to 23 years. They were recorded by buoys or at meteorological stations situated on

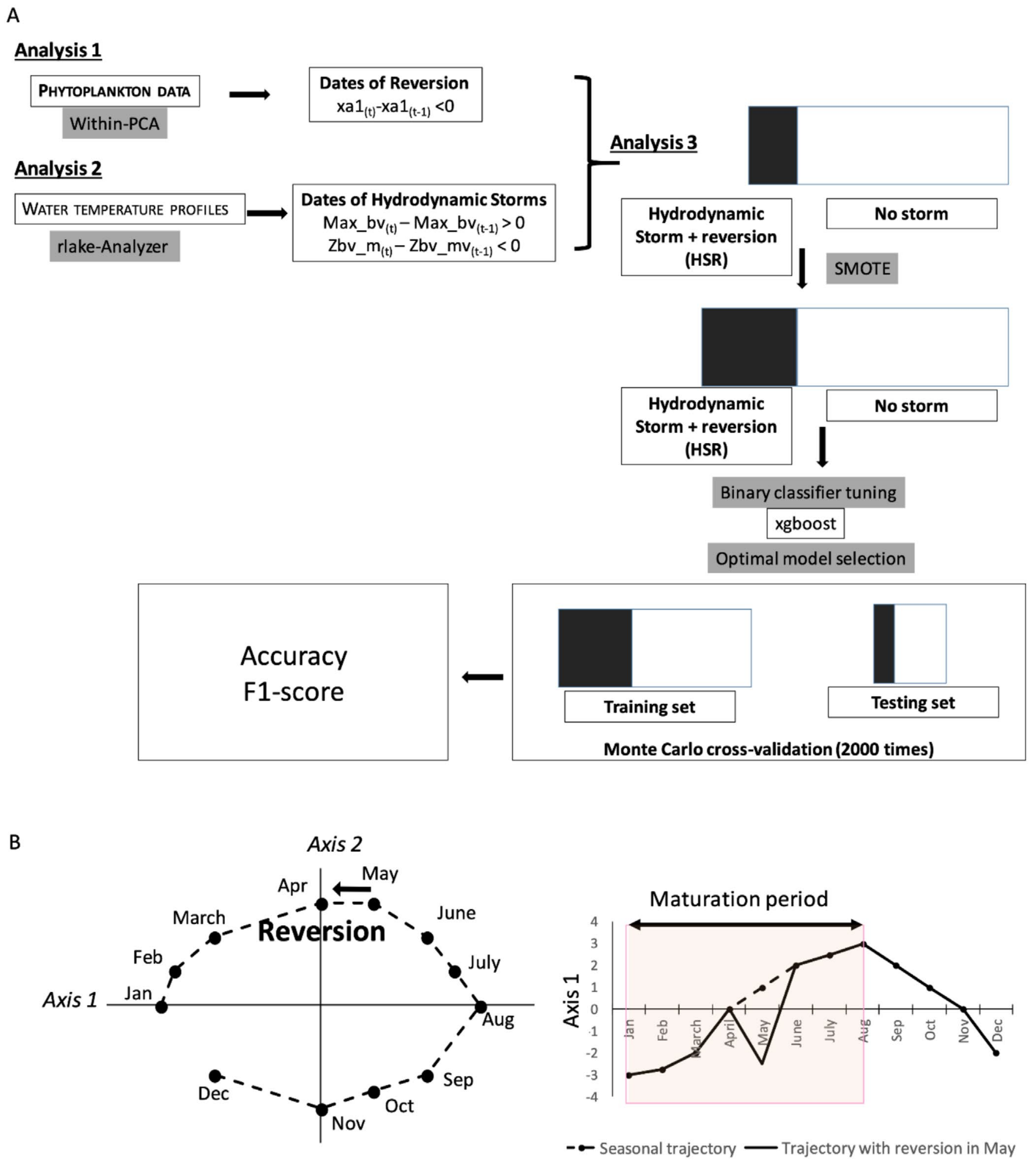

FIGURE 2 | (A) Flowchart of the three-step strategy employed in the study. The dates of reversion and hydrodynamic storms are determined by calculating the difference in variables between field campaign (*t*) and the previous field campaign (*t*–1), see method section. The black area represents the portion of hydrodynamic storms inducing reversions. (B) Illustration of the approach used in Analysis 1. The diagrams illustrate the concept of reversions within the first plane of the within-PCA.

the shores of Lakes Taupo, Võrtsjärv, Kinneret, Kasumigaura, Windermere, Bourget, Oneida, and Geneva. Meteorological conditions during the 5 days prior to in situ sampling were processed to calculate mean and maximum values. The 5-day means and maxima were then standardised by month for each lake, so that the intensity of meteorological parameters could be compared between HS dates and non-HS dates among all lakes (Figure S1). The recorded HS reflected anomalies in meteorological conditions, with low pressure systems resulting in strong wind events and cooling of the atmosphere. For instance, meteorological conditions associated with HS presented significant differences compared to the other dates in average air temperatures, solar

TABLE 2 | Contribution of the within-year variability to the overall temporal variability recorded for each study lake, and percentage of within-year variability explained by the axes at each lake.

Lakes	Within-year variability %	Axis 1%	Axis 2%
Kinneret	75.2	21.3	11.5
Bourget	77.9	11.6	7.4
Geneva	81.3	11.9	7.6
Kasumigaura	63.1	20.1	9.4
Oneida	81.0	10.7	10.3
Taupo	83.6	17.6	15.9
Võrtsjärv	81.7	19.1	6.8
Windermere	86.2	5.7	3.9

radiation, and wind speed (Figure S1). Finally, half of the recorded standardised maximum wind speeds associated with HS were among the highest in the time series and close to the 3rd quartile of maximum wind speed (Figure S1).

2.2.3 | Analysis 3: Hydrodynamic Features That Induce Storm-Induced Changes in Seasonal Trajectories

We identified all phytoplankton community reversions that co-occurred with HS, which we hereafter refer to as hydrodynamic storm with reversions (HSR). We fitted a binary classification model, based on the statistical learning technique “Tree Boosting” (Chen and Guestrin 2016) to assess whether HSR could be consistently predicted from lake physical conditions (predictor variables listed in Table S1).

We used the “Synthetic Minority Over-Sampling Technique” (Chawla et al. 2002) to address the problem of highly unbalanced data between storm events (minority class) and non-storm periods (majority class) in our original dataset, which can reduce the performance of classification models. Specifically, storm events were statistically oversampled at 200% of the original number to maintain the same percentage of storm events between the datasets (Figure 2A).

Several key parameters of Tree Boosting models, such as the number of boosting iterations or trees (nrounds), maximum depth of each decision tree (max_depth) and the fraction of features randomly selected at each tree (colsample_bytree), were tuned to obtain the best combination of lake physical conditions associated with HSR (Chen and Guestrin 2016). A grid of manually specified parameter values was tested, with the best combination of parameters that maximised prediction accuracy retained in the final model configuration (Figure 2A).

To assure reproducibility and avoid overfitting of the gradient boosted trees model, the dataset was randomly split into two subsets: a training set (approximately 70% of the data) and a testing set (approximately 30% of the data) for model validation (Figure 2A). The ratio of storm events and no-storm events in both the training and testing data sets was maintained at the ratio of 30%–70%. The model training and validation were repeated 2000 times for each lake following Monte Carlo cross-validation.

The binary classifier performance was evaluated using accuracy and the F1-score obtained from 2000 individual model runs. Accuracy represents the percentage of the total number of predictions that are correct:

$$\text{Accuracy} = \frac{\text{TPo} + \text{TNo}}{\text{TPo} + \text{TNo} + \text{FPo} + \text{FNo}} \tag{1}$$

where TPo = True HSR Positives, TNo = True HSR Negatives, FPo = False HSR Positives, and FNo = False HSR Negatives.

The F1- score is the harmonic weighted average of the precision (P) and recall (R) values.

$$F1 = 2\frac{P.R}{P + R} \tag{2}$$

where $P = \frac{\text{TPo}}{\text{TPo} + \text{FPo}}$ and $R = \frac{\text{TPo}}{\text{TPo} + \text{FNo}}$.

Partial dependence plots were used to assess the importance of each physical variable to the model performance and their relationship (linear, monotonic or complex) with the predicted outcome (HSR or normal situation; Friedman 2001). Partial dependence probabilities were calculated by varying the interested feature and fixing the remaining features (R package randomForestSRC; Ishwaran and Kogalur 2023). The partial dependence plot shows the marginal effect of one variable on the predicted outcome of the binary classifier.

Inter-lake differences in the performance of the model were analysed by a PCA run on a matrix constituting four model performance indices computed for each lake: the median accuracy, the median F1, the standard deviation of accuracy, and the standard deviation of F1. These indices were calculated from the outcomes of the 2000 models runs. Correlations between scores on axis 1 of the PCA and lake physical variables (Table 1) were used to identify lake characteristics influencing the performance of the model.

3 | Results

3.1 | Analysis 1: Seasonal Trajectories and Their Driving Factors

The average seasonal trajectory of phytoplankton community (AvST) represented 81% (median) of the lakes' temporal variability in community composition. AvST was described by the first 2 axes of the within-PCA, with axis 1 explaining between 5.7% and 21.3% of the within-year variability (Table 2). Axis 1 consistently discriminated between winter and summer months in the eight lakes (Figure 3). The negative scores on axis 1 of the within-PCA represented diatom and cryptophyte communities that often occur in weakly stratified environments (e.g., *Plagioselmis lacustris, Ulnaria japonica, Asterionella formosa*). These communities were

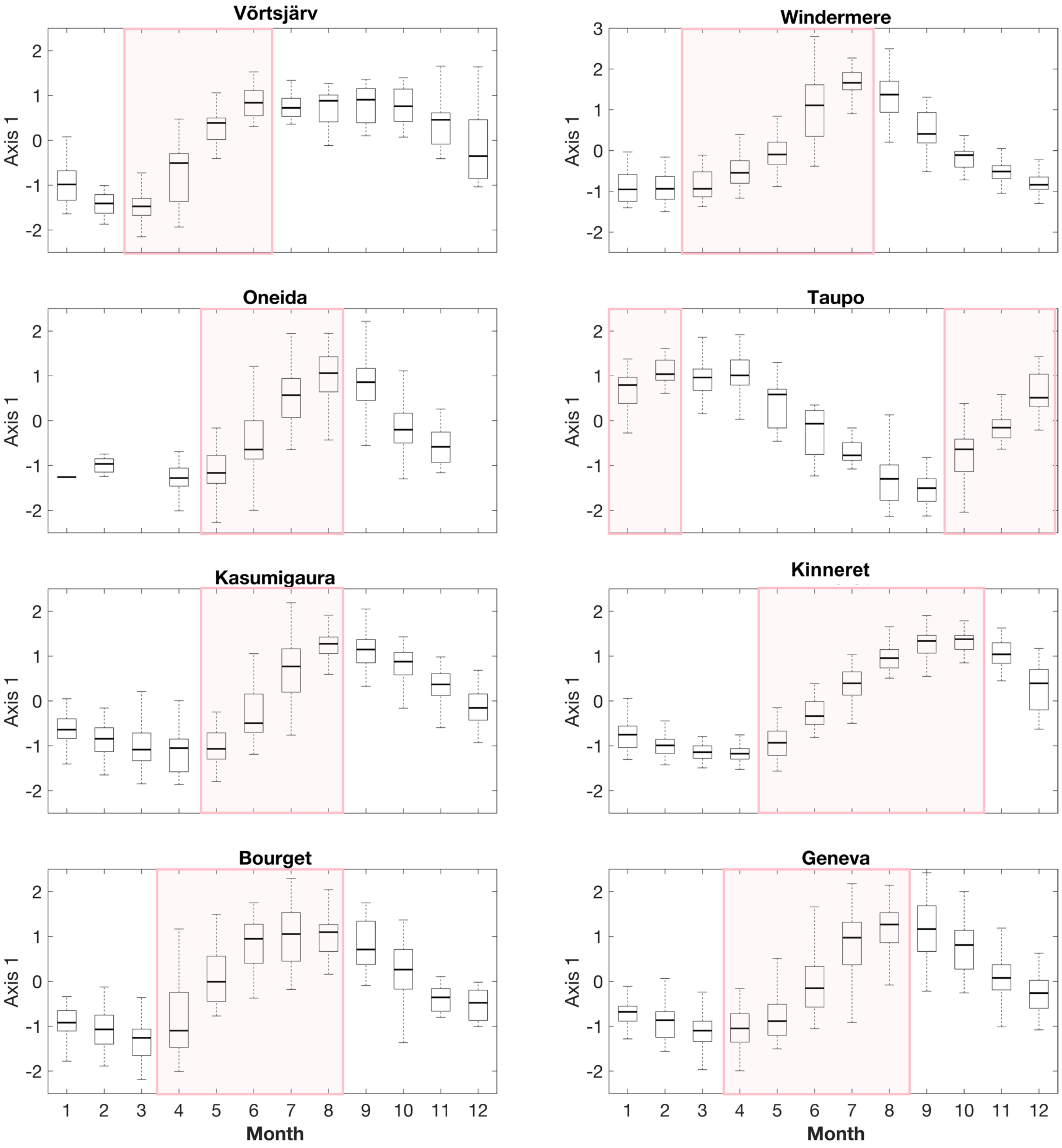

FIGURE 3 | Box-plots of standardised axis 1 scores from within-PCA ordinations based on phytoplankton species biomass measurements (for seven lakes) or cell density (for Windermere). The pink windows indicate the phytoplankton-maturation periods for each lake, a period of transition towards a phytoplankton community dominated by species adapted to stratified summer conditions, reflected by a steady directional shift in median monthly ordination scores. Note the mirror-image pattern of Lake Taupo located in the Southern Hemisphere. All other lakes are in the Northern Hemisphere. The black horizontal bars in the boxes indicate median values, the limits of the boxes indicate 25% and 75% quartiles, and the whiskers extend to the most extreme data points not considered outliers.

distinguished from summer communities which, in most lakes, were characterised by a greater diversity of taxa, including cyanobacteria and microplanktonic species (Table S2).

All lakes showed a clear seasonal trajectory of phytoplankton community change from early spring to summer (Figure 3). These changes in the monthly average axis 1 scores of the within-PCA depicted the maturation period of the phytoplankton community from early spring species that included diatoms and cryptophytes to large cyanobacteria, diatoms, green algae, or dinophytes in summer (Table S2). The time-of-year and duration of the maturation period showed slight differences among lakes (Figure 3): the maturation period lasted four months in lakes Võrtsjärv (March to June), Kasumigaura, and Oneida (both May to August), but was five months in Windermere (March to July) and lakes Bourget and Geneva (April to August), and six months (May to October) in Lake Kinneret. The trajectory of Lake Taupo, in the Southern Hemisphere, was a mirror image of the other lakes, with its maturation period lasting five months (October to February) during the austral spring and summer. AvST were correlated with seasonal warming (Figure 4) for all lakes, especially for the monomictic mid-latitude lakes (Windermere, Bourget, Geneva and Taupo). AvST and thermal stability indices (max_Bv, Schmidt) were also positively correlated for all lakes except the two polymictic lakes, Oneida and Võrtsjärv. In shallow Lake Kasumigaura, correlations between AvST and thermal stability indices were significant but weak. Secchi depth was correlated with AvST in lakes Bourget, Kasumigaura, and Võrtsjärv. In Lakes Kasumigaura and Võrtsjärv, AvST appeared more strongly linked with water clarity and the ratio of euphotic to mixing depth than in the other lakes.

3.2 | Analysis 2: Dates of Reversions and HS

Strong temporal variability in community structure, and thus variability in axis 1 scores, was evident for each month during the maturation period of the phytoplankton communities. Reversion was a common feature of seasonal trajectories, whereas HSR occurred less frequently (Figure 5A,B). Although HSs were relatively rare, HSRs were associated with 20 to 40% of these events in most of the studied lakes (Figure 5C).

3.3 | Analysis 3: Hydrodynamic Features of Storm-Induced Changes in Seasonal Trajectories

The occurrence of HSRs was predicted by hydrodynamic features with high accuracy for all lakes. The interquartile range of predictive accuracy (% of correctly predicted HSR and non-HSR events) was 0.87 and 0.92 on a scale ranging from 0 to 1 (Figure 6). The F1 scores, which represent the weighted average of precision and recall values (equation 2), were invariably high but variability was low or moderate in five of the lakes (Geneva, Oneida, Kinneret, Bourget and Kasumigaura). In Lake Taupo, only one HSR was observed, so our approach based on the re-sampling technique was not applicable for this dataset. We assessed model performance using several metrics: the standard deviation of accuracy (Acc_std) and the F1-score (F1_std), as well as the mean of accuracy (Acc_m) and the F1-score (F1_m). We then combined all metrics using a Principal Component Analysis to derive a single index of model performance, except Taupo (Figure 7). The first component of the PCA (axis 1) accounted for 92.4% of the total variability and was associated with all four metrics selected

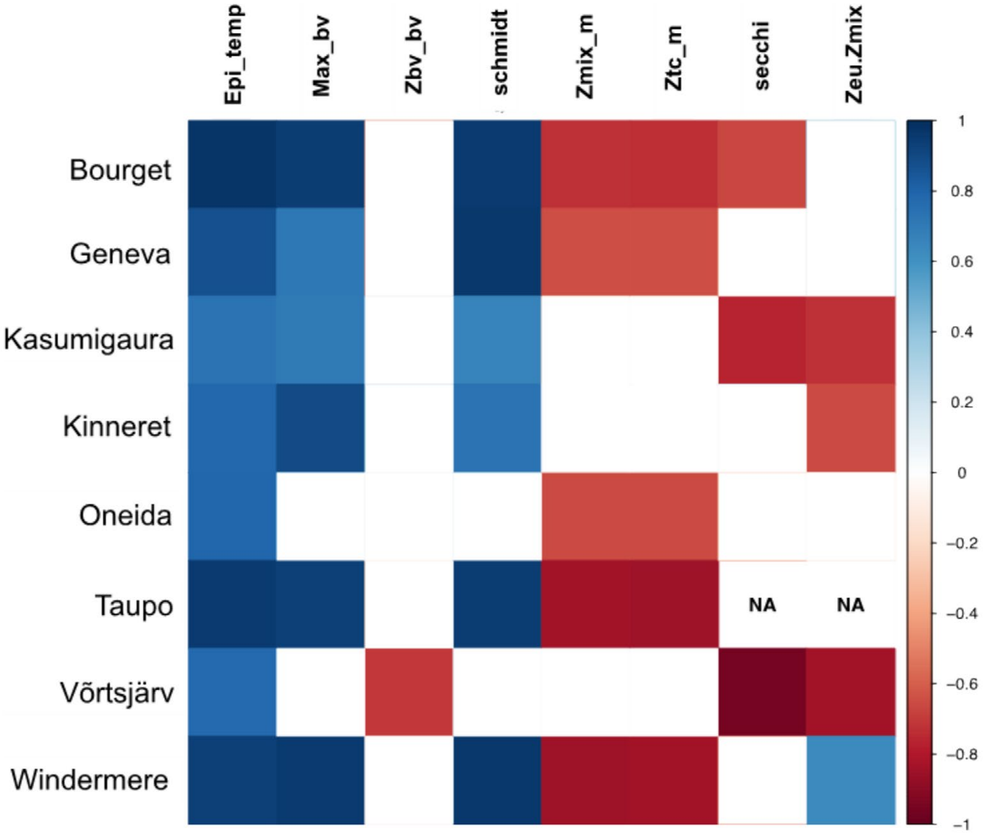

FIGURE 4 | Summary of correlations between monthly average coordinates (or centroids) on axis 1 of within-PCAs and eight variables characterising the physical conditions of the eight study lakes. Coloured squares indicate significant correlations ($p < 0.05$), with colour indicating the value of Pearson's correlation coefficients. NA indicates that data were unavailable. The physical variables included in the analysis were epilimnetic temperature (epi_temp), maximal Brunt-Väisälä frequency (max_bv), depth at maximal Brunt-Väisälä frequency (Zbv), Schmidt stability (schmidt), mixing depth (Zmix), thermocline depth (Ztc), Secchi depth (secchi) and the ratio of euphotic to mixing depth (Zeu.Zmix).

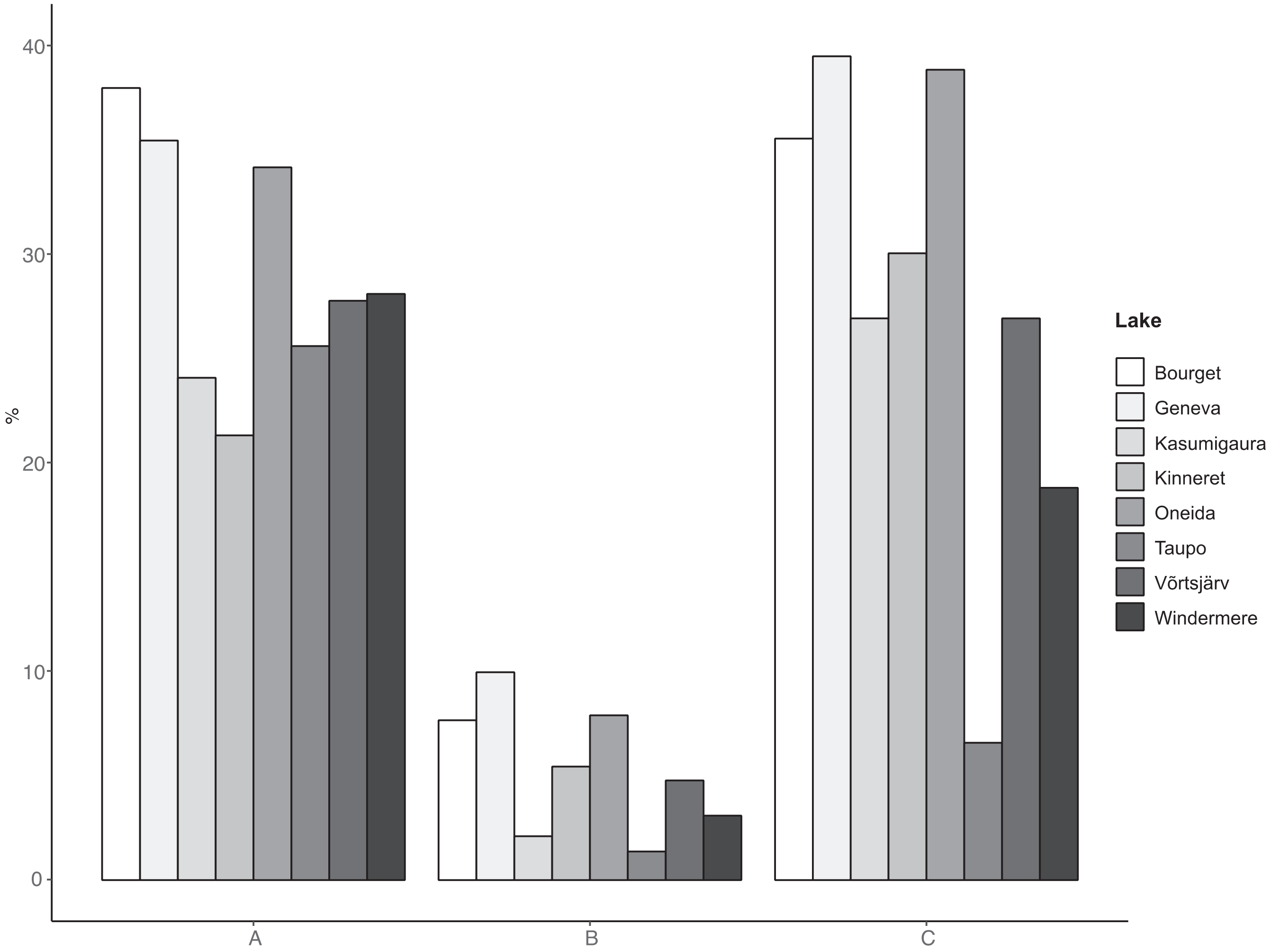

FIGURE 5 | Frequency (%) based on original data of (A) reversions per observation: observed reversions disrupting phytoplankton community maturation during seasonal succession, (B) HSR events per observation: HS associated with a reversion during the maturation period, and (C) HSR events per HS: HS associated with a reversion compared to the total number of HS.

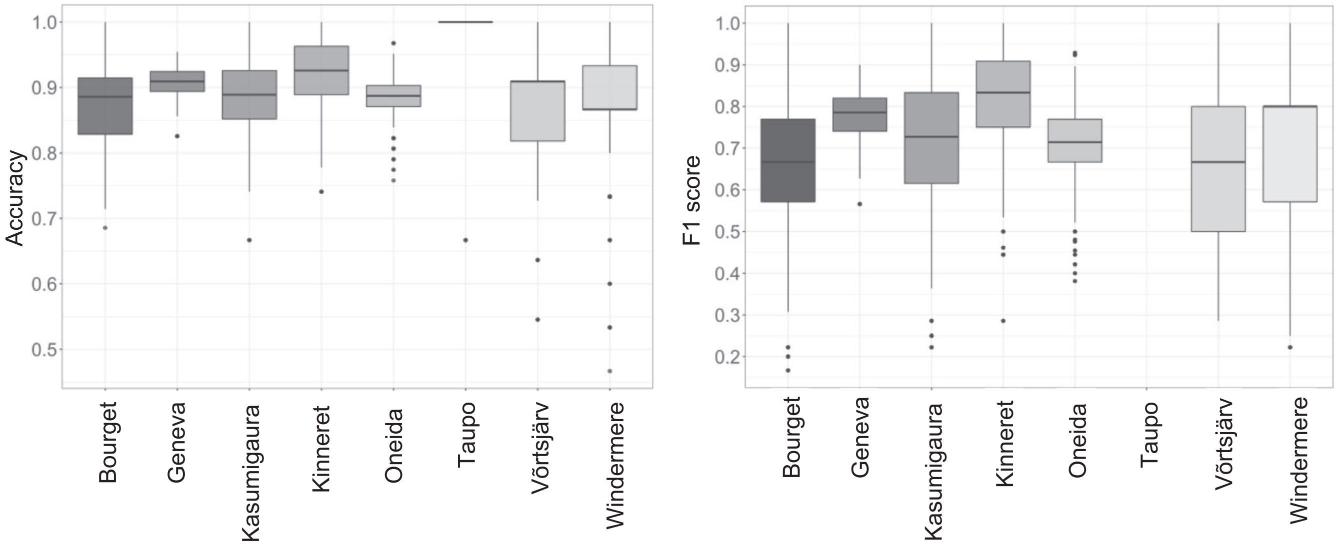

FIGURE 6 | Box-plots of the accuracy and F1-score obtained from 2000 individual model runs. Accuracy denotes the ratio between the number of correct predictions and the total number of predictions. The F1-score is the weighted harmonic mean of precision and recall values.

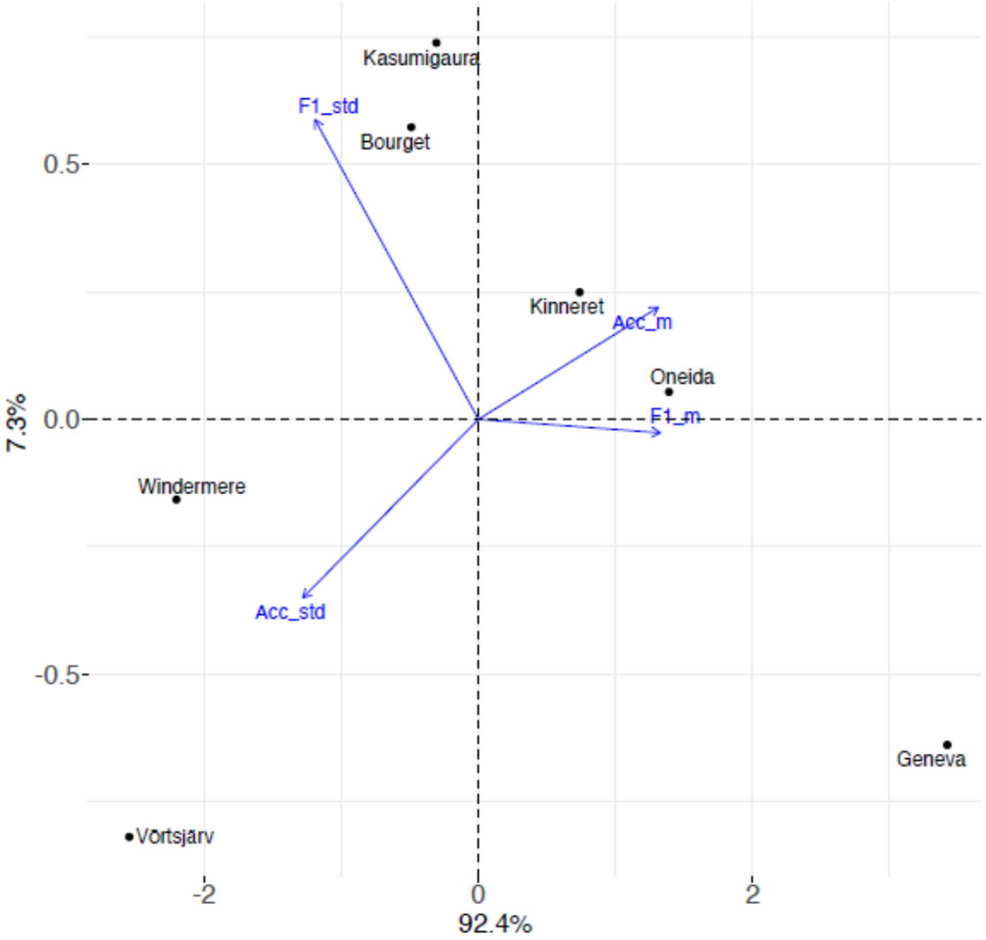

FIGURE 7 | PCA on four performance metrics of the final boosting trees models: The standard deviation of accuracy (Acc_std) and the F1-score (F1_std), and the mean of accuracy (Acc_m) and the F1-score (F1_m). For each lake, the means and standard deviations were computed based on the metrics from 2000 model runs.

to reflect model performance—the mean and standard deviation of both accuracy and the F1-score. Thus, the first component represented an accurate proxy for model performance (Figure 7). The PCA also indicated large variability in model performance among lakes (Figure 7). Lakes showing the best performance, high averages, and low variability in accuracy and F1-scores were Lakes Geneva, Oneida, and Kinneret. In contrast, Windermere and Lake Võrtsjärv showed very poor model performance because of high variability and reduced accuracy or F1-scores.

Because the intensity of physical changes associated with HSR did not systematically vary between lakes showing poor (Windermere, Taupo and Võrtsjärv) and good model fits (Figure 8), the intensity of physical changes did not explain differences in model performance. In contrast, the performance of the models described by axis 1 of the PCA (Figure 7) was strongly correlated with the number of available observations for each lake (Figure S2), which ranged between 62 and 337 ($p = 0.006$, Pearson's $r = 0.90$). The performance of the models was also correlated with the number of HSRs, which ranged between 3 and 34 ($p = 0.006$, Pearson's $r = 0.90$), and the ratio of the number of HSRs to observations ($p = 0.02$, Pearson's $r = 0.83$). None of the other lake characteristics listed in Table 1 (e.g., surface area, average and maximum depth) were significantly correlated with model performance (Figure S2).

Among the quantitative variables number of available observations for each lake, ratio of the number of HSRs to observations, lakes characteristics in Table 1 tested to explain differences in model performance (succeeded or failed) among lakes, only the ratio of the number of HSRs to observations was identified as a significant factor (ANOVA, $p = 0.032$). The number of HSRs could not be tested because this variable did not meet the normality assumption. Nevertheless, the five lakes where models were successful (Bourget, Geneva, Kinneret, Kasumigaura and Oneida) had at least 7 HSRs, whereas the three others (Windermere, Võrtsjärv and Taupo) had very few (4, 3 and 1, respectively; Table 1).

For lakes Bourget, Geneva, Kinneret, Kasumigaura, and Oneida, the model identified which specific environmental variables were correlated with reversions. These variables were either related to thermal structure (Zmix, Zbv_m, Ztc_m, max_bv, Schmidt and Epi_temp) or to water transparency (Secchi) (Figure 9) and their combinations were lake-specific. However, the first of the three main explanatory variables (Zmix, Zbv_m or Ztc_m) represented a proxy of the shape of the temperature

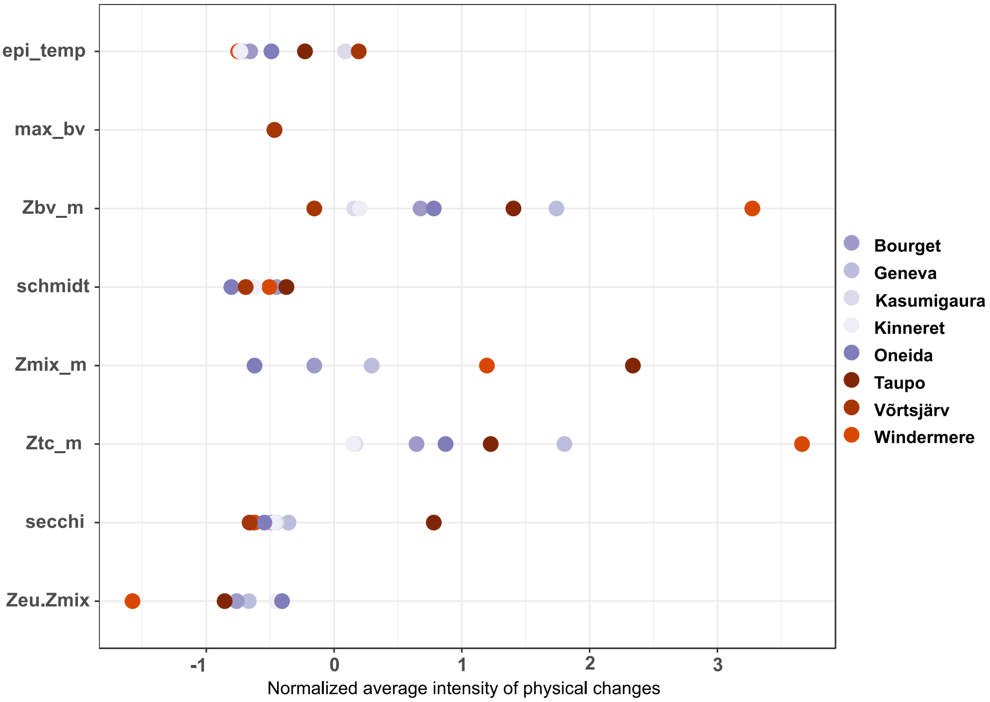

FIGURE 8 | Normalised mean intensity of physical changes associated with an HSR computed for epilimnion temperature (Epi_temp), maximal Brunt-Väisälä frequency (max_bv), depth of maximal Brunt-Väisälä frequency (Zbv_m), Schmidt stability (schmidt), mixing depth (Zmix_m), thermocline depth (Ztc_m), Secchi depth (secchi) and the ratio of euphotic to mixing depth (Zeu.Zmix). Blue symbols represent lakes where models performed better, and red symbols represent lakes where the models did not perform well (low averages and high variability in accuracy and F1-scores). Normalisation was achieved by standardising the average intensity of each physical parameter over the mean and standard deviation from all lakes in the dataset.

profile in all lakes. HSRs were consistently associated with stratification indices (Figure 9), such as a deeper metalimnion (Kinneret), deeper Zbv (Geneva, Oneida, Kasumigaura), or a deeper mixed layer (Bourget). HSRs were thus generally associated with deeper mixing and a deeper thermocline than other dates (Figure 10). The remaining explanatory variables differed among lakes, indicating that physical conditions inducing HSRs were lake-dependent. For instance, the shape of the thermal vertical profiles and stratification strength were important for the monomictic Lakes Geneva, Bourget, and Kinneret. In contrast, water transparency was associated with HSR in addition to other variables only in the polymictic lakes (Oneida and Kasumigaura). In those two lakes, reversions coincided with elevated water transparency. Finally, epilimnetic temperature was identified as an explanatory variable in Kasumigaura, where HSRs were associated with a relatively cool epilimnion (Figure 10).

4 | Discussion

Disentangling storm-induced changes from the other sources of phytoplankton variability is necessary to properly evaluate the ecological impacts of storms, which are predicted to increase in frequency and intensity with ongoing climate change. In this study, the average temporal trajectory of phytoplankton composition was used as a reference against which to evaluate the impacts of meteorological storms identified via changes in stratification or light climate (HS). The recorded HSs properly reflected anomalies in atmospheric conditions that can be associated with low pressure systems resulting in strong wind events and cooling of the atmosphere (Figure S1). Our study allowed us to distinguish between drivers of changes in species composition resulting from storm events and revealed that the combination of key drivers resulting in reversions of phytoplankton succession might differ depending on lake mixing regimes (polymictic versus monomictic).

4.1 | Patterns and Drivers of Seasonal Phytoplankton Succession: Towards the Description of Reference Seasonal Trajectory

Results of our within-PCA underlined strong recurrent trajectories for each of the eight lakes we analysed, following the well-described seasonal succession of phytoplankton communities in temperate regions (Sommer et al. 2012). The drivers for the trajectories were related to annual stratification regimes, with the patterns of phytoplankton succession related to water temperature and water-column stability, especially for monomictic lakes. These variables were strongly coupled with seasonal warming trends and the development of stratification, resulting in strong relations with epilimnetic temperature, Schmidt stability, and maximum buoyancy frequency. In lakes Oneida, Kasumigaura, and Võrtsjärv, the weak or non-significant correlation between the average phytoplankton seasonal trajectory and physical water-column stability can be explained by the lack of a persistent seasonal thermocline

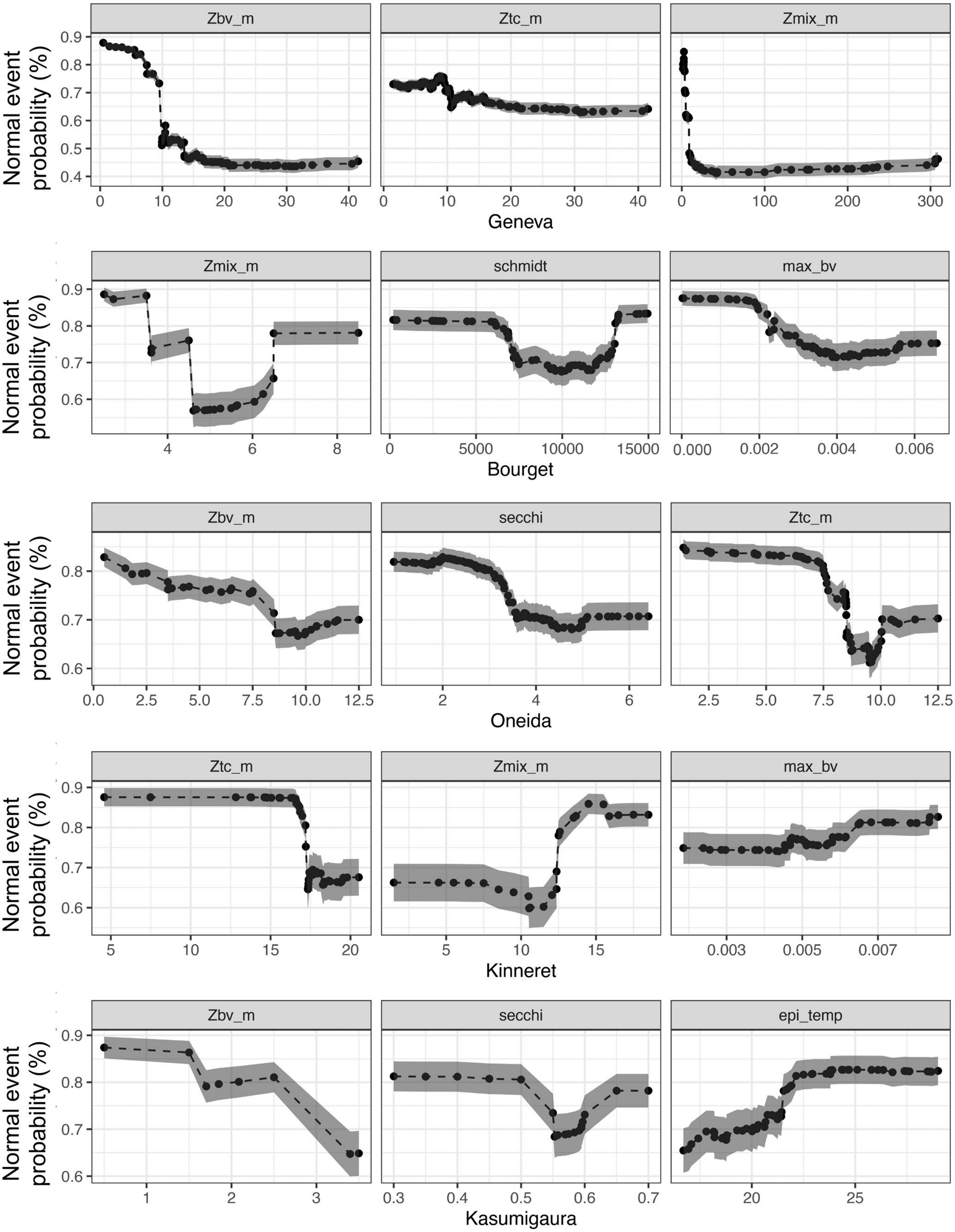

FIGURE 9 | Partial dependence plots of the six main physical variables inducing reversions in the trajectories of phytoplankton communities (Zbv_m, Ztc_m, Zmix_m, max_bv, epi_temp, secchi) and the predicted probability of an event being a "normal" observation not influenced by a storm. The x-axes represent the values of each variable and the y-axis represents the probability of normal, non-HSR events (i.e., 1- the probabilities of HSR occurrence). The dashed lines indicate the average predicted probability and the shading 95% confidence intervals.

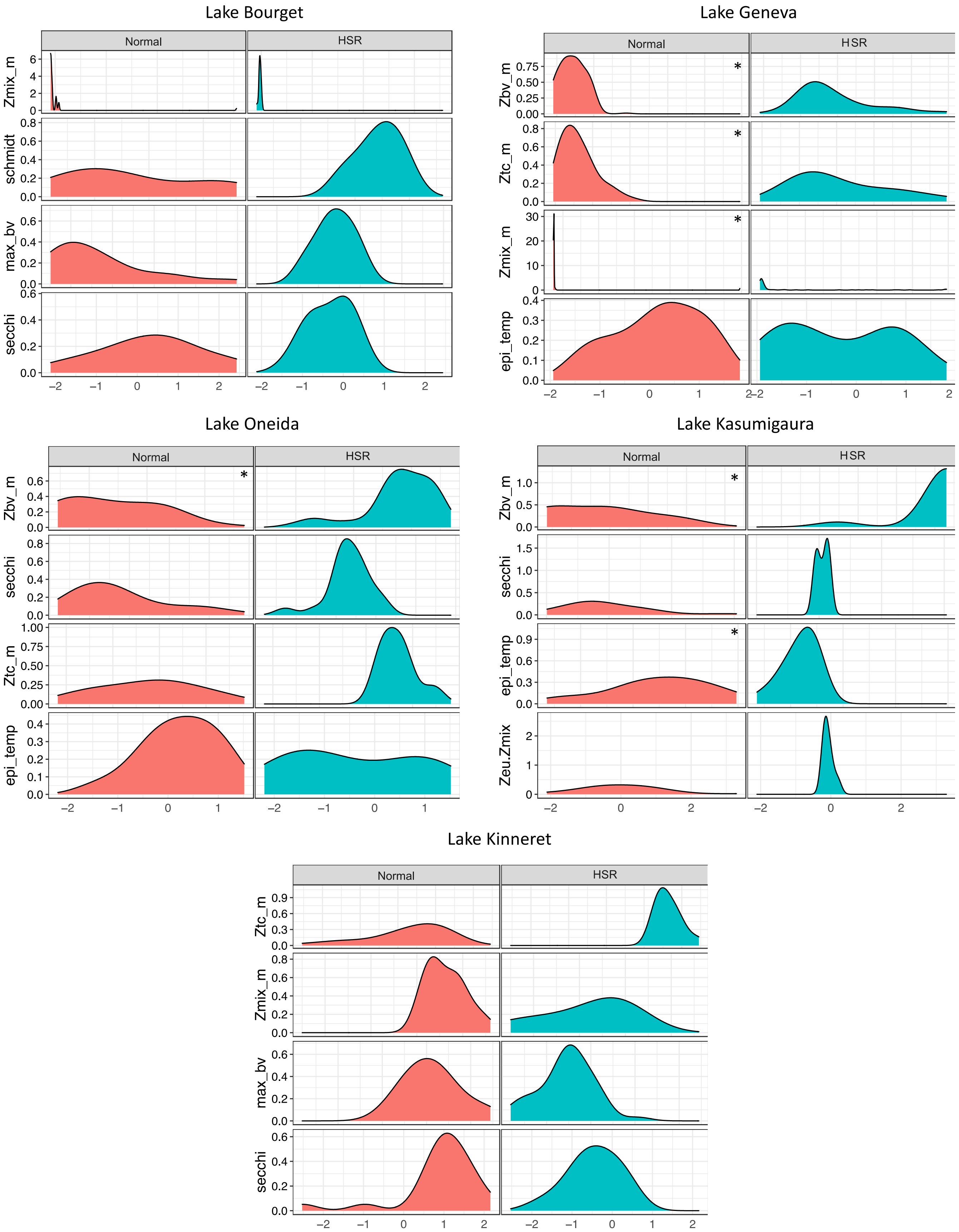

FIGURE 10 | Density plots of physical variables inducing a reversion in trajectories of phytoplankton communities based on normalised shape-values for Lakes Bourget, Geneva, Oneida, Kasumigaura and Kinneret. The x-axes represent the normalised value of the variables and the y-axis represents the probability density. The asterisks (*) indicate statistically significant differences (Kruskal-Wallis test) between normal situation (orange) and HSR events (turquoise) when variables are not used in combination with other explanatory variables.

in polymictic lakes. Instead, diurnal thermoclines may develop for only a few hours or days in these lakes (Augusto-Silva et al. 2019) and remain highly sensitive to wind events (Hetherington et al. 2015), resulting in high temporal variability in stratification indices.

Correlations between phytoplankton community structure during seasonal successions and lake physical variables do not necessarily imply a causal relationship. Instead, they reflect concurrent seasonal variation caused by a multitude of factors, including concentrations of limiting nutrients, light availability, or biotic interactions (Sommer et al. 2012). Nevertheless, the consistency of the seasonal trajectories we identified with patterns typical of temperate lakes (Sommer et al. 1986; Sommer et al. 2012) enables the use of these trajectories as a reference to analyse the impact of storms on phytoplankton succession.

4.2 | Causal Links Between HS Impacts and Reversions in Seasonal Phytoplankton Trajectories

Some of the numerous reversions we identified in the seasonal succession of phytoplankton communities co-occurred with HS, but more than half of them did not. This result likely reflects the many possible drivers of phytoplankton community structure, and deviations from seasonal trajectories that did not match with HS could have partly resulted from species interactions, such as competition, grazing, and/or parasitism (Sommer et al. 2012; Mariani et al. 2013; Gerphagnon et al. 2013), in addition to hydrodynamic events that failed to cause a change in the stratification indices. The latter could include frequent mixing of the upper mixed water layer without concurrent deepening or wind-induced vertical movement of the thermocline. Whether the changes in stratification were sufficient to affect our calculated stability indices may have depended on the position in the lake of our sampling site relative to the position of the thermocline. These events cause horizontal currents and turbulences at the thermocline that favour water exchange between the hypo- and epilimnion, resulting in local or lake-wide impacts on resource availability with consequences on phytoplankton communities (Corman et al. 2010; Comesaña et al. 2021).

The overall limited match we observed between hydrodynamic signals of storm events and phytoplankton community reversions possibly also reflects low-frequency sampling at low spatial resolution. Earth rotation affects the motion of the thermocline in many of the lakes we studied, given their large size. For example, Kelvin and Poincarée waves (nearshore and offshore waves caused by Coriolis forces) occur in Lake Kinneret (Antenucci et al. 2000). These water movements may result in up- and downwelling with short-term changes in the mixed-layer depth, without inducing a reversion in the phytoplankton seasonal trajectory. Such internal waves have also been documented in Windermere and Lake Geneva (Horn et al. 2001; Bouffard and Lemmin 2013; Woolway et al. 2018). Wind-induced changes in mixed-layer depth depend on the wind force relative to stratification strength (which changes seasonally), which together determine the degree of up- and downwelling of the thermocline and the likelihood of internal waves becoming non-linear and inducing appreciable mixing (Horn et al. 2001; MacIntyre et al. 2006). Some mixed-layer deepening may be transient due to the passage of non-linear waves and may have a minimal influence on phytoplankton communities. Given the spatial and temporal variability of lake responses to wind forcing, the metrics we used to identify hydrodynamic storms may not always capture the relevant changes in lake physics capable of causing reversion events. Nevertheless, the links we observed between hydrodynamic signals of storms and reversions in phytoplankton succession are an important discovery. Further insights could be derived by calculating metrics such as the Lake number or Wedderburn numbers, two indices that would directly represent the strength of upwelling and vertical mixing (Read et al. 2011), but these metrics would have required additional data that were not available for all lakes. Our analysis could also be improved through the collection of physical measurements (e.g., conductivity, temperature, and depth) at both inshore and offshore sites during routine phytoplankton sampling.

Twenty percent to 40% of the identified HS were associated with phytoplankton reversions. This relatively low percentage of HSR relative to the number of HS can be attributed to the ability of lake phytoplankton either to resist storm-induced disturbances or to rapidly recover to antecedent conditions (Thayne et al. 2022). The identified 20%–40% might also be an underestimate because the temporal resolution of sampling, typically fortnightly, could often be insufficient to fully resolve the temporal variability in hydrodynamic and biological processes. Lake physical conditions often respond rapidly to changing meteorological conditions, with storm-induced deepening of the thermocline potentially occurring within hours following strong winds (Imboden et al. 1983; MacIntyre et al. 1999; Fourniotis 2018). In contrast, generation times of most phytoplankton taxa are between two and six days (Reynolds 1993; Yacobi and Zohary 2010) and strong responses such as algal blooms to deep mixing may even arise only after several weeks (Giling et al. 2017). Consequently, effects on phytoplankton communities likely lag behind storm events, even when strong physical changes occur in the lake water column. Conversely, the probability of detecting the hydrodynamic signals of a storm that happened days before sampling might often be too low because physical conditions can recover from strong winds within a few days (Giling et al. 2017; Kasprzak et al. 2017). This discrepancy in the time scales of responses between physical and phytoplankton responses could partially explain the $<50\%$ match between HS events and reversions that we observed.

Concomitant changes in phytoplankton community structure and hydrodynamic conditions may also link to biogeochemistry. For example, in addition to flushing out phytoplankton (Jacobsen and Simonsen 1993), high inflows of water from heavy rainfall associated with storms have the potential to alter lake metabolism and nutrient fluxes (Reichwaldt and Ghadouani 2012), and result in high water exchange rates around major inflows that may prevent cyanobacteria growth (Nõges and Tuvikene 2012). Conversely, enhanced nutrient supply as a result of deep mixing or external inputs promotes fast-growing species like cryptophytes (Elber and Schanz 1990) and diatoms (Znachor et al. 2008). Nutrient inputs may also trigger cyanobacterial blooms that can persist for months (Michalak et al. 2013), although the stimulation in oligotrophic lakes may be brief (MacIntyre et al. 2006). The depth at which the inflowing stormwater is introduced in the water column and the extent of subsequent water-column mixing also influence whether the supplied nutrients become available in the euphotic zone or whether they are sequestered in deep water (Rueda and MacIntyre 2009). For example, a typhoon caused considerable changes in the water-column structure of Lake Biwa, Japan, but mixing in the lake's northern basin was not deep enough to entrain appreciable quantities of soluble reactive phosphorus, which was the limiting nutrient in the lake (Robarts et al. 1998). Thus, whether mismatches occur between physical impacts of storm events and phytoplankton reversions likely depends on (i) the time scales of hydrodynamic and phytoplankton responses and (ii) the extent to which storm-induced mixing modifies resource supply, suggesting that both aspects need to be considered to assess the consequence of storms for lakes.

4.3 | Variation in Driver Combinations Among Lakes

The binary classification approach we used effectively identified potential drivers linking phytoplankton community reversions to the hydrodynamic effects of storms in 5 of the 8 lakes we studied (Bourget, Geneva, Kinneret, Kasumigaura, and Oneida). These five lakes were all represented by large datasets and numerous HSR events, in contrast to the other three lakes. Our ability to detect storm impacts on phytoplankton may thus depend on the number of storm events captured in the dataset, with longer time series capturing more storm events. Long-term monitoring of lakes is essential to develop robust predictive models of the ecological effects of rare events and to improve water resource management in the face of global environmental change.

Although the model correctly predicted phytoplankton reversions based on a small set of selected physical variables in five lakes, the relative importance of those drivers varied among lakes, with different physical characteristics as important factors influencing lake responses to storms (Stockwell et al. 2020). Water transparency was among the key drivers in two polymictic lakes (Oneida and Kasumigaura) but had no notable influence in deeper and monomictic lakes. Unexpectedly, reversions observed in polymictic lakes were associated with high water transparency, possibly due to a storm-induced loss or dilution of phytoplankton biomass (Stockwell et al. 2020). Strong grazing pressure can be another lake characteristic affecting outcomes of storm events. For example, invasive zebra mussels (*Dreissena polymorpha*) in Lake Oneida gain access to pelagic resources from storm-induced vertical and horizontal mixing (Idrisi et al. 2001). Finally, ecological preferences of species involved in the ordinary seasonal pattern of succession may play a role. In lakes where summer communities are associated with low water transparencies, storm-induced decreases in water transparency likely favour species characteristics of summer conditions, and hence prevent reversions. In contrast, storms leading to increased water transparency likely produce phytoplankton reversions. This mechanism could be enhanced when flushing rates increase during and after rainstorms resulting in increased transparency due to dilution by rainwater. In Lake Kasumigaura, such increases in transparency may result in delayed growth of summer species, especially species adapted to low light intensity such as the cyanobacterium *Cuspidothrix issatschenkoi* (Fukushima et al. 2021), thereby causing phytoplankton reversions.

In conclusion, we identified typical seasonal trajectories of phytoplankton succession in diverse large lakes that are globally distributed and found that reversions of phytoplankton communities to an earlier successional state were associated with thermal stratification and epilimnetic temperature in monomictic lakes, and on water transparency and the ratio of euphotic to mixing depth in polymictic lakes. Our analysis illustrates the value of examining patterns in phytoplankton community structure in long-term time series to identify events that disrupt the normal seasonal succession (Reynolds 1993; Sommer et al. 2012). Overall, the patterns and potential drivers identified in our analysis are an important step that paves the way for comprehensive global analyses of large data sets to assess variation of lake responses to extreme events such as storms or heatwaves in the face of global change.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data have been uploaded to the FEMC archive/portal system hosted by the University of Vermont (Stockwell et al. 2021). Datasets were contributed by a variety of public and private providers from multiple countries, and data for some lakes are available only upon request owing to the proprietary interests of individual data providers. See Stockwell et al. (2021) for data provider contact information and instructions on how to submit a data request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.