LIMNOLOGY and OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 67, 2022, S101–S120

doi: 10.1002/lno.11859

Antecedent lake conditions shape resistance and resilience of a shallow lake ecosystem following extreme wind storms

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Abstract

Extreme wind storms can strongly influence short-term variation in lake ecosystem functioning. Climate change is affecting storms by altering their frequency, duration, and intensity, which may have consequences for lake ecosystem resistance and resilience. However, catchment and lake processes are simultaneously affecting antecedent lake conditions which may shape the resistance and resilience landscape prior to storm exposure. To determine whether storm characteristics or antecedent lake conditions are more important for explaining variation in lake ecosystem resistance and resilience, we analyzed the effects of 25 extreme wind storms on various biological and physiochemical variables in a shallow lake. Using boosted regression trees to model observed variation in resistance and resilience, we found that antecedent lake conditions were more important (relative importance = 67%) than storm characteristics (relative importance = 33%) in explaining variation in lake ecosystem resistance and resilience. The most important antecedent lake conditions were turbidity, Schmidt stability, $\%O_2$ saturation, light conditions, and soluble reactive silica concentrations. We found that storm characteristics were all similar in their relative importance and results suggest that resistance and resilience decrease with increasing duration, mean precipitation, shear stress intensity, and time between storms. In addition, we found that antagonistic or opposing effects between the biological and physiochemical variables influence the overall resistance and resilience of the lake ecosystem under specific lake and storm conditions. The extent to which these results apply to the resistance and resilience of different lake ecosystems remains an important area for inquiry.

Extreme storms that produce high wind speeds, rain deluges, and floods can have meaningful effects on the functioning of lake ecosystems (Tsai et al. 2008; Tsai et al. 2011; Kasprzak et al. 2017; Ji et al. 2018; Stockwell et al. 2020). Severe storms can affect a variety of physical lake processes primarily through the runoff of terrestrial nutrients from precipitation (Gaiser et al. 2009; de Eyto et al. 2016; Zwart et al. 2017), wind induced mixing of the water column (Klug et al. 2012; Shade et al. 2012; Giling et al. 2017), lake sediment resuspension (Qin 2004; Zhu et al. 2014), and the heating/cooling of surface waters (Wüest and Lorke 2003; Woolway et al. 2018). Collectively, storm-induced effects on lake processes may have consequences for the resistance, resilience, and overall functioning following storm disturbances (Holling 1973, 1996; Havens et al. 2016; Hillebrand et al. 2018). The resistance and resilience of lake ecosystems are considered to be a critical aspect of a lake's intrinsic ability to oppose change in the face of a disturbance (resistance) and to recover (resilience) to antecedent functions following exposure to extreme storms (Holling 1973; Pimm 1984; Carpenter et al. 1992; Scheffer et al. 1992, 1994; Holling 1996; Carpenter et al. 2001; Pimm et al. 2019). A definition of resilience introduced by Holling (1973) encapsulates both ideas of resistance and resilience and states "that resilience is a measure of the persistence of systems and of their ability to absorb change

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

Special Issue: Nonlinear dynamics, resilience, and regime shifts in aquaticcommunities and ecosystems
[Correction added on 07 July 2021, after first online publication]

and still maintain the same relationships between populations, or state variables." The definition integrates resistance and resilience, and allows for local asymptotic recovery (Pimm 1984) to multiple equilibria (Holling 1973; Donohue et al. 2016). In addition, we used this definition because it avoids assumptions of steady states and associated global equilibria, and rather assumes that ecosystems operate far from any steady state, or global equilibrium, and that ecosystems are in constant flux and continuously undergoing gradual changes through time (Gunderson 2000; Gunderson et al. 2012). More generally put, the definition has come to be interpreted as whether a system returned to its pre-disturbance equilibrium, or entered a new one (Gunderson 2000; Gunderson et al. 2012; Donohue et al. 2016). Using this interpretation, *resistance* is the degree to which a system or system variable is able to resist (i.e., absorb) change in the face of a disturbance and *resilience* is then the level to which the system recovered to (i.e., either to the same or different equilibrium) following the disturbance. We use the term equilibrium in the sense that lakes are able to find a new balance following a disturbance by adapting, or reorganizing through changes in population relationships and/or state variables.

As a result of climate change, the frequency and intensity of extreme storms are expected to increase (Rockel and Woth 2007; Gastineau and Soden 2009). Increases in peak wind intensities will ultimately expose many inland waters to more extreme wind storms sometimes including heavy precipitation (Donat et al. 2010; Haarsma et al. 2013; Baatsen et al. 2015). Long-term changes in regional storm frequency, duration, and intensity may have meaningful effects on the resistance and resilience of lake ecosystems following storms by affecting physical, chemical, and biological interactions (Tsai et al. 2011; Shade et al. 2012; Stockwell et al. 2020).

Lake responses to extreme wind disturbances depend on antecedent lake conditions and storm characteristics (Havens et al. 2001, 2011, 2016; Jones et al. 2008, 2009; Perga et al. 2018; Stockwell et al. 2020). For example, a small alpine lake exposed to severe storms was not strongly modified as a result of storm characteristics, but rather as a result of unusually warm dry spells preceding the storms (Perga et al. 2018). The antecedent conditions of the catchment basin allowed for large suspended solid inputs, which persistently modified the lake's metabolic and thermal dynamics. In addition, physical and biological modifications experienced in lakes as a result of extreme storms result from interactions between atmospheric and catchment processes (Jennings et al. 2012; Klug et al. 2012; Favaro and Lamoureux 2014; Kuha et al. 2016). While previous studies demonstrate that severe storms induce variable responses in lakes, it is unclear if storm characteristics are more important than the lake's antecedent conditions. Resolving the relative role of these two classes of variables will substantially enhance our understanding of how climate driven alterations to storm characteristics are interacting with alterations in catchment processes and lake conditions to shape lake ecosystem resistance and resilience.

Here, we analyzed how physiochemical and biological properties of a shallow lake resist and recover from extreme wind storms. An extreme storm is generally defined as those events lying in the outermost 90th, 95th, or 99th percentile of the local weather history (IPCC 2012). For the purpose of this research, we used extreme value theory to estimate the probability of a given shear stress quantile and analyze those events in the 99th percentile (IPCC 2012). The primary research goal was to determine whether storm characteristics (frequency, duration, intensity, wind direction, and precipitation), or average antecedent lake conditions (pH, $\%O_2$ saturation, water temperature, turbidity, conductivity, Schmidt stability, photosynthetic active radiation, total and soluble reactive phosphorus, soluble reactive silica, and total nitrogen) were more important for explaining the resistance and resilience of the lake ecosystem following storms. Here, we tested whether antecedent lake conditions are more important than storm characteristics in shaping the resistance and resilience of the lake. We tested this by: (1) classifying and examining extreme shear stress events observed from high-frequency wind data collected on a shallow lake; (2) quantifying resistance and resilience indices based on short-term effects of extreme shear stress events on lake ecosystem response variables; and (3) determining the relative importance of storm characteristics vs. antecedent lake conditions for explaining variation in the resistance and resilience of the lake's physiochemical (pH, $\%O_2$ saturation, and water temperature) and biological (chlorophyll *a*, phycocyanin, and turbidity) properties by fitting boosted regression trees (BRT). By characterizing the drivers of variation in lake ecosystem resistance and resilience, our results provide useful heuristics for understanding the complexity of lake ecosystem resistance and resilience responses to storms in the context of overall warming trends.

Methods

Study site

Located southeast of Berlin, Germany, Müggelsee is a shallow polymictic, eutrophic lake with a mean depth of 4.9 m, a max depth of 7.9 m, and surface area of 7.2 km^2 (Köhler et al. 2005). The River Spree is the lake's major tributary which influences the lake's bio-physical processes and retention times, which ranges between 6 and 8 weeks. The catchment area is approximately 7000 km^2 and consists of urban, agriculture, and forest (Köhler et al. 2005). When atmospheric conditions become unstable due to warming in spring, westerly winds flow across the lake, steadily increasing in frequency and speed through June when atmospheric conditions begin to stabilize. Westerly winds give way to southwesterly winds in July and the frequency of high-speed wind gusts decreases through October. However, extreme wind events have been recorded across seasons. Because of the lake's morphology and east to west orientation, the wind often travels across the lake's lengthiest fetch, resulting in frequent mixing with only short periods of stratification lasting from less than a day up to several weeks (Wilhelm and Adrian 2008). Frequent mixing makes the lake prone to upwelling, or resuspension events, especially in spring (Kozerski and Kleeberg 1998). In addition to atmospheric forcing, Müggelsee experiences strong seasonal and periodic algal blooms that can influence the thermal structure and mixing dynamics of the lake, particularly in spring (Shatwell et al. 2016). Shallow lakes similar to Müggelsee are potentially more sensitive to extreme storms because they are more immediately susceptible to changing meteorological conditions (Gerten and Adrian 2001) and due to stronger interactions that occur between lake sediment and the water column (Qin 2004; Havens et al. 2016). The resuspension of lake sediment may affect resistance and resilience of Müggelsee through changes in nutrient concentrations, light availability, and algal biomass following storms (Kozerski and Kleeberg 1998; Duarte et al. 2004; Guadayol et al. 2009; Zhu et al. 2014).

High-frequency data collection

Müggelsee is equipped with a high-frequency monitoring station that is anchored at 5.3 m depth and 300 m from the northern shoreline (52°26′46.1″N; 13°39′0.2″E). The station simultaneously measures meteorological and limnological parameters. Data used here were collected between 2002 and 2017, and span the months between March and November. Five-minute measurements of pH, %O_2 saturation, water temperature, chlorophyll *a*, phycocyanin, and turbidity were collected using a multi-parameter probe (YSI 6600 V2-4/YSI6560; YSI Inc.) at a depth of 1.5 m. In addition, hourly measurements of water temperature are taken every 0.5 m through the water column to a depth of 5 m, which was used to calculate Schmidt stability. Measurements of water temperature are made with a physical sensor, while determination of hydrogen ion concentrations was measured using a pH electrode. Optical sensors equipped with antifouling wipers designed for lens cleaning take measurements of oxygen saturation, chlorophyll *a*, turbidity, and phycocyanin. Measurements of underwater light were collected using two spherical photosynthetic available radiation (PAR) sensors (LI-193SA, LICOR, Nebraska) placed at 0.75 and 1.25 m depth. To characterize wind, we used the anemometric measurements of maximum wind speed and mean direction, which are taken every 5 min at 10 m above the lake surface (Schalenanemometer; Thies GmbH).

Shear stress quantification

We chose shear stress as our primary stressor driving changes in lake characteristics during extreme wind storms because it is the best predictor of wave-generated sediment resuspension events, which may strongly affect ecological dynamics in Müggelsee (Kozerski and Kleeberg 1998). Resuspension events in Müggelsee are short lived local events that tend to be higher in the spring and into the summer, and decrease in the fall due to spring time resuspension and subsequent redistribution of sediment in the lake (Kozerski and Kleeberg 1998). Resuspension events in Müggelsee primarily re-suspend finer sediments and debris from the shallower and sheltered parts of the lake (Kozerski and Kleeberg 1998). Following the methodology described by Rohweder et al. (2008) and Laenen and LeTourneau (1996), shear stress was calculated for every given wind speed and direction as a function of lake depth. Maximum wind speed (ms^{-1}) data was collected in 5 min intervals and used to calculate shear stress between March and November.

Using the R packages "rgdal" (version 1.4-3) and "proj4" (version 1.0-8) (Urbanek 2012; Bivand et al. 2016), a list of shoreline coordinates and grid of points every 100 m within the lake were extracted from a shapefile in QGIS (version 2.18.15). The output data were then used to calculate effective fetch using the function fetch_len_multi from the R package "waver" (version 0.2.1) (Marchand and David 2018). Bottom shear stress was then calculated in Newtons/m^2 (N/m^2) for all possible fetches and for Müggelsees' average lake depth of 5 m. This required the computation of the wave geometry following wave forecasting equations for shallow waters and linear wave theory (Komar and Gaughan 1972; U.S. Army Corps of Engineers Shore Protection Manual 1984) (*see* Supporting Information for equations and specific details on calculating fetch and shear stress).

Extreme wind storm classification

Extreme shear stress events were classified by calculating the return period, or the maximum shear stress which is exceeded, on average, once every T days (*see* Eq. 1) during the growing season (i.e., March to November) (Palutikof et al. 1999). Return periods were estimated following methods based on generalized extreme value (GEV) distributions and L-moments summary statistics for parameter estimation (Hosking 1990;Palutikof et al. 1999; Gilleland and Katz 2006, 2016). GEV is considered to be a family of distributions: Gumbel ($k=0$), Fréchet ($k>0$), and Weibull ($k<0$) and is determined by the tail behavior of each distribution (Laib and Kanevski 2016). We use L-moment statistics as it has been suggested to provide better parameter estimation when the time series under consideration is less than 20 yr. The cumulative probability of a shear stress quantile (X_T) with a return period (T) is given by:

$$X_T=\beta+\frac{\alpha}{k}\left\{1-\left[-ln\left(1-\frac{1}{T}\right)\right]^k\right\} k\neq 0 \qquad (1)$$

Where X_T is the return period, β is the mode of the extreme value distribution (location parameter), α is the dispersion (scale parameter), and k is the shape parameter which determines the type of GEV distribution (Palutikof et al. 1999; Gilleland and Katz 2006, 2016). By calculating the return period, we are able to determine the return level, or the probability of a given daily peak in shear stress level exceeding 1/ T days. For example, a daily shear stress event estimated to occur every 100 d or more in a system would have a probability of occurring on any given day of $1/100 = 0.01$. Before the shear stress data were fitted to an extreme distribution model, it was transformed from the 5 min maxima collected at the monitoring station to daily maxima. We then fitted an extreme value distribution model and return periods were computed using the fevd and return.level functions in the R package "extRemes" (version 2.0) (Gilleland and Katz 2006, 2016). To see an example of R code, *see* Supporting Information.

Quantification of resistance and resilience indices

Indices provide a useful tool for standardizing the storm responses across variable type and for interpreting and comparing the resistance and resilience of different ecosystems including lakes (Orwin and Wardle 2004; Tsai et al. 2011; Cantarello et al. 2017; Guillot et al. 2019). Resistance is the amount of change induced by the initial disturbance when compared to the mean antecedent conditions, while resilience is the level to which the lake parameter under scrutiny recovered to after being disturbed (Holling 1973; Pimm 1984; Donohue et al. 2016). To calculate the resistance (RS) index for each individual lake parameter, we used the following function (Orwin and Wardle 2004):

$$RS(t_0) = 1 - \frac{2|D_0|}{(C + |D_0|)} \tag{2}$$

Where t_0 is the time at which the lake parameter has reached max displacement (P_0) and D_0 is the difference between the baseline conditions (C) and the max displacement point P_0, or the maximum value to which a lake parameter has been disturbed to (Fig. 1 and S1). It is necessary before quantifying resistance and resilience to define a baseline from which the two components can be calculated for each lake parameter. Because we were trying to capture the immediate conditions of the lake, we determined 3 d would represent the baseline (C) or antecedent conditions for calculating resistance and resilience for each lake parameter. This was determined by calculating the mean of each lake parameter 3 d, 1 week, and 2 weeks prior to the event. The further back in time we went, the closer to the annual mean was calculated, which we considered not representative of the immediate state of the lake conditions.

The resilience index was calculated when the lake parameter under observation had returned to antecedent conditions, or when it returned to an alternative conditional state and it was clear that the system variable was more than likely not responding to the storm, but rather being governed by other system dynamics at time t_x. To determine this point of recovery, an initial time window was pre-defined, beginning after the peak in the lake parameter response and extending to the end of the 3-d post storm condition period. Post storm conditions were defined as the 3-d period beginning when shear stress returned to zero. The recovery point D_x was then determined by calculating the standard error in the lake parameter in a rolling window P_x with a minimum length of 72 h and starting at P_0 (Fig. 1). The lake parameter was then averaged over the window with the lowest standard error and selected as its recovery level. Because it is impossible to know, or predict when and at what level a lake parameter will recover, the time series could be narrowed or widened respectively upon visual inspection if it appeared the lake parameter recovered faster, or did not recover within the pre-defined post storm time window. Thus, the resilience (RL) index was calculated as follows:

$$RL(t_x) = \frac{2\,|\,D_0\,|}{(D_0| + |D_x|) - 1} \tag{3}$$

Where t_x is time at which the value of the lake parameter returned to antecedent conditions, or to an alternative equilibrium, and D_x is the difference between (C) and the recovery mean value P_x at time t_x (Fig. 1). Seasonal variation at times prevented lake variables from returning to their antecedent states. For example, following storm-driven cooling of the water column, water temperature rarely recovered to antecedent conditions during the fall because the general cooling trend of the lake at those times of year prevailed over the temperature recovery. Thus, to calculate resistance and resilience, we seasonally adjusted the data so that resilience can be interpreted as a return to conditions expected at the specific time of year. All lake parameters were seasonally decomposed and adjusted using the msts and mstl function as part of the R package "forecast" (version 8.5) (Hyndman and Khandakar 2008). We did this by first determining the number of hourly observations for a given variable and sampling year and then transforming the time series into a multi-seasonal time series (msts) and then decomposing the seasons and trends using Loess function (mstl). The mstl function is fully automated and requires just a single setting which is a vector of the seasonal components being tested (for algorithm equations, *see* de Livera et al. 2011). We tested for daily oscillations (24 h seasonality) in pH, $\%O_2$ saturation, water temperature, chlorophyll *a*, and phycocyanin. However, it was determined that turbidity, phycocyanin, and water temperature all display annual seasonality, while chlorophyll *a*, pH, and $\%O_2$ saturation displayed weak daily oscillations and annual seasonality. Each lake parameter was then seasonally adjusted by subtracting the identified seasonal component from the original data. To see an example of R code, *see* Supporting Information.

Resistance and resilience range between −1 and 1, where a value of 1 indicates maximal resistance and resilience of the observed lake parameter. A resistance of 0 indicates there has been a 100% reduction or enhancement in the observed parameter. A resilience value of 0 indicates no recovery (e.g., $D_0 = D_x$). Negative values of resistance indicate there has

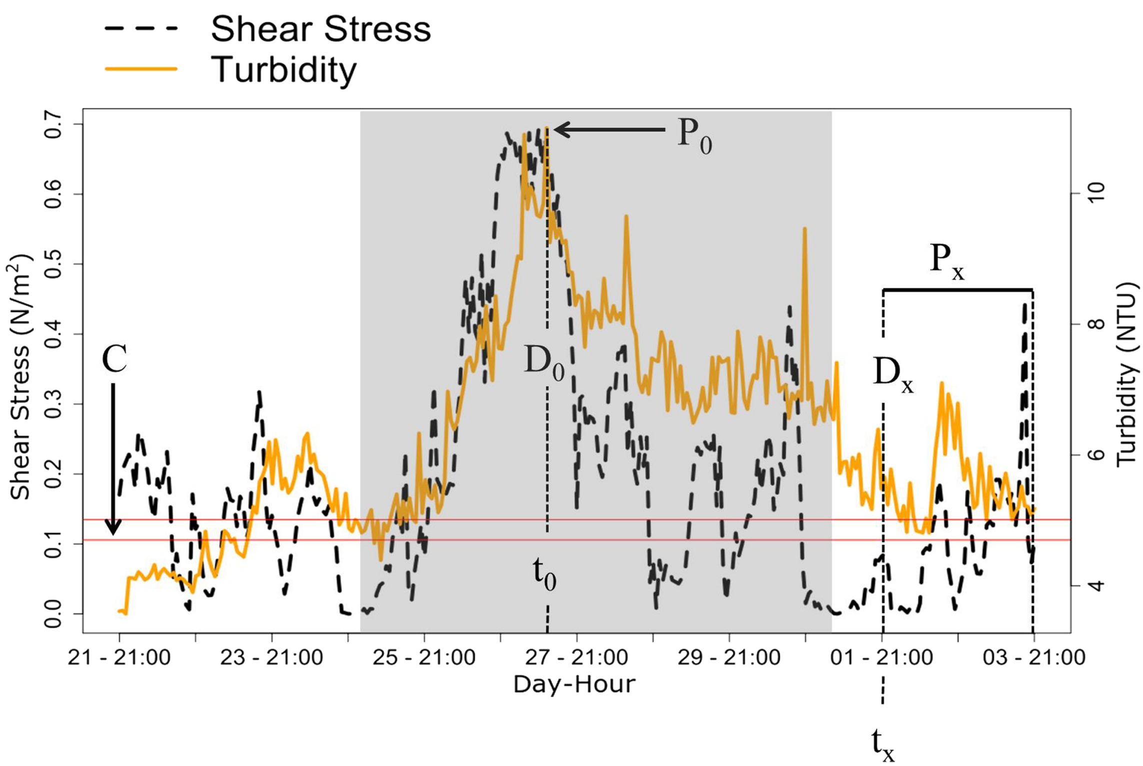

Fig. 1. Example of how to quantify resistance (RS) and resilience (RL) of a lake parameter (*z* axis) during a resuspension event in June 2007 that has a mean antecedent value of C (red lines are the 95% confidence interval surrounding the true mean of C). An extreme shear stress event occurs during a given time frame (gray blocked area) and a lake parameter reaches its maximum response P_0 at time t_0 where resistance is an index of the absolute magnitude of this change $D_0 = |C - P_0|$. Resilience is then an index of the level to which the lake parameter has recovered beginning at time t_x, where $D_x = |C - P_x|$, or the absolute difference between C and the average value P_x taken over a 72 h window with the lowest standard error in the lake parameter.

been more than a 100% change in the observed parameter (e.g., $|D_0| > C$), while negative values for resilience indicate that the parameter continued to move away from (C). In the case, it was not clear where P_0 was occurring and/or if the overall response was positive or negative, we used BRT to determine the overall response of the lake parameter under scrutiny. This step helps break down the direct and indirect effects of the storm to properly identify whether there was a positive or negative reaction toward the storm. In more general terms, it can be the case that there was an initial response to the storm which was a positive one, but as the storm progressed there was also a negative response which ends up being approximately equal distant from antecedent conditions as the positive response. To break the resulting tie and to determine the correct peak, we used BRT models and visualized results using partial dependency plots to determine the overall effect. BRT models to aid in the identification of P_0 were fitted with a maximum of 10,000 trees, a tree complexity of 2, a learning rate starting at 0.82, and decreasing by a factor of two with an ending rate at 0.1×10^{-9}, and to introduce randomness into the model stochastic bag fractioning of (0.5, 0.6, 0.7) was used (Elith et al. 2008). Models were selected based on the combination of model hyper-parameters; number of trees, tree complexity, and learning rate that resulted in the least predictive error, or the model that results in a mean deviance standard error that is closest to 0. The selection of model parameters was optimized by cross-validating model results with those data that are excluded as an independent test set. The optimization and selection of hyper-parameters are automated by fitting models using the function gbm.step as part of the R package “dismo” (version 1.1-4) (Hijmans et al. 2017). The function uses a 10-fold cross-validation process to determine the optimal number of boosting trees to be used in the final model (Hastie et al. 2001; Elith et al. 2008). The algorithm works by first dividing the data into 10 subsets and then fits gradient boosted models (gbm) of increasing complexity along the fold sequence, where which the residual deviance is calculated at each step. Each fold processed results in a gbm model and its associated holdout residual deviance, standard error, and the optimal number of trees fitted. The model that results in the lowest holdout deviance is then fit and selected as the final model (Hijmans et al. 2017). The predictor variables for these models were shear stress, pH, $\%O_2$ saturation, water temperature, chlorophyll *a*, phycocyanin, and turbidity (see model formula in following section). In the case that there was no distinguishable response, either a reduction, or enhancement in the lake parameter, the parameter under observation was assigned a “1” for resistance and resilience (i.e., no perturbation and complete recovery). Lastly, because calculating resistance and resilience was an automated process with pre-defined time windows, it was also the case that the function would in some storm scenarios select points in time for P_0 which were not associated with the storm. In these cases, we specified a time window for the function to find an appropriate P_0.

Lake resistance and resilience analysis

To determine if the storm characteristics or antecedent lake conditions were more important for predicting the resistance and resilience of all measured lake parameters (i.e., resistance and resilience indices of pH, $\%O_2$ saturation, water temperature, turbidity, chlorophyll *a*, and phycocyanin), we combined all resistance and resilience indices into a single BRT model where the values of resistance and resilience were the response (we call this the combined indices model). Before being introduced into the model, we conducted a co-linearity analysis to reduce the number of correlated predictors. When predictors showed a Pearson correlation of $r > 0.50$ we selected the predictor that made more sense in predicting lake ecosystem resistance and resilience. For example, water temperature was chosen over air temperature and day of the year over atmospheric pressure and humidity. The 3-d baseline period used as the control conditions for quantifying resistance and resilience was considered to be the antecedent lake conditions. Antecedent lake conditions included the following predictor variables: pH, $\%O_2$ saturation, turbidity (NTU), water temperature (°C), conductivity (μS/cm), Schmidt stability (J/m^2) (i.e., stratification strength), photosynthetically active radiation (PAR) (W/m^2), total phosphorus (μgP/l), total nitrogen (mgN/l), and total soluble reactive silica (mgSi/l). Characteristics associated with the storm were mean wind direction (°), precipitation (mm), duration (h), maximum shear stress (N/m^2), and time between storms (months). Time between storms was calculated as the time accrued since the last storm, which provides insight into how storm frequency influences resistance and resilience of the lake. All other storm characteristics were measured during a defined storm period which was centered on the peak in shear stress, and was defined as beginning when shear stress was zero prior to the peak and ended when shear stress returned to zero after the peak. The year in which the storm occurred was converted to decimal year and included in the model. Also to control for independence in resistance and resilience of response variables, we included in the model a two-level factor representing resistance and resilience metrics and a six-level factor representing each response variable's resistance and resilience indices. Lastly, because antecedent lake conditions were seasonally adjusted to be consistent with the conditions under which resistance and resilience were quantified, we also included the day of year on which the shear stress peak occurred as a proxy for seasonality in the model. All data and statistical analysis were carried out using the program R (R Core Team 2019). Schmidt stability was calculated using the R package "rLakeAnalyzer" (Winslow et al. 2018). Nutrient data were collected once weekly from the epilimnion of which the most recent nutrient measurement (i.e., 1–4 d) prior to the storm was used as a predictor in the model. Total phosphorus, nitrogen, and silica all showed annual seasonality and were seasonally decomposed and adjusted using the mstl function as part of the R package "forecast" (version 8.5) (Hyndman and Khandakar 2008). The BRT model formula was as follows (for full details on BRT, *see* Elith et al. 2008):

$$Y_{(\mathrm{RSRL})} = f0(x) + f1(x) + f2(x).$$

Where $Y_{(\mathrm{RSRL})}$ is resistance (RS) and resilience (RL) index values and f_i are decision trees where x is the predictor variables including antecedent lake conditions and storm characteristics. The model followed the same structure described in the quantifying resistance and resilience section, however, to select the final model we compared the performance of models with varying tree complexities of 1,2,3,4,5 to allow for more interactions and bag fractioning was decreased to (0.3,0.4,0.5) which decreased the sensitivity of the models to outliers. Models were selected based on the combination of model hyper-parameters; number of trees, tree complexity, and learning rate. The combination of hyper parameters that resulted in a model with the lowest mean deviance standard error and highest predictive power was selected. Partial dependency plots of the fitted values were created to visualize and interpret the most influential variables describing lake ecosystem resistance and resilience. Partial dependency plots provide the marginal effects, or the greatest instantaneous change in resistance and resilience relative to each storm characteristic and antecedent lake condition. Partial dependency plots were generated using the R packages "ggplot2" and "ggpubr" (Wickham 2016; Kassambara 2020). In addition to fitting the above described combined indices model (i.e., model combining both physiochemical and biological variables), we also fitted two separate models, one with only the biological indicators of resistance and resilience as a response (i.e., resistance and resilience of chlorophyll *a*, phycocyanin, and turbidity), and another with physiochemical indicators of resistance and resilience as a response (i.e., resistance and resilience of pH, $\%O_2$ saturation, and water temperature). Fitting these models provided further clarity on the roles of antecedent lake conditions and storm characteristics on the two groups of variables independently.

Results

Wind storm classification

Results from fitting the extreme distribution model suggest that the shear stress maxima follow a Weibull distribution, which is typical of wind extremes (for model fit and results, *see* Fig. S2). We decided to analyze those shear stress events which were estimated to have return periods of 100 d or more

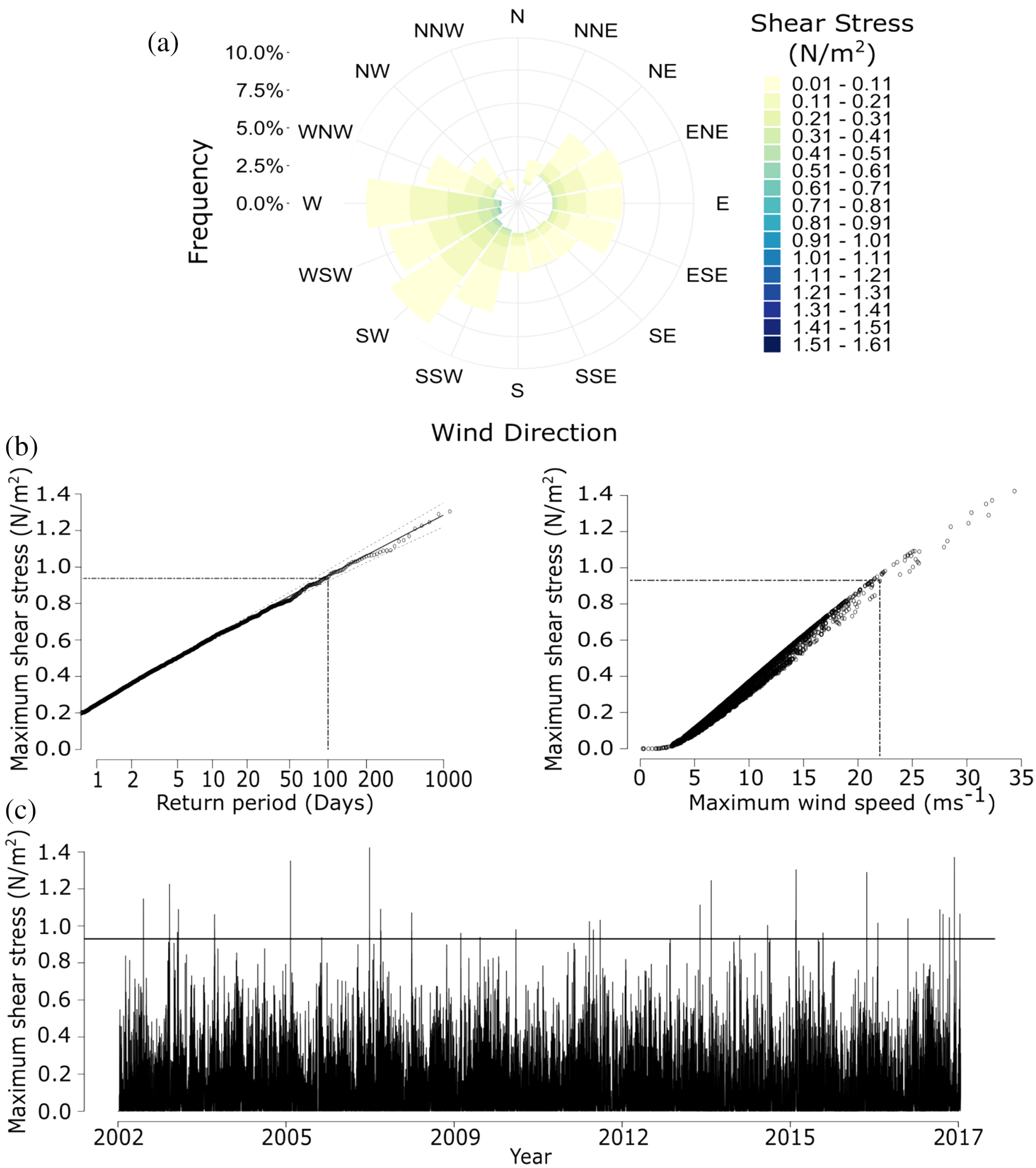

Fig. 2. (**a**) Wind rose depicting the frequency of shear stress events and wind direction for Müggelsee. The legend shows the shear stress levels for a given wind direction. (**b**) Left shows the estimated return times of shear stress events, where the vertical dashed line represents the estimated return period in days and the horizontal dashed line represents the shear stress level that is expected to occur for the given return period. The relationship is not exactly 1 to 1 because shear stress measurements include the effect of fetch and wave characteristics. (**b**) Right shows the relationship between wind and shear stress. Here we have analyzed those events that are estimated to occur on the lake every 100 d or more, or daily peak shear stress > 0.93 N/m^2 and max wind speeds between 21 and 35 ms^{-1} which was a total of 30 storm events identified. (**c**) Is the time series of 5 min maximum shear stress used to classify extreme events. The black line shows the 0.93 N/m^2 threshold used to classify events.

(i.e., probability of occurring on any given day = 0.01), which corresponds to wind extremes that generated peaks in shear stress ≥ 0.93 N/m^2 (Fig. 2). Applying this 100 d threshold to the 5 min time series resulted in the identification of 30 storms, of which 25 were suitable for our study because they had minimal data gaps for all response variables analyzed here. All wind storms were then analyzed at hourly time scales. The identified events occurred throughout the seasonal spectrum, with 5 between the months of March and May, 13 between June and August, and 7 between September and

October. Duration varied among the events and ranged between 42 and 157 h with an average of 110 h. These types of events are estimated to occur on the lake every 0.27–3.5 yr and generated hourly shear stress means between 0.1 and 0.3 N/m^2 with peaks between 0.2 and 0.9 N/m^2 (Fig. S3). In terms of wind speed, these events produced maximum wind speeds between 21 and 35 (ms^{-1}) (Table S1). Wind primarily traveled across the lengthiest fetch and on average was in contact with the surface of the water for 3.2 km with storms having a mean wind direction of southwest. However, wind directions ranged between less frequent directions such as S to ESE, to more frequent directions such as SSW to W (Fig. 2). Observations were complete for pH, $\%O_2$ saturation, and water temperature for each storm event between 2002 and 2017. However, there were missing observations for turbidity during events in July 2002 and June 2003, and for chlorophyll *a* in July 2002. Phycocyanin was not collected at the monitoring station until 2008 and was complete through 2017.

Resistance and resilience indices

The identified storms induced varying effects in the observed lake parameters which were divergent in their response to the storms (Fig. 3). Spearman correlations suggest the most significant relationships ($P \leq 0.05$) between the different indices were between the resistance and resilience of water temperature, turbidity, pH, and $\%O_2$ saturation (Fig. 4). Water temperature resistance and resilience were found to be negatively correlated with resistance of chlorophyll *a* and with the resilience of phycocyanin conditions, suggesting that changes in phytoplankton conditions following storms were more likely when there were strong changes in water temperature. Furthermore, water temperature resilience was more likely when antecedent turbidity conditions were resistant toward the storms. Water temperature generally decreased with a mean of $-0.5°C$ sd ± 1.6 with one storm decreasing temperature by $-4°C$. Two of the storms resulted in no change in temperature, while eight of the storms generated increases in water temperatures between 0.2 and 2.4°C. Water temperature had a resistance mean of $\bar{x} = 0.71$. However, the changes in temperature that did occur were generally persistent and water temperature resilience on average was low and had an index mean of $\bar{x} = 0.33$ (Figs. 5 and S4). Resistance of pH was significantly ($P \leq 0.05$) and negatively correlated with water temperature resilience, which suggests greater changes in pH were more likely when water temperature did not return to antecedent levels. However, pH resistance and resilience were found to be significantly ($P \leq 0.05$) and positively correlated with the resistance and resilience of $\%O_2$ saturation, and negatively correlated ($P \leq 0.05$) with the resilience of turbidity conditions, suggesting that changes in pH conditions are significantly related to the displacement and recovery of algal conditions following the storms. pH departed very little from antecedent conditions and had an resistance mean of $\bar{x} = 0.90$, however, small changes in pH were moderately persistent in the system with a resilience mean of $\bar{x} = 0.49$ (Figs. 5 and S4). In the most extreme cases, pH conditions were either enhanced or reduced by 0.6 pH units, respectively. Percent O_2 saturation resistance was significantly ($P \leq 0.05$) and negatively correlated with turbidity resilience, suggesting that greater changes in oxygen saturation conditions can be expected when turbidity conditions did not return to antecedent conditions (Fig. 4). Percent O_2 saturation was moderately resistant and resilient to change and had a mean of $\bar{x} = 0.50$ and $\bar{x} = 0.49$, respectively (Figs. 5 and S4). Storms had opposing effects on $\%O_2$ saturation depending on whether saturation levels were below or above 100% at the onset. The storms tended to reduce $\%O_2$ saturation when levels were >100% (10 of 25 storms, with 2 storms further enhancing $\%O_2$ saturation), while storms enhanced $\%O_2$ saturation when levels were below 100% (also 8 of 25 storms, with 5 storms further reducing $\%O_2$ saturation). Results from a regression analysis suggest that $\%O_2$ saturation level is significantly related to whether storms increase or decrease oxygen saturation levels ($R^2 = 0.48$, $F = [1, 23.6]$, $P < 0.001$).

Turbidity resilience was significantly and negatively correlated to the resistance of pH and $\%O_2$ saturation, suggesting that greater changes in pH and $\%O_2$ saturation are expected when turbidity conditions are not resilient as a result of sediment resuspension and/or changes in phytoplankton biomass (Fig. 4). Turbidity enhancement following storms can mostly be interpreted as a result of sediment resuspension (16 of 23 storms), while turbidity reductions most likely result from short term vertical mixing of phytoplankton (6 of 23 storms). At least one storm in August 2011 enhanced turbidity conditions due to bloom formation (Fig. 3). Storms on average changed the turbidity conditions in the lake by ~87% with a resistance mean of $\bar{x} = 0.17$, with eight storms registering negative values of resistance. However, turbidity conditions in the lake tended to be resilient with a mean of $\bar{x} = 0.54$. Nevertheless, in 3 of the 23 storms, turbidity conditions continued to move away from antecedent conditions (i.e., negative values of resilience). In all three storm events, the lake was in an unseasonably clear state, and took place in early April 2014 and in October 2002 and 2017 (Figs. 5 and S4). In relation to chlorophyll *a*, the storms tended to change chlorophyll *a* concentrations on average by 100% with a mean resistance of $\bar{x} = 0$, with 50% of storms causing more than 100% change in chlorophyll *a* concentrations (12 of 24 storms). Overall, chlorophyll *a* conditions tended to be moderately resilient with a mean of $\bar{x} = 0.55$ (Figs. 5 and S4). Chlorophyll *a* on average increased by 3.2 $\mu g/L$ following storms (10 of 24 storms) and nearly equally decreased by -3.3 $\mu g/L$ (14 of 24 storms). Phycocyanin showed low resistance with a mean of $\bar{x} = 0$, with storms able to induce more than 100% change in phycocyanin (9 of 18 storms). Phycocyanin was moderately resilient with a mean of $\bar{x} = 0.53$, where only 1of the 18 storms caused phycocyanin fluorescence to move away from antecedent algal conditions (Figs. 5 and S4). Phycocyanin fluorescence

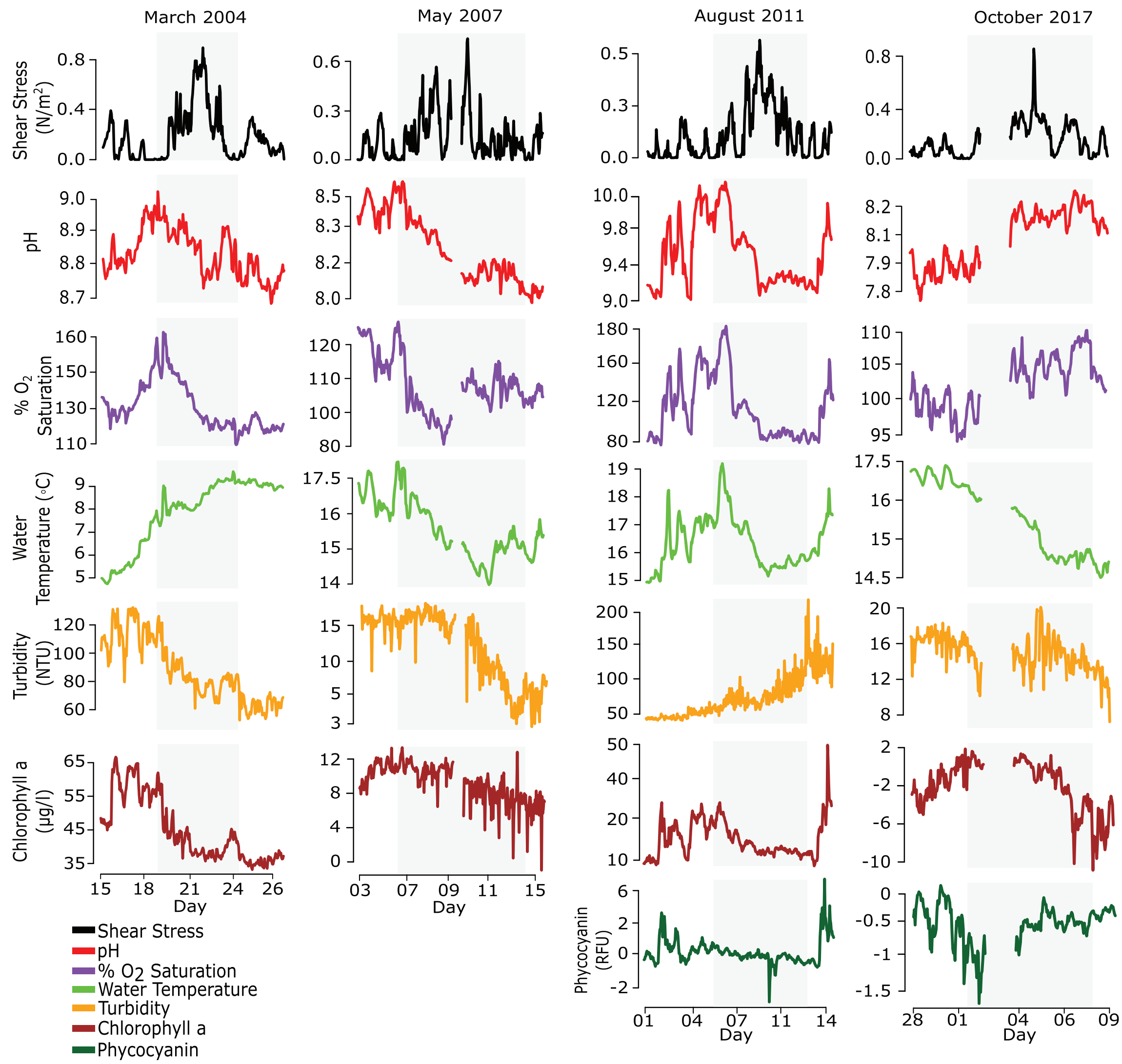

Fig. 3. Four of the 25 analyzed shear stress events and the responses of lake ecosystem variables used to calculate resistance and resilience. The figure provides an indication of the variability in storm events (i.e., shear stress = top row) and the responses of pH, $\%O_2$ saturation, water temperature, turbidity, chlorophyll *a*, and phycocyanin (see legend). The gray-shaded areas represent the time during which the identified storm event occurred. Because the response variables are seasonally adjusted negative values are present in some figures. For example, the storm in October 2017 hit the lake when chlorophyll *a* and phycocyanin concentrations were unseasonably low.

in the lake on average decreased by 0.50 RFU following 7 of 18 storms. Lastly, in four of the storm scenarios, there were no discernable response and were assigned a 1 for resistance and resilience for water temperature (1/25), chlorophyll *a* (2/24), and phycocynin (1/18).

Storm and antecedent lake condition effects on lake ecosystem resistance and resilience

To determine if the storm characteristics or antecedent lake conditions were more important, BRT results provide a ranking of predictor variables in terms of each variable's relative importance. The relative importance of each variable is calculated as a function of the frequency with which it was included in the BRT's individual regression trees and the improvement to the model that resulted from its inclusion (Elith et al. 2008). The final combined indices model ($n = 280$) was fitted with a tree complexity of 5, 1700 trees, a learning rate of 0.0128, a mean deviance standard error of 0.14, and had a cross-validated correlation mean of 0.56 (adjusted $R^2 = 0.76$) (Table S2).

Variability in the individual predicted indices was the most important predictor of lake ecosystem resistance and resilience with a 29.6% relative importance in the model (Fig. 5), which suggests that the individual variability in the predicted resistance and resilience of the biological and physiochemical indices is important for describing the lake's resistance and

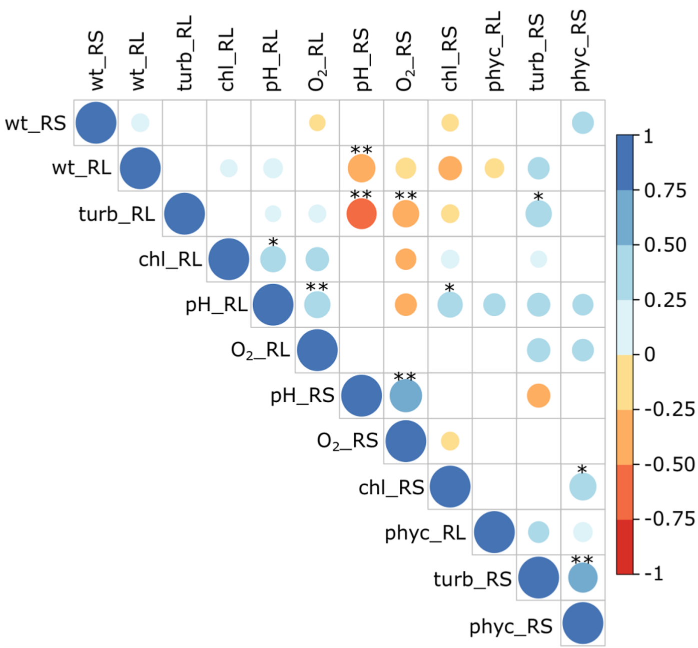

Fig. 4. Hierarchical clustering of spearman correlations between the varying resistance (RS) and resilience (RL) indices. Those relationships that have two stars above them were significant at $P \leq 0.05$ level, one star indicates a correlation at a $P \leq 0.10$ level. Blue circles represent positive correlations while red circles represent negative correlations. The size of the circle indicates the strength of the relationship, with bigger circles representing stronger correlations between indices.

resilience following storms. The resistance and resilience of the biological variables (i.e., chlorophyll *a*, phycocyanin, and turbidity) under certain antecedent conditions suggest that the storms were capable of changing these variables by 100% or more (Fig. 5). The second most important variable (9.2%) was the factor representing the independence of resistance and resilience, which suggests that exploring these individually and among the two groups of variables may be important. Because the model contained several neutral variables (i.e., RS/RL factor, variable indices factor, year, and day of the year), we rescaled the relative importance of the antecedent lake conditions and storm characteristics by summing their relative importance and then dividing the overall sum of antecedent lake condition and storm characteristic by the sum of the two. These results suggest that the rescaled antecedent lake conditions were more important (scaled relative importance 67%) than storm characteristics (scaled relative importance 33%) (Fig. 5). The relative importance of antecedent physiochemical conditions effecting lake ecosystem resistance and resilience were turbidity (7%), Schmidt stability (6.8%), % O_2 saturation (3.4%), PAR (3.4%), conductivity (3.3%), water temperature (3.1%), and pH (2.2%). Lake resistance and resilience increased with increased levels of turbidity, stratification, PAR, and pH, while it decreased with increasing oxygen saturation, conductivity, and water temperature (Fig. 6). Antecedent nutrient concentrations of soluble reactive silica, total phosphorus and total nitrogen had relative importance levels of 3.3%, 2.7%, and 1.9%, respectively. Low to moderate levels of antecedent soluble reactive silica and total nitrogen lead to increased resistance and resilience (Fig. 6). Storm characteristics were fairly equal in describing the resistance and resilience of the lake which tended to decrease with increasing duration (3.9%), shear stress intensity (3.8%), time between storms (3.7%), and when storms came from less frequent wind directions (2.9%) (Figs. 6 and 8). However, the results suggest that increasing mean precipitation was equally as important (3.9%) as duration, and increased resistance and resilience following storms. The relative importance of the day of the year and the year in which the storm took place was 2.3% and 2.2%, respectively. Lake ecosystem resistance and resilience varied with season and greater negative effects were observed in mid-summer to fall (Figs. 6 and S6). Lastly, storms occurring after 2012 increasingly had negative effects on the resistance and resilience of the lake (Figs. 6 and 8).

Storm and antecedent lake conditions antagonistic effects on lake biological and physiochemical resistance and resilience

Modeling the two groups of variables separately provided insight into the nonlinear effects of the antecedent lake conditions and storm characteristics, we see in the combined indices model described in the previous section. To clarify how antecedent lake conditions and storm characteristics were influencing the lake's biological and physiochemical resistance and resilience responses independently, we fit two models, one with only the biological indicators of resistance and resilience as a response, and another with physiochemical indicators of resistance and resilience as a response. Both models were identical in structure as the combined indices model. The biological model ($n = 130$) was fitted with tree complexity of 5, 1250 trees, a learning rate of 0.0032, a cross-validated correlation mean of 0.50 (adjusted $R^2 = 0.50$), and a mean deviance standard error of 0.19. The physiochemical model ($n = 150$) was fitted with a tree complexity of 5, 1950 trees, a learning rate of 0.0016, a cross-validated correlation mean of 0.51 (adjusted $R^2 = 0.49$), and a mean deviance standard error of 0.07.

While the same antecedent lake conditions and storm characteristics were similar in their relative importance between the biological and the physiochemical models, the order in which they affect the two groups of variables changed (Fig. S5). In Figure 6, we can see that resistance and resilience tended to go in the same direction when considering all response variables. However, underlying antagonistic, or opposing effects on the resistance and resilience of the two groups of variables and independently within the physiochemical group of variables are driving some of the uncertainty and nonlinear dynamics, we see in Fig. 6. Antagonistic effects on the resistance and resilience of the two

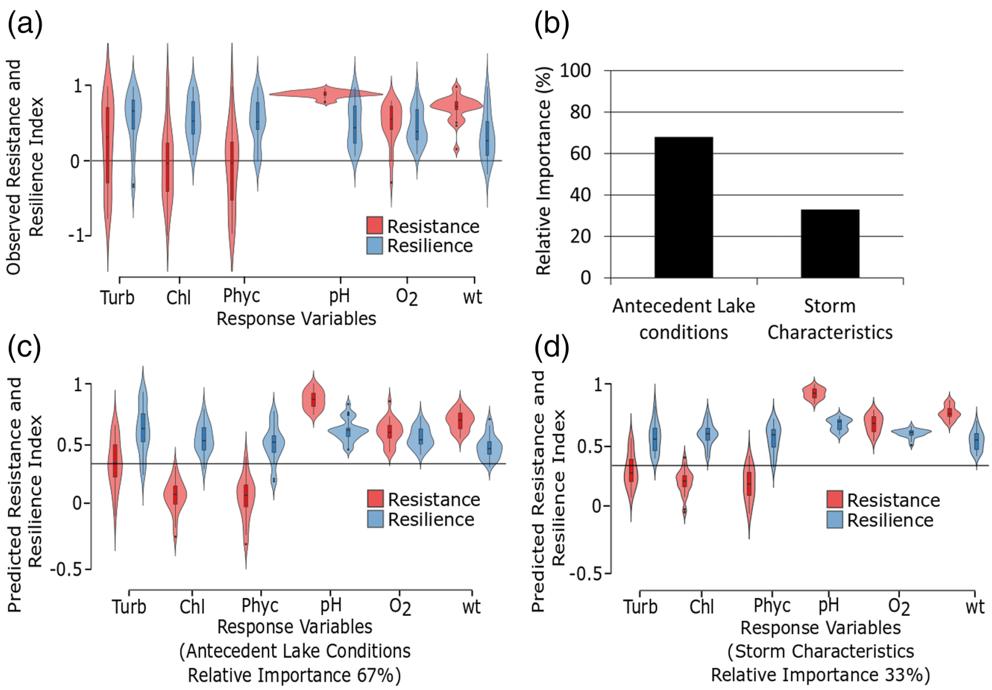

Fig. 5. Observed lake ecosystem resistance and resilience is given in (**a**). (**b**) The rescaled percent relative importance of antecedent conditions and storm characteristics, while the results from the antecedent lake condition predictions and storm characteristic predictions are given in (**c**) and (**d**), respectively. The indices are interpreted in terms of percent change where 0 represents either 100% change regarding resistance, or 0% recovery regarding resilience. (**c**) and (**d**) The predicted lake ecosystem resistance and resilience (quantified on a standardized scale from −1 to 1), relative to each of the response variables. The violin plots are box plots which are surrounded by kernel density distributions which give the probability of resistance and resilience following a storm for each of the response variables. The predictions made using the antecedent lake conditions suggests that the conditions prior to the storm hitting were relatively more important than the storms characteristics themselves. The black line in (**a**) shows at which point storms were causing more than 100% change/0% recovery, while in (**b**) and (**c**) it represents the median resistance and resilience across the individual predicted indices.

groups of variables were identified for both antecedent lake conditions and storm characteristics, which include the effects of $\%O_2$ saturation, water temperature, pH, soluble reactive silica, total nitrogen, storm duration, day of the year, and the year in which the storm took place. Antagonistic effects between resistance and resilience within the physiochemical variables were present as a result of antecedent total phosphorus, mean precipitation, and wind direction.

Antagonistic effects resulting from varying antecedent $\%O_2$ saturation suggests that when saturation levels were greater than 100% resistance and resilience of the physiochemical environment increased, while the biological resistance and resilience decreased (Fig. 7). Surface water temperatures greater than 15°C resulted in increased resistance and resilience of the biological variables and vice versa for the physiochemical variables, suggesting that increased water temperatures increases the biological variables' (i.e., algal conditions) ability to recover from storm-induced effects (Fig. 7). Antecedent pH conditions led to antagonistic effects between the groups of variables and suggest that increasing pH levels decreases the resistance and resilience of the physiochemical environment, while resistance and resilience of the biological conditions increased with increasing pH (Fig. S6). Storm durations over 100 h resulted in decreased resistance and resilience of the biological variables, while it increased the resistance and resilience of the physiochemical variables, which suggests that long-duration mixing homogenizes the physiochemical environment resulting in increased resistance and resilience (Fig. 7). Seasonality led to antagonistic effects with spring to early summer conditions increasing the resistance and resilience of the biological variables and vice versa for the physiochemical variables (Fig. S6). Lastly, during the time series, the lake experienced a step change in conductivity in 2012 and decreased turbidity conditions after 2013. Changes in conductivity and turbidity may have led to differences in how the two groups of variables respond to storms, with biological resistance and resilience decreasing after 2013 and vice versa for the physiochemical variables (Fig. 7; *see* Fig. S6 to see all antagonistic effects which are not shown in Fig. 7).

Antecedent total phosphorus, mean precipitation, and wind direction drove the resistance and resilience of the physiochemical variables in different directions, while the resistance and resilience of the biological variables were driven in the same direction (Fig. 8). Increasing antecedent total phosphorus led to increased resistance and decreased resilience, which when compared with the combined indices

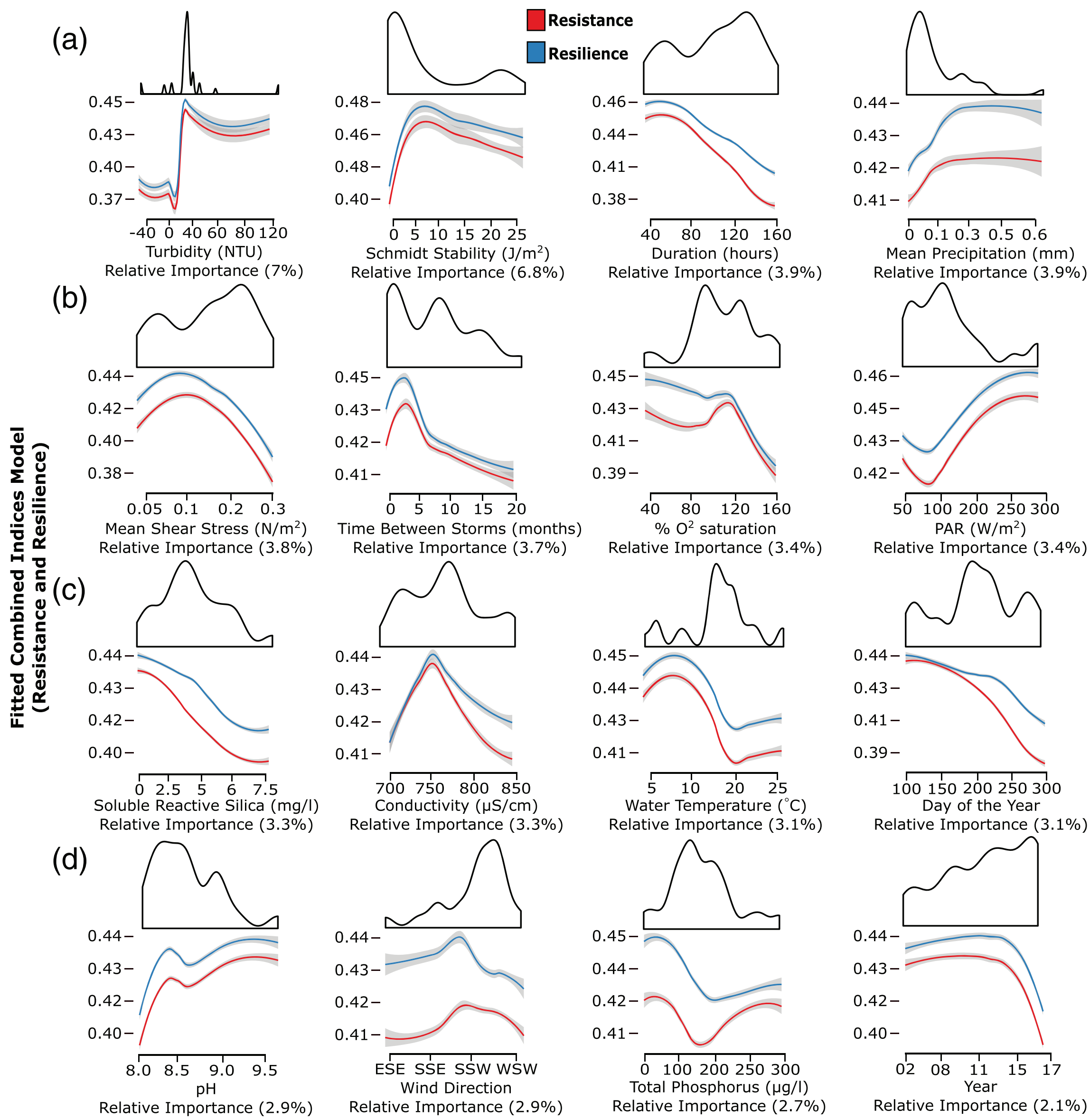

Fig. 6. Line graphs show partial dependence of both the physiochemical and biological (i.e., combined indices model) resistance (RS = red line) and resilience (RL = blue line) (quantified on a standardized scale from −1 to 1), relative to antecedent lake conditions and storm characteristics. The graphs are in order of importance (see percentages) based on the variable on the *x*-axis. The gray-shaded area around the lines is the standard error or the uncertainty surrounding the predicted median. The density plots above each line graph show the distribution of each antecedent lake condition or storm characteristic along the *x*-axes. For example, most storms hit Müggelsee when Schmidt stability was low and relatively few storms hit during high Schmidt stability. Thus, the rapidly increasing relationship in resistance and resilience depicted in the associated line graph is most robust due to the richness of data over those ranges of Schmidt stability. Only total nitrogen is not shown due to low importance (1.9%).

model suggests that the decreased resilience in the physiochemical environment is driving that pattern (Figs. 6 and 8). Similarly, the increased resistance and resilience in the combined indices model as a result of increased mean precipitation is primarily being driven by the resistance in the physiochemical environment (Figs. 6 and 8). In relation to wind direction, there is not any clear picture drawn from the combined indices model (Fig. 6), but here we find that wind directions from less frequent directions decreased the resistance of the physiochemical variables and increased resilience (Fig. 8). Those storms coming from less frequent directions are also those that were the shortest in duration, which suggests why the physiochemical environment would recover quicker under those conditions. Resistance and resilience of the biological variables decreased when storms came from less frequent wind directions (Fig. 8). However, it seems changes in wind direction are mostly driving lake resistance dynamics (Fig. 6).

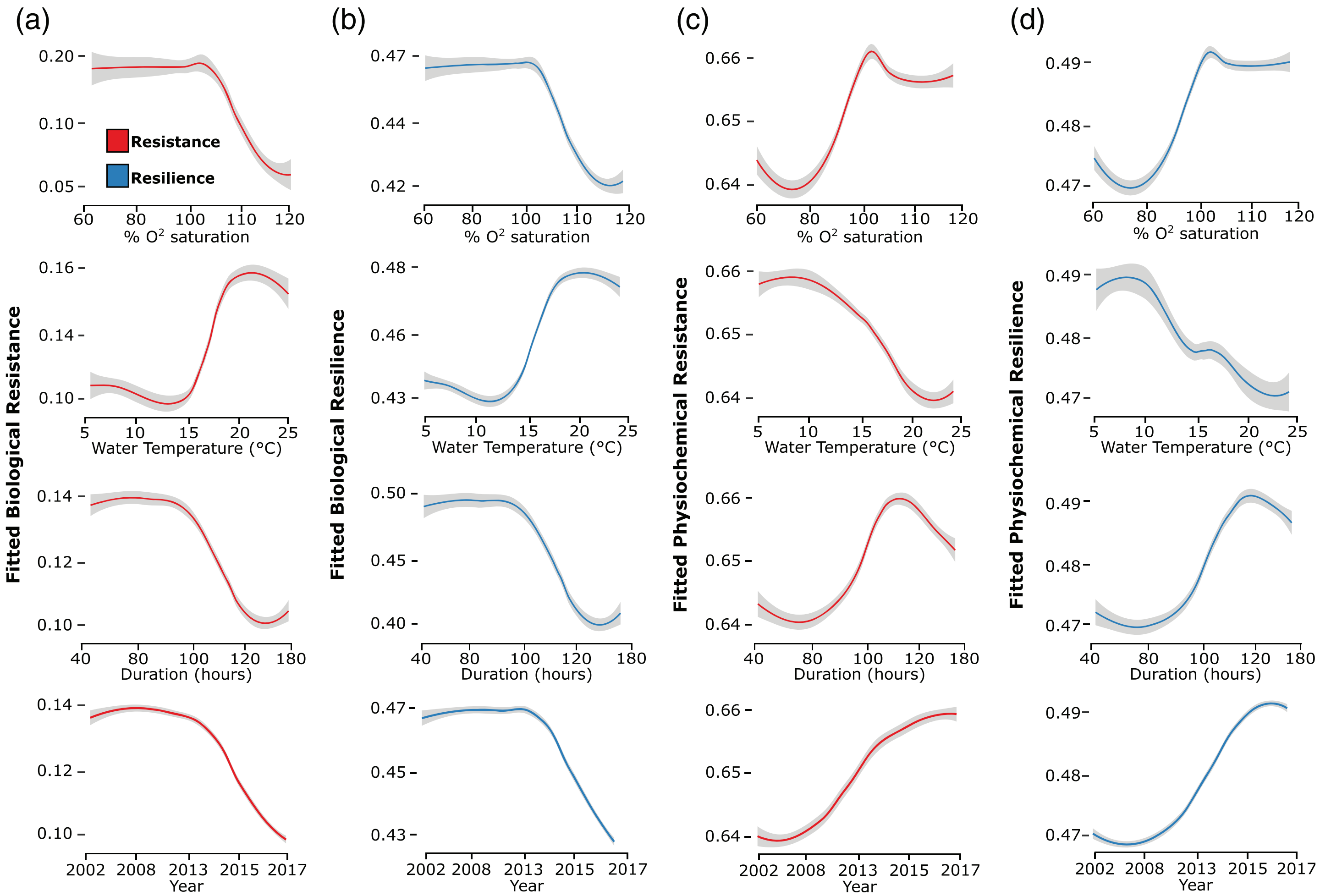

Fig. 7. The partial dependency plots (quantified on a standardized scale from −1 to 1), in columns (**a**) and (**b**) show the marginal effects of antecedent lake conditions and storm characteristics on the resistance and resilience of the biological variables, while columns (**c**) and (**d**) show the marginal effects in relation to the physiochemical variables. In the figure, we see the resulting effects of %O_2 saturation, water temperature, duration, and year in which the storm took place. When comparing the two groups of variables we can see that there are antagonistic effects on the resistance and resilience of the two groups of variables. For example, %O_2 saturation above 100% increases resistance and resilience of the physiochemical variables, while the resistance and resilience of the biological variables decreases.

Discussion

We identified 25 extreme wind storms and analyzed their effects on the resistance and resilience of Müggelsee, a shallow, polymictic lake ecosystem in Berlin, Germany. We then determined if storm characteristics or antecedent lake conditions were more important in describing the lake's ability to be resistant and resilient following the analyzed storms. Although storms analyzed produced high wind speeds which suspended sediment, and were accompanied by varying levels of precipitation, we found that antecedent lake conditions were more important than the storms' frequency, duration, and intensity (Fig. 5). The most important antecedent lake conditions affecting lake ecosystem resistance and resilience following the storms were antecedent turbidity conditions and level of thermal stratification followed by %O_2 saturation, light conditions, silica concentrations, conductivity, and water temperature (Fig. 6). In relation to storm characteristics, we found that storm duration was the most important followed by mean precipitation, mean shear stress, and storm frequency (Fig. 6). Here, we focus on the lake conditions and storm characteristics which were found to be the most influential for determining the lake's resistance and resilience. Throughout the discussion, resistance, and resilience are discussed in tandem because the varying biological and physiochemical resistance and resilience values tended to vary together (Fig. 6). This does not mean that resistance and resilience of the physiochemical and biological variables were always affected in the same direction (Figs. 7 and 8), but that the lake showed higher—or lower—probabilities for being both resistant and resilient under certain conditions. We further found that results from the models which consider the lake's biological and physiochemical resistance and resilience

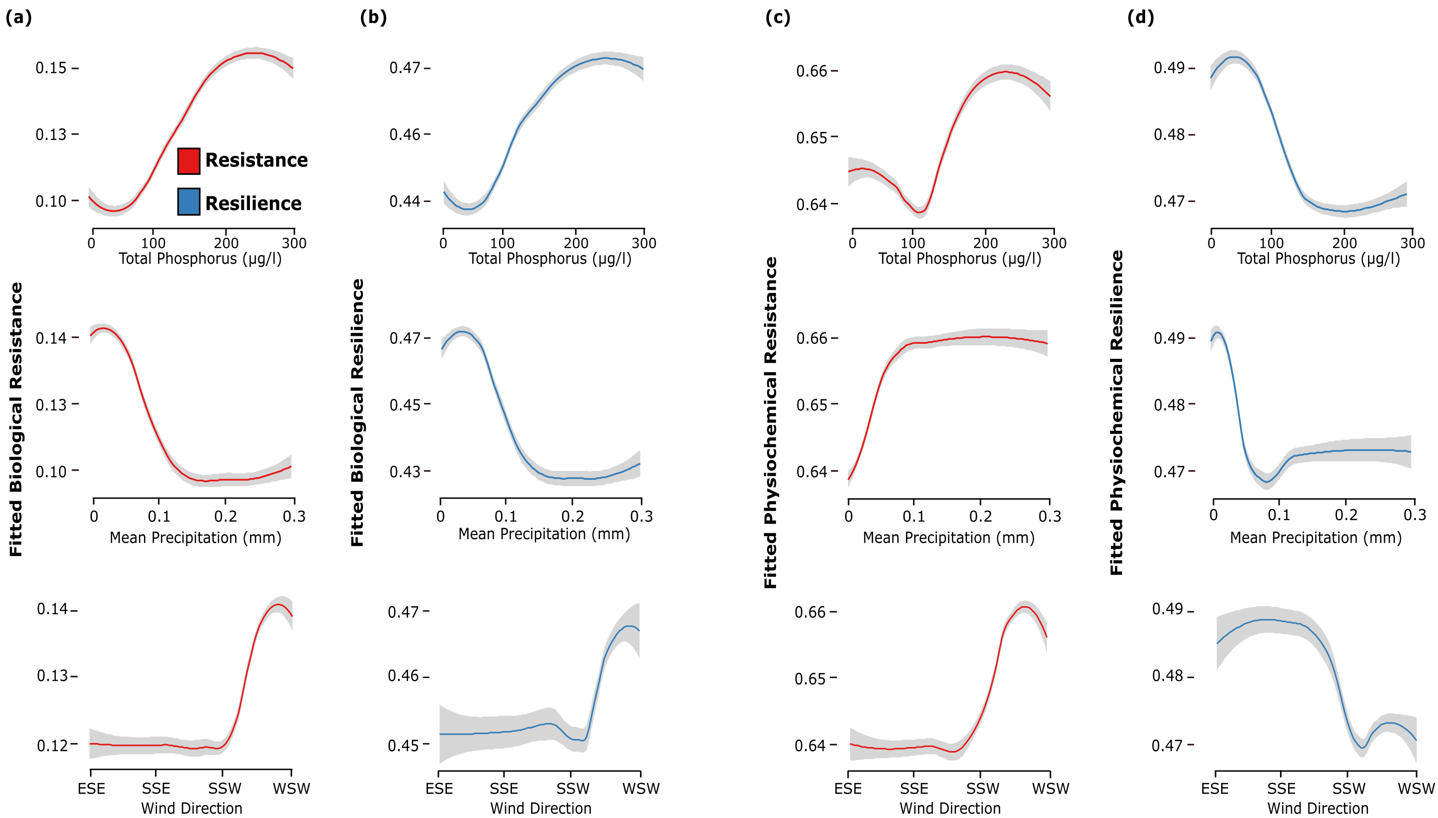

Fig. 8. The partial dependency plots (quantified on a standardized scale from −1 to 1), in columns (**a**) and (**b**) show the marginal effects of antecedent lake conditions and storm characteristics on the resistance and resilience of the biological variables, while columns (**c**) and (**d**) show the marginal effects in relation to the physiochemical variables. In the figure we see the resulting effects of total phosphorus, mean precipitation, and wind direction. When comparing the two groups of variables we can see that the resistance and resilience of the biological variables are driven in the same direction, while there were antagonistic effects on the resistance and resilience of the physiochemical variables as a result of these antecedent lake conditions and storm characteristics.

independently, suggest that antecedent lake conditions and storm characteristics leading to antagonistic effects on the resistance and resilience of the two groups of variables, respectively, is driving some of the nonlinear dynamics we see in the combined indices model (i.e., model combining both physiochemical and biological variables) (Figs. 6, 7, and 8). Lastly, it is important to note that the results also suggest that the lake ecosystem is less resistant and resilient to storms of increasing duration and intensity.

Lakes are often simultaneously disturbed by natural- (e.g., from storms, droughts, and floods) and human-induced impacts (e.g., from urban, agriculture, and other nonpoint sources of pollution) which are likely interacting to determine antecedent lake conditions (Huber et al. 2008; Kuha et al. 2016; Perga et al. 2018). In the case of Müggelsee, the results suggest variability in antecedent biological and physicochemical dynamics such as turbidity, Schmidt stability, % O_2 saturation, and light conditions are affecting Müggelsee's ability to resist and recover from storm driven changes (Figs. 6 and 7).

Antecedent lake conditions

Antecedent turbidity conditions were found to be the most important lake condition shaping resistance and resilience of the lake. Being a eutrophic lake, antecedent turbidity is primarily driven by algal conditions in the lake, especially through mid to late summer. However, at certain times of the year, primarily in spring and fall, the lake can experience sediment resuspension which can also drive antecedent turbidity conditions (Kozerski and Kleeberg 1998). Changes in turbidity conditions are generally the primary effect of a wind storm blowing over a shallow lake that is prone to resuspension. The results suggest that the lake was more resistant and resilient under turbid rather than clear antecedent conditions. However, if the lake is already turbid, for example as a result of high algal biomass, any sediment that is suspended as a result of a storm is mostly negligible and not the primary driver of the water column dynamics. Therefore, higher turbidity as a result of increased algal biomass increases the resistance and resilience of the lake's physiochemical variables (Figs. 6 and 7). On the other hand, when a lake is in a clear water phase, it is more susceptible to storm induced turbidity through sediment resuspension. In cases where shear stress is indeed high enough to resuspend sediment, the likelihood that the storm will temporarily change the state of the lake from clear to turbid increases. Therefore, a clear lake would be less resistant to changes in turbidity, whereas even if resilience is affected, it is primarily related to the resettling of sediment. Previous work found that extensive macrophyte coverage can provide enhanced resistance and resilience to turbidity resulting from a storm (Ibelings et al. 2007). However, since antecedent turbidity conditions are dependent on algal biomass and considering algal metabolic processes like photosynthesis and nutrient consumption, exploring how changes in $\%O_2$ saturation and soluble reactive silica are linked with the resistance and resilience of the lake ecosystem can be insightful.

Whether the lake was resistant and resilient following the storm was partially dependent on whether antecedent $\%O_2$ saturation was above or below 100% (Figs. 6 and 7). Oxygen saturation levels in the lake are driven by a number of factors including seasonal driven changes in water temperature and stratification, atmospheric diffusion, and primary production (Fondriest Environmental Inc. 2013). Storms were more likely to increase $\%O_2$ saturation when the antecedent level was below 100% while storms tended to decrease $\%O_2$ saturation when antecedent levels were above 100% (Figs. 3 and 7). Changes in antecedent $\%O_2$ saturation levels below 100% that are enhanced by a storm can partially be explained by the increased gas exchange at the atmosphere-water interface due to waves, which also partially shapes the resistance and resilience of the lake under such saturation conditions. On the other hand decreases in $\%O_2$ saturation levels above 100% can partially be explained by diffusion of O_2 into the atmosphere as a result of an oversaturated system. Oxygen saturation levels above 100% led to increased resistance and resilience of the physiochemical environment, which is a strong indication that metabolic processes are to some extent engineering water column dynamics before and after the storms. In relation to the biological variables, resistance and resilience decreased with antecedent $\%O_2$ saturation levels above 100%, which makes sense, as we would expect higher algal biomass to be displaced and/or reduced under such conditions. At the lake ecosystem level (i.e., model combining both physiochemical and biological variables) we see that resistance and resilience decreased with $\%O_2$ saturation above 100%, which suggests that when a bloom is present that resistance and resilience of the lake is largely determined by biological rather than physiochemical processes following a storm (Fig. 6).

Antecedent soluble reactive silica concentrations, a proxy for diatom biomass, were also found to be an important antecedent lake condition shaping the resistance and resilience of the lake. Siliceous lake sediments have been used in paleoenvironmental studies to infer changes in historical storminess periods spanning hundreds of years, which provides some indication that silica concentrations are sensitive to changes in regional storm patterns (Krawiec and Kaufman 2014). Silica concentrations in Müggelsee are primarily driven by seasonal variation, sedimentation and become more bio-available in the water column through wind driven mixing in spring and fall (Köhler and Nixdorf 1994; Kozerski and Kleeberg 1998; Sommer et al. 2012). Concentrations of silica may represent whether the lake was well mixed with cool water temperatures and low diatom biomass (i.e., high concentrations of soluble silica prior to the storm), or when a diatom bloom was present (i.e., low to moderate concentrations of soluble silica) (Saunders et al. 2009; Ngupula et al. 2014). In our study, we found that mixed conditions (i.e., high concentrations of silica) was linked to storm driven decreases in the resistance and resilience of the lake ecosystem (Fig. 7). However, silica concentrations had antagonistic effects on the biological and physiochemical variables respectively (Fig. S6). Resistance and resilience of the lakes physiochemical conditions tended to increase with low to moderate concentrations of silica (i.e., when a diatom bloom was present), while the opposite was found for the biological conditions (Fig. S6). This confirms the strong linkage of the lake's diatom community to antecedent thermal conditions, in a way which reduces the impacts of a storm and increases the lake's ability to recover to its pre-storm physiochemical structure. Spring blooms in Müggelsee, mostly dominated by diatoms, have been shown to have a direct effect on the transparency, stratification length, and thermal dynamics of the lake (Shatwell et al. 2016). We found that spring to early summer time conditions, the presence of stratification, and moderate concentrations of silica leads to a higher probability of the biological and physiochemical lake conditions to be more resistant and resilient following the storms (Figs. 6 and S6). The study conducted by Shatwell et al. (2016) provides some indication to why silica is an important antecedent condition influencing the recovery of the lake's physiochemical environment, at least as it pertains to spring time storms and lake conditions. However, many interacting effects are possible when relating the effects of storms on an algal community. High antecedent algal biomass can lead to light limitation (Rinke et al. 2010; Shatwell et al. 2016), which is exacerbated by suspended sediments, potentially leading to decreasing biomass. On the other hand, antecedent algal communities with low biomass may not be light, but nutrient limited and could benefit from any increase in nutrients (i.e., silica and/or phosphorus) as a consequence of resuspension (Figs. 8 and S6). For example, phycocyanin (i.e., cyanobacteria) may benefit from an increase in other nutrients such as phosphorus or nitrogen as a result of resuspension, which may increase the resilience of the cyanobacteria community following a storm (Shade et al. 2012). Similarly, diatom community composition may be leading to different resistance and resilience responses due to functional groups having adaptations related to chemical gradients, uptake of nutrients, position in the water column, or light harvesting, which are all affected by antecedent lake conditions and storms (Saunders et al. 2009; Krawiec and Kaufman 2014; Ngupula et al. 2014). Saunders et al. (2009) found that the two most important predictors of diatom abundance across nutrient and chemical gradients of 50 coastal and inland lakes were conductivity and pH, both of which were found to be relatively important in shaping lake ecosystem resistance and resilience (Figs. 5 and 6).

The resistance and resilience of the lake were partially shaped by antecedent conductivity and pH conditions (Figs. 6 and S5). Lake pH and conductivity dynamics are determined by similar factors such as hydrogeological processes, lake size relative to watershed size, point, and nonpoint sources of pollution and atmospheric inputs (Eilers et al. 1983; Fondriest Environmental Inc. 2013, 2014; Pal et al. 2015). Additionally, pH variability is being driven by seasonal variation in water temperature and stratification, and phytoplankton biomass. While these variables are important for the resistance and resilience of the lake, it is difficult to isolate a single mechanism, or interaction that determines the pH and conductivity of a water body. Müggelsee's conductivity, while continuously high through the time period we consider, made a shift from an average of 725 ± 40.6 (μS/cm) between 2002 and 2012 (storms; $n = 14$), to 819 ± 45 (μS/cm) between 2013 and 2017 (storms; $n = 11$). The shift in mean conductivity was caused by gradual increases in sulfates in the lake as a result of groundwater infiltration into the river Spree containing old mine tailings (Graupner et al. 2014). The results suggest that the resulting increase in average hourly conductivity led to a greater likelihood of storm induced effects on the resistance and resilience of the lake ecosystem. While it is unclear which processes pH and conductivity are affecting, their overall importance in maintaining stable metabolic states, influence on various life stages of aquatic organisms, and roles in the cycling of nutrients is most likely why they are an important component of lake ecosystem resistance and resilience following storms (Caraco et al. 1993; Fondriest Environmental Inc. 2014).

Storm characteristics

Low antecedent turbidity conditions and high shear stress levels from less frequent wind directions led to higher probabilities of low resistance and resilience (Fig. 6 and S5). Turbidity conditions during the time series analyzed shifted from a mean of 1.7 ± 1.2 (NTU) between 2002 and 2012 (storms; $n = 14$), which decreased to a mean of 0.4 ± 1 (NTU) between 2013 and 2017 (storms; $n = 11$). The shift in turbidity conditions of the lake also coincides with decreasing trends in chlorophyll *a* and phycocyanin levels. The results suggest that the shift toward a more clear water state led to higher probabilities of the lake's physiochemical environment to be more resistant and resilient following storms. Wind frequently blows from the west to south west (Fig. 2), which likely results in lateral deposition of sediment in more sheltered areas of the lake, which sets the stage for resuspension when storms come from less frequent directions (Figs. 2 and S5). The storm, however, would need to be long enough in duration and high in shear stress intensity to see a subsequent impact on the lake's ability to be resistant and resilient following the storm. However, the extent to which the storm affects the overall turbidity conditions, as stated prior depends on the antecedent turbidity conditions (i.e., the presence of an algal bloom or not). With the shift to more clear antecedent conditions the likelihood of resuspension does not increase, but the likelihood that resuspension events play a greater role in changing turbidity conditions likely does increase. In addition to duration, shear stress, and wind direction, the resistance and resilience of the lake were equally influenced by mean precipitation and storm frequency (Figs. 6 and 7).

While climate change is expected to change the regional patterns in storms (IPCC 2012), a dramatic change in the average wind direction is mostly transitive, meaning that if the average wind direction changes to what is now a less frequent direction, we speculate that the impacts will only last until sediment has been deposited elsewhere in the lake. Furthermore, it is unlikely that single pulse storm disturbances are able to change the overall long-term state of a lake. Only in rare examples have lakes shifted in functional states (e.g., clear to turbid) as a result of a single, short lived weather event (Bachmann et al. 2005; Gaiser et al. 2009). However, compounded extreme storm events that previously tended to be rare are becoming more frequent as a result of climate change, making long-term effects and regime shifts more probable (Paine et al. 1998; IPCC 2012; Havens et al. 2016). According to resilience theory, a higher frequency of disturbances is expected to have longer-term consequences for the resilience of an ecosystem due to the overlapping of storm impacts (Paine et al. 1998). Here, we found the opposite, the greater the time-interval between storms, the greater the effect of the storm on the resistance and resilience of the lake ecosystem (Fig. 7). However, the results also show that there were partial antagonistic effects as a result of time accrued between storms, which suggest resistance and resilience of the biological variables sharply decreased with decreasing time between storms (Fig. S6). While mean precipitation was found to be the second most important storm characteristic, we mention it last as there is more uncertainty surrounding how it effects lake ecosystem resistance and resilience. In Fig. 6, we see that increasing mean precipitation increases the resistance and resilience of the lake ecosystem, however, this pattern is largely being driven by the high resistance of the physiochemical variables (Fig. 8), and the fact that many of the storms were not accompanied by high levels of precipitation. It is more likely that increasing mean precipitation decreases the resistance and resilience of the lake ecosystem under mean lake conditions (Fig. 8). Regardless of the primary effect, precipitation was found to be strongly influencing the resistance and resilience of the lake lending further evidence that storms accompanied with moderate to high levels of precipitation have a strong influence on maintaining a clear or turbid state (Bachmann et al. 2005; Gaiser et al. 2009).

Results suggest that if storms simultaneously (1) become longer in duration, (2) are accompanied by higher levels of precipitation, and (3) increases in intensity, the likelihood of storms impacting the resistance and resilience of the lake will increase. However, duration of storms had an antagonistic effect on the biological and physiochemical variables independently. Physicochemical variables increased in resistance and resilience following long duration storms but vice versa for the biological variables. Given the strong role of antecedent lake conditions and their potential interactions with storm characteristics in determining the resistance and resilience of the lake, and the fact that lake conditions and storm characteristics vary locally and regionally, the way in which a particular lake responds to extreme wind storms likely depends on size, depth, trophic state and stratification regimes (Jones et al. 2008, 2009; Stockwell et al. 2020).

Conclusion

Antecedent lake conditions and storm characteristics play a critical role in shaping a lake's ability to be resistant and resilient following extreme wind storms. However, changes in baseline antecedent lake conditions such as in turbidity, stratification, %O_2 saturation, soluble reactive silica, water temperature, conductivity, and pH may be more important for driving lake ecosystem resistance and resilience following storms. Enhancing lake ecosystem resistance and resilience following storms may be partially accomplished by controlling anthropogenic inputs which affect the lake's transparency and chemical dynamics. However, while near-term management strategies may enhance lake ecosystem resistance and resilience, there is nothing that can manage the increasing duration, precipitation, and frequency of storms except slowing the rate of global climate change. Further research in the area of resistance and resilience is promising for increasing our understanding of how different ecosystems respond to extreme disturbances of different types in varying conditional states (Pimm et al. 2019).

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Acknowledgments

We would like to first acknowledge the funding received from Marie Sklodowska-Curie Actions (Marie Skłodowska-Curie grant agreement no. 722518) and EU-ITN MANTEL project which made this research possible. Benjamin M. Kraemer and Rita Adrian acknowledge the 2017-2018 Belmont Forum and BiodivERsA joint call for research proposals under the BiodivScen Era-Net COFUND program and with funding from the German Science Foundation (AD 91/22-1). In addition, we acknowledge the work carried out by Kerstin Reinsberg (Doctoral Degree and Habilitation Office at the Freie Universität Berlin) and Markus Edler (Dahlem Research School at the Freie Universität Berlin) in negotiating the contract for Michael Thayne to receive a European Joint-Doctorate Degree from Freie Universität Berlin and the University of Geneva. We would also like to thank colleagues at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB) whom job it is to collect, maintain, and preserve the data collected from the lake. Lastly, we would like to acknowledge both big and small contributions from colleagues from the Leibniz-Institute of Freshwater Ecology and Inland Fisheries, and University of Geneva for contributing their knowledge and expertise in furthering this research.

Conflict of interest

None declared.

Submitted 01 December 2020
Revised 19 April 2021
Accepted 17 May 2021

Deputy editor: Julia C. Mullarney