The determination of critical processes shaping lake ecosystem resistance and resilience following extreme storms

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Müggelsee High Frequency Lake Monitoring Station During Storm Xavier 2017

Photo captured by IGB webcam ©

This dissertation was conducted at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries between October 2017 through March 2022 under the supervision of Prof. Dr. Rita Adrian, a faculty member of the Department of Biology Chemistry and Pharmacy at the Freie Universität Berlin, and Prof. Dr. Bastiaan Ibelings, a faculty member of the Department F.-A. Forel for Environmental and Aquatic Sciences at University of Geneva. The research was conducted under a cooperation agreement between the Freie Universität Berlin and University of Geneva as part of a European International Training Network. The disputation took place on October 26, 2023 at the Freie Universität Berlin. Furthermore, intellectual property of other authors has been marked accordingly. I also declare that I have not applied for an examination procedure at any other institution and that I have not submitted the dissertation in this or any other form to any other faculty as a dissertation.

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Declaration of Independence: Herewith I certify that I have prepared and written my thesis independently and that I have not used any sources and aids other than those indicated by me.

This cumulative dissertation is based on the following two publications:

1. **Thayne**, M. W., Kraemer, B. M., Mesman, J. P., Ibelings, B. W., & Adrian, R. (2021). Antecedent lake conditions shape resistance and resilience of a shallow lake ecosystem following extreme wind storms. *Limnology and Oceanography*. https://doi.org/10.1002/lno.11859 (Special Issue: Non-linear dynamics, resilience, and regime shifts in aquatic communities and ecosystems)

Own contribution to this publication: compiled and processed high frequency data, co-developed methods and R-code for analyzing the data, and wrote the manuscript.

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“This grand show is eternal. It is always sunrise somewhere; the dew is never all dried at once; a shower is forever falling; vapor ever rising”

-John Muir

And the river is always roaring and the lake is always calling. This dissertation is dedicated to nature and its unending bounty of love and acceptance. As a young boy of eight years old I would spend my days after school fly fishing in the cool swift waters of the Provo River in Utah. My father would drop me off and then go back to work after planning a pick-up time and spot on the river. It was these years of my life that I grew a strong connection to nature and especially to water. The fish taught me about currents and the seasonal patterns of aquatic insects. While the changing seasons and river flows taught me the water cycle. My experiences in nature is what drew me to science as it allowed me to explore my curiosities about nature and its complexities. And so, I want to thank my father for teaching me the art of fly fishing and allowing me to immerse myself into nature and develop the curiosities that have brought me to writing this dissertation. I want to acknowledge his support throughout my academic career. Without his support I would not have gone to Iceland where I met the most supportive and important person in my life, my wife Sophie Thayne. Thus, I would like to acknowledge her for her unwavering love and support for me, and the two humans we brought into this world while conducting this work. In that light I would like to acknowledge my mother-in-law Steffi Berthold for being the best Oma and helping free up time for me to finish my PhD. Lastly, I want to acknowledge the professors, senior scientists, and mentors who have taken a chance on me and allowed me the freedom to explore my curiosities. The list is long, but since I am here at this stage, I would like to acknowledge Dr. Rita Adrian, my doctor mother, for giving me this opportunity.

Table of Contents

Summary

Climate change is impacting the timing, frequency, intensity and duration of extreme storms worldwide, and the susceptibility of lake ecosystem resistance and resilience to changing storm dynamics is mostly unknown. The development of a systematic, standardized and quantitative methodology for synthesizing resistance and resilience following storms could be useful for predicting future impacts of extreme storms. Furthermore, the development of such methodology could perhaps help identify management strategies that work in conjunction with lakes to optimize physiographic specific processes which enhance resistance and or resilience following extreme storms. Therefore, the central goal of this thesis was to develop a systematic, standardized and quantitative methodology (i.e. Chapter 1) that allowed for the synthesis of resistance and resilience of multiple ecosystems (i.e. Chapter 2) relative to long-term (non-transitory) and short-term (transitory) lake and storm conditions. We developed an approach which incorporates high frequency limnological and meteorological data into boosted regression tree models to determine the hierarchical importance and partial dependency of lake characteristics and storm conditions in shaping lake ecosystem resistance and resilience. The results presented in this thesis provide a comprehensive view of the methodology we developed to disentangle and determine the critical lake processes that shape lake ecosystem resistance and resilience following extreme storms.

Zusammenfassung

Der Klimawandel wirkt sich weltweit auf den Zeitpunkt, die Häufigkeit, die Intensität und die Dauer extremer Stürme aus, und die Widerstandsfähigkeit und Resilienz von Seeökosystemen gegenüber der sich verändernden Sturmdynamik ist weitgehend unbekannt. Die Entwicklung einer systematischen, standardisierten und quantitativen Methodik zur Synthese von Resistenz und Widerstandsfähigkeit nach Stürmen könnte für die Vorhersage künftiger Auswirkungen extremer Stürme nützlich sein. Darüber hinaus könnte die Entwicklung einer solchen Methodik dazu beitragen, Managementstrategien zu identifizieren, die in Verbindung mit Seen physiografisch spezifische Prozesse optimieren, die die Resistenz und/oder Widerstandsfähigkeit nach extremen Stürmen erhöhen. Das zentrale Ziel dieser Arbeit war daher die Entwicklung einer systematischen, standardisierten und quantitativen Methodik, die eine Synthese der Resistenz und Widerstandsfähigkeit verschiedener Ökosysteme in Bezug auf langfristige (nicht vorübergehende) und kurzfristige (vorübergehende) See- und Sturmbedingungen ermöglicht. Wir haben einen Ansatz entwickelt, der hochfrequente limnologische und meteorologische Daten in verstärkte Regressionsbaummodelle einbezieht, um die hierarchische Bedeutung und partielle Abhängigkeit von Seemerkmalen und Unwetterbedingungen bei der Gestaltung der Resistenz und Widerstandsfähigkeit von Seeökosystemen zu bestimmen. Die in dieser Arbeit vorgestellten Ergebnisse bieten einen umfassenden Überblick über die von uns entwickelte Methodik zur Entflechtung und Bestimmung der kritischen Seeprozesse, die die Resistenz und Widerstandsfähigkeit von Seeökosystemen nach extremen Stürmen beeinflussen.

General Introduction

Observations from the field

Working as a range-trend biologist in the southwestern United States gave me a unique opportunity to interact with nature. Identifying plants can be one of the more intimate practices a scientist can experience. All plants go through stages of growth and evolution through a single season, which makes identifying them a complicated task at times. Most grasses, for example, as they emerge from the ground in spring look strikingly similar, which takes a trained practitioner to identify individual species, often growing side by side. The botanist develops unique ways to identify plants. First and always are using key identifying features; shape of the blade/leaf, number of veins, or the most important, is there a seed head, or flower present. However, if the botanist is stumped they will employ other senses such as the smell, taste or feel. And when those fail they can turn to the soil it is growing in, and/or what other plants are growing nearby. The reason I point this out in the introduction of my dissertation is that nature has a way of creating functional redundancy in ecosystems to the point that is sometimes difficult to differentiate species. It’s the redundancy that makes many believe that ecosystems are mostly unchanging, or return to what they were. When one species disappears, there is one that looks strikingly similar and performs similar functions, but the underlying processes and relationships of the ecosystem may have changed.

One day working with a senior range-trend biologist on a vegetation transect in Utah proved to be one of the most powerful moments in my scientific career in furthering my understanding of; 1) how much ecosystems can change in relatively shorts amount of time, and 2) the power of long-term data collection. I can remember the day quite clearly, as my supervisor had found an exquisite obsidian arrow head laying in the sand along his transect. As we were identifying plants a rancher on horseback rode upon us with several cattle dogs. In the Western United States there is large swaths of public land where cattle associations, an organized group of ranchers, are allowed to graze cattle on the land. As he approached us he asked what we were doing. We described to him that we were there as part of a long-term initiative to restore Utah’s sensitive watershed habitat and wildlife wintering ground. He stated to us that he had been grazing cattle in the area for 30 years and very little had changed in terms of the range conditions. That particular transect had close to a decade of vegetation data and geo-located photo documentation. My supervisor asked him to wait a moment and he walked backed to our truck to retrieve a binder with all the photos for the transect.

When my supervisor returned he asked the rancher to come have a look. He slowly turned through the pages of the binder. And as each page flipped the rancher's eyes grew wider and wider with astonishment. The photos told a very different story than what was in the mind of the rancher. In that short time frame of ~10 years many perennial bunch grasses and forbes had been replaced by annual grasses and weeds. The grass and sagebrush had become overgrazed, juniper tree saplings had become juveniles, and the soil around had started to become compact from cow and wild horse trails. In other words that microcosm of the larger ecosystem had changed dramatically in the 10 years data had been collected, and the photos told the story without a single word spoken. While surely cattle and horse grazing played a role in the dramatic change in the landscape, other compounding environmental and weather factors such as pro-longed droughts in the area had not helped the vegetation to recover from summertime cattle and wintertime wildlife foraging. Nonetheless I was left thinking how many times and different biophysical states that little patch of nature had gone through since the Native American dropped that arrowhead on the ground. The rancher didn't say much and got on his horse and left, but I am sure that experience changed his view of the range forever just as much as it did for me.

This story provides an example of how the functional redundancy of nature can trick us into believing nothing is changing. The rancher saw that there was grass, trees, and sagebrush, but after seeing the photos, he likely saw perennial grasses vs. annual grasses, sagebrush vs. unhealthy sagebrush, he saw the changes with his eyes and knows intimately what that means for his livelihood. What I noticed is that the little patch of land had gone from one functional state to another by replacing the biomass that was there with equally as much biomass that would not attract foraging animals. Sagebrush with pokey ends making it difficult for deer and elk to eat, and annual grasses and forbes that have little nutritional value for large ungulates like cattle and horses. The story provides an observational view and understanding of how ecosystems respond to external pressures (Walker et al. 1981, 1997). The little patch of land had adapted to the biological and environmental pressure it was receiving, however, it did not cease to exist and at first glance looked similar to what it once was, but the underlying biophysical structure had dramatically changed.

As humans we tend to look at ecosystems as changing rather slowly. The water in the lake we swim in seemingly never changes and there is always waves on its surface. The forest we walk through always has trees and the wind is always blowing. However, we take for granted that these seemingly unchanging ecosystems are constantly adapting (i.e. changing) to maintain structure and functionality, and are in fact in a constant state of change. The lake, the moment you left from swimming is not the same lake you come back to. The temperature has changed, the sediment has moved, and countless other bio-physical relationships and interactions have taken place, but yet the next time we come back we dive in and to our skin and eyes nothing has changed. But is it that way because the lake is always returning to what it was, or is it because the lake is always changing to maintain balance, structures and functions?

Lakes, similar to the little patch of land in the desert, are microcosms of their external surroundings and can change rapidly to environmental pressures such as extreme storms (Kasprzak et al. 2017; Calderó-Pascual et al. 2020; Andersen et al. 2020). The location of a lake and its supporting watershed and riverine ecosystems play a critical role in shaping the biophysical dynamics of lake conditions (Stockwell et al. 2020). I further draw on personal experience to draw a picture of the value lakes play in human society and life. Strawberry reservoir, is a 69 km^2 lake with an average depth of 61 m, and is perched at 2,320 m in the Uinta-Wasatch-Cache National Forest in the state of Utah, United States. The lake is a beautiful display of human-made ingenuity and engineering. Despite being a reservoir the lake and the ecosystem it now supports are indispensable for the socio-ecological services it provides to the state of Utah. Fishing in the state has a net worth of 259 million U.S. dollars, of which 30% is directly linked to fishing activities at Strawberry reservoir (Salt Lake Tribune 2013). While its economic value is important, the lake supports a thriving ecosystem, where it serves as a resting and feeding lake for migrating birds, beaver lodges and damns dot the lake and river banks, and bears and other wildlife can be seen cruising its shores.

Working as a fisheries biologist for two summers on Strawberry gave me a unique opportunity to see how science, and the biases of biologists can play out in the management of an ecosystem. However, this story is about the creel surveys we conducted to gauge the health of the game fish population and economic value of the lake. The surveys started at randomly designated starting points and times, with the possibility of starting at sunrise. One morning I got the sunrise survey time and found myself at Renegade bay drinking coffee and watching the sunrise. When the official time of sunrise hit I began driving the truck and looking for fisherman along the lake shores, or coming to launch their boats. It was the middle of the week, which were always slow days for fishing, but if there were fisherman they would be at Haws point.

Pulling into the parking lot at Haws point I could see there was a car parked, so I got my survey questions ready and walked down the hill to where I could see two men by a small fire. I greeted them and they were startled and became visibly nervous with my presence, which was the case quite often as people think we are coming to check for illegal activities. I stated why I was there and they relaxed. Over their fire was a beautiful hand-crafted tea pot and cups, which for Utah is unusual to see. When I asked where they were from, they hesitated, and one stated they were from Persia. I laughed, and I asked if Persia is still a place? They laughed too and said they were from Iran. After complimenting their tea set, I conducted my survey. At the end of the survey I asked them what the fishing was like where they were from. They proceeded to tell me a story about their home lake. While the name of the lake now escapes my mind, the men both spoke with great passion about their lake. They described to me how the lake used to support many fish and it was tradition for people to fish with nets on the lake. Over the years the lake became polluted and dams were built on its tributaries. Eventually the external pressures and overfishing with nets made it impossible to reliably catch fish anymore. At the end of their story one man walked to the edge of the lake and pulled his stringer of fish from the water and said with a big smile, this is why your job is important.

Similar to the first story, this experience had a major impact on me as a scientist and gave me a deeper understanding of how delicate our ecosystems are. And that while extremely resistant and resilient to change, with enough external pressure lakes can become like that little patch of land in the desert. Despite looking like the same lake, the underlying biophysical structure had changed, and just like the patch of rangeland to the foraging animals, the lake had become undesirable to those men, and to an extent lost its socio-ecological purpose. As we continue through the Anthropocene epoch, lake ecosystems are going to continue to be pressed to their limits via human induced and natural disturbances. Lake ecosystems face a wall of challenges in the future, which may impact their underlying biophysical structures, and subsequently affect their ability to be resistant and resilient to internal and external pressures (Thayne et al. 2022). And with environmental pressures such as extreme storms, predicted to become more frequent and intense with climate change, assessing the magnitude of lake ecosystem responses to extreme storms (resistance) and their capacity to recover (resilience) is critical for predicting the future of lake ecosystems (Pimm et al. 2019).

Resistance and resilience of lakes

Resistance and resilience are the theoretical abilities of ecosystems, including lakes to resist and re-establish biological and physiochemical relationships and processes following disturbances (Holling 1973; Pimm 1984; Thayne et al. 2022). To understand dynamic systems, it is often the case that scientists study systems in a perturbed state to better breakdown the mechanics of the system. In lake ecosystems extreme wind storms can act as a strong perturbing force. Thus, researching how lakes respond to extreme storms can help us understand the processes shaping resistance and resilience of lake ecosystems. Or in other words, resistance and resilience are metrics which provide a standardized and quantitative way for evaluating disturbances and the underlying mechanics driving ecosystem responses (Thayne et al. 2022; Patrick et al 2022). While the concepts of resistance and resilience have been around since the 70's, virtually no studies have applied the concepts to naturally occurring disturbances in lakes. Generally, the concepts have been experimental and applied to biological communities of lakes by conducting whole lake manipulations via the introduction and or removal of species, or induced mixing events (Carpenter et al. 2001; Shade et al. 2012a; Stelzer 2022). Such experiments provide general indications of alternative stable states and processes related to the recovery of phytoplankton communities. However, they do not provide an understanding of ecosystem level resistance and resilience, and how they are shaped by continually changing lake and climatic conditions.

Humans have long had impacts on the land and water they inhabit and utilize, respectively (Buscardo et al. 2021). The damning of rivers, use of nutrient rich fertilizers, poor planning of large urban areas, and the manipulation of upstream watershed habitats all effect the functionality of lake ecosystems (Søndergaard and Jeppesen 2007). Most importantly for the work presented here, is those activities can partially shape the resistance and resilience of lakes by influencing their biophysical processes and relationships (Thayne et al. 2022). For example, overland flow produced by heavy precipitation can transport sediment and excess nutrients from agricultural fields, and/or polluted urban areas into nearby waterways, which eventually accumulate in lakes. The result of excess nutrients and pollutants into a lake ecosystem fundamentally changes the biological and physiochemical relationships that determine a lakes trophic status and subsequently the transitory lake characteristics that determine resistance and resilience following extreme storms (Thayne et al. 2022, 2023). In addition to pressing issues such as eutrophication, lake processes important for lake resistance and resilience are additionally shaped and influenced by climate change. Climate change is affecting ice cover, thermal stratification/mixing regimes, and primary productivity of lakes (Woolway et al. 2020). Moreover, climate change is impacting the frequency, intensity and duration of extreme storms worldwide (Webster et al. 2005; Zhang et al. 2013; Lehmann et al. 2015). As we start to list some of the dynamics that maybe shaping resistance and resilience, we quickly see that there are many, and each are having their effect at varying temporal scales and spatial extents (Carpenter et al. 1997). Resistance and resilience are therefore being shaped by non-transitory, or long-term pressing disturbances such as eutrophication and or climate change, which consequently effect more transitory, or rapidly changing lake conditions such as primary production and or thermal stratification. Thus, to measure resistance and resilience in ever-changing lake ecosystems, we merged the two primary theories of resilience, engineering and ecological, to respectively capture how short-term responses to disturbances can be used to determine the importance of both transitory and non-transitory lake conditions (Thayne et al. 2023).

Ecological resilience in basic terms is the ability of an ecosystem to return to what it was, or not following extreme changes in environmental conditions (Holling 1973). Ecological resilience holds the view that ecosystems adapt and change in relation to disturbances, and operate far from any steady state, or global equilibrium. And that systems may undergo catastrophic shifts where the outcome is an alternative stable state (Scheffer et al. 2007). Therefore, ecological resilience recognizes the existence of multiple stable states, which are generally described by the dominant biophysical characteristics of an ecosystem (Gunderson et al. 2000, 2012). For example, in shallow lakes the qualitative differences between clear (i.e. macrophyte dominated) vs. turbid (algae dominated) describe two stable states governed by differing biophysical interactions and processes (Scheffer et al. 1993). Consequently, changes in ecological resilience tend to happen over long-time scales making it difficult to develop metrics to measure the resistance and resilience of one ecosystem state versus another (Müller et al. 2016). On the other hand, engineering resilience views ecosystems in the light of functional design, such that when a system is disturbed it tends to undergo asymptotic recovery to a well-established pre-disturbance global equilibrium to maintain functionality (Pimm 1984; Holling 1996). The longer a system takes to return to its global equilibrium, the less resilient it is following a disturbance. Thus, engineering resilience provides us with clear metrics of how to measure resistance and resilience. Here, we combine these ideas by viewing the lake ecosystem as one that is continually undergoing change through time via non-transitory pressing disturbances such as eutrophication and/or climate change (i.e. ecological resilience), which subsequently drives the short-term variation in transitory antecedent lake processes shaping resistance and resilience following extreme storms (i.e. engineering resilience). Therefore, rather than time to a well-established equilibrium, such as a long term mean, we allowed the control conditions to shift through time based on when an extreme storm occurred. Consequently, we measure resistance and resilience (i.e. lake stability states) relative to the immediate antecedent lake conditions, and whether the lake returned to those conditions, or not. Measuring resistance and resilience this away provides us with a view of how "stable states", which include the terms resistance and resilience (Pimm 1984; Worm and Duffy 2003; Shade et al. 2012b), are being shaped by short term lake dynamics relative to background changes in long-term lake and climate conditions. In short, like a scientist in the lab manually perturbing their system, we allow the extreme storms to be the perturbation of transitory, or short-term lake characteristics, which are being shaped by non-transitory, or long-term trends and regime shifts in lake and climate conditions (Figure 1).

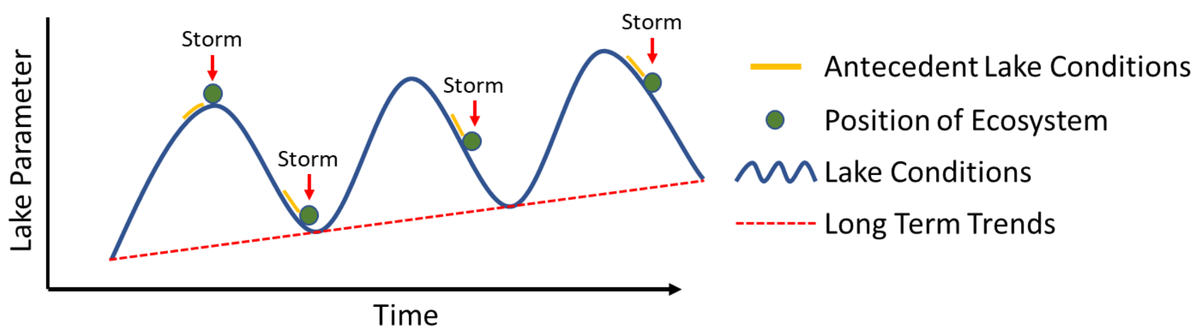

Figure 1. Shows a simple conceptual diagram of how we can combine the theories of ecological and engineering resilience to describe various "stable states", or the resistance and resilience of varying lake parameters (x-axis) through time (y-axis). Lake conditions (blue line) are shaped by interdependent physical and biological relationships, and processes which determine the ecosystems (green circle) resistance and resilience relative to short term (short yellow lines) and long term (dashed red line) changes in lake and climate conditions. At each storm disturbance (marked by red arrow) we measured into standardized indices the hourly asymptotic resistance and resilience of ecosystem proxies such as water temperature, oxygen saturation, pH, chlorophyll *a*, phycocyanin, turbidity, and dissolved organic matter. Measuring resistance and resilience this way allows for statistically determining the importance of changing short- and long-term changes in lake and climate conditions, and the importance of changing storm characteristics such as frequency, duration, and intensity.

Thesis outline

The following chapters of this dissertation were aimed at understanding the mechanics shaping resistance and resilience relative to non-transitory and transitory lake and storm conditions. In chapter one we address whether changes in transitory lake conditions are more important than storm characteristics in shaping resistance and resilience of biological and physiochemical proxies of a shallow lake ecosystem. The central goal of the first study was to develop a systematic, standardized and quantitative approach for synthesizing resistance and resilience following storms, and then determine the hierarchal importance of pre-storm, or antecedent lake and storm conditions. Chapter one is focused on research conducted using hourly high frequency data collected on Müggelsee, a shallow, eutrophic, and polymictic lake in Berlin, Germany. In chapter two, we expanded the methodology developed to include 8 lakes across a trophic state and depth gradient to further our understanding of cross-ecosystem controls on the susceptibility of lake ecosystem resistance and resilience following extreme storms. In the general discussion we provide a comprehensive view of how lake ecosystem resistance and resilience is being shaped as a result of both non-transitory and transitory lake, watershed, and storm characteristics. I close the general discussion by providing an outlook of possible pathways of research such as using the methodology developed to identify and predict ecosystem thresholds between two alternative stable states.

Chapter 1

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

by

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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.

Introduction

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, 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. 2016), wind induced mixing of the water column (James et al. 2008; Klug et al. 2012; Shade et al. 2012; Giling et al. 2017), lake sediment resuspension (Qin et al. 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 is 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 et al. 1973, 1996; Pimm 1984, 2019; Scheffer et al. 1992, 1994; Carpenter et al. 1991, 2001). 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 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; Donahue 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 et al. 2000, 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, 2012; Donahue 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 is 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 depends on antecedent lake conditions and storm characteristics (Jones et al. 2008, 2009; Havens et al. 2001, 2011, 2016; 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 versus 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. 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 & Adrian 2001), and 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 were measured using a pH electrode. Optical sensors equipped with anti-fouling 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 minutes 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 re-suspension 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 re-distribution of sediment in the lake (Kozerski et al 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 average wind speed (ms^{-1}) data collected in 5-minute intervals was 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. 2017) 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 was then used to calculate effective fetch using the function fetch_len_multi from the R package "waver" (version 0.2.1) (Marchand and Gill 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 et al. 1972; U.S. Army Corps of Engineers 1984) (see supplemental text 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 equation 1) during the growing season (i.e. March – 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 years. The cumulative probability of a shear stress quantile (X_T) with the return period (T) is given by:

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

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 days 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-minute 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 example R code, see supplemental text file.

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; Donahue et al. 2016). To calculate the resistance (RS) index for each individual lake parameter, we used the following function (Orwin and Wardle 2004):

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

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 (Figure 1 and S.1). 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 days 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 days, 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.

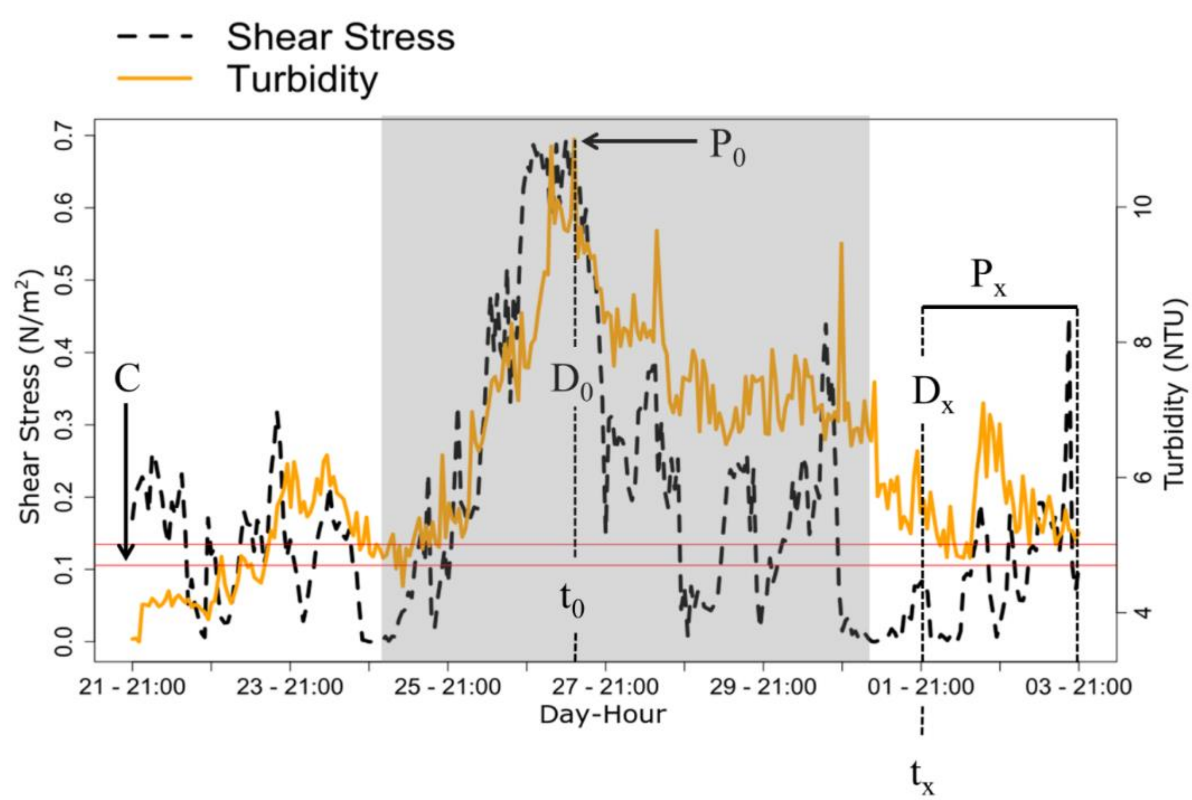

Figure 1: Example of how to quantify resistance (RS) and resilience (RL) of a lake parameter (z axis) during a resuspension event in June 2007 that has a mean antecedent value of C (red lines are the 95% confidence interval surrounding the true mean of C). An extreme shear stress event occurs during a given time frame (grey 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-hour window with the lowest standard error in the lake parameter.

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-day post storm condition period. Post storm conditions were defined as the 3-day 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 hours and starting at P_0 (Figure 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:

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

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 (Figure 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 Livera et al. 2011). We tested for daily oscillations (24-hour 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 example R code, see supplemental text file.

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 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 boosted regression trees (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 towards 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. Boosted regression tree 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 is 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 (Hastings 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 this is 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-day 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 (hours), 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 2-level factor representing resistance and resilience metrics and a 6-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. Schmidt stability was calculated using “rLakeAnalyzer” (Winslow et al. 2018). Nutrient data were collected once weekly from the epilimnion of which the most recent nutrient measurement (i.e. 1 to 4 days) 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 2016). The BRT model formula was as follows (for full details on BRT see Elith et al. 2008):

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

Where $Y_{(RSRL)}$ 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 conditions. 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 Figure S.2). We decided to analyze those shear stress events which were estimated to have return periods of 100 days or more (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 (Figure 2). Applying this 100-day threshold to the 5-minute 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 amongst the events and ranged between 42 and 157 hours with an average of 110 hours. These types of events are estimated to occur on the lake every 0.27 to 3.5 years and generated hourly shear stress means between 0.1-0.3 N/m^2 with peaks between 0.2-0.9 N/m^2 (Figure S.3). In terms of wind speed, these events produced maximum wind speeds between 21 and 35 (ms^{-1}) (Table S.1). 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 (Figure 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.

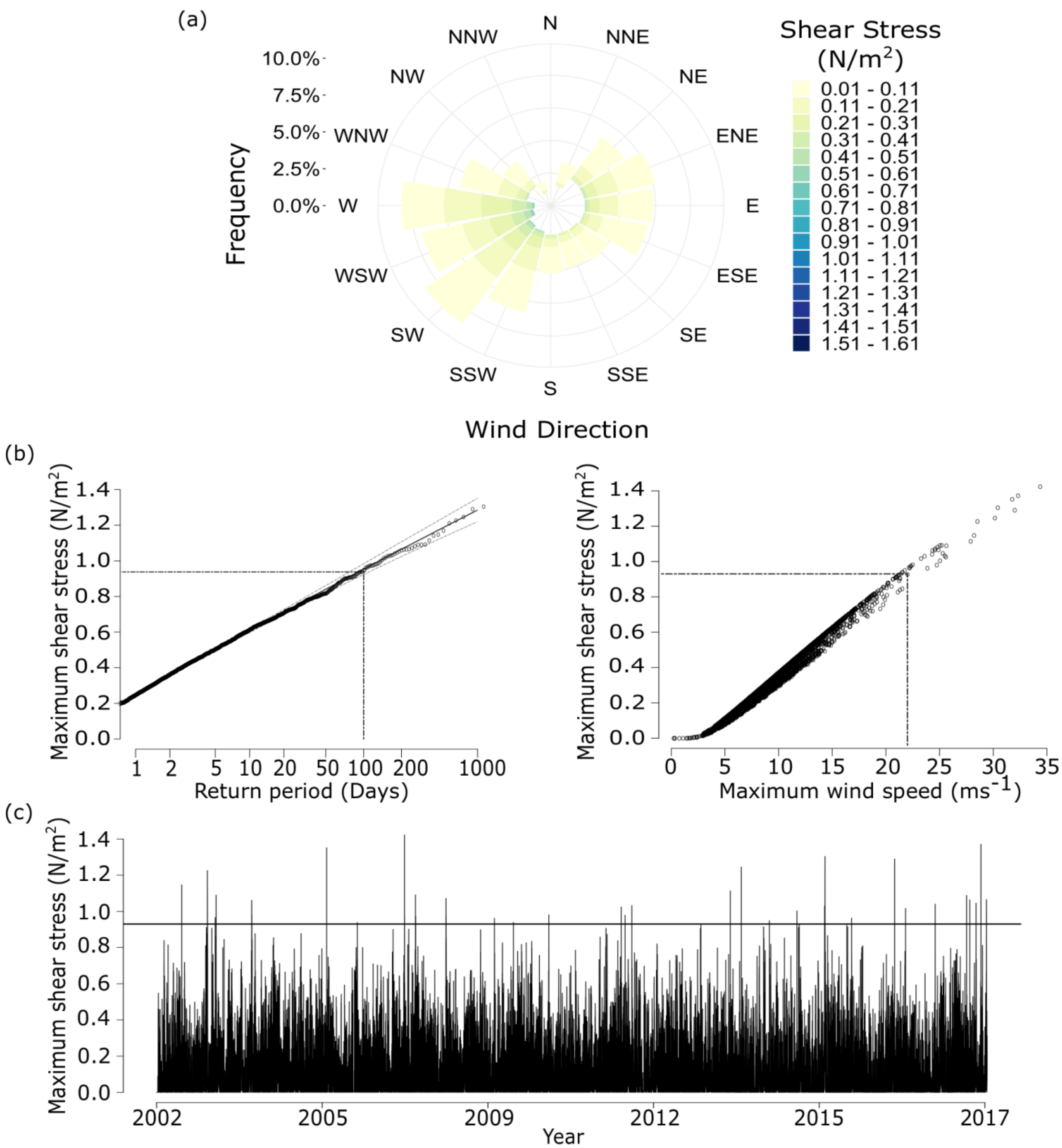

Figure 2: Figure (a) is a wind rose depicting the frequency of shear stress events and wind direction for Müggelsee. The legend shows the shear stress levels for a given wind direction. Figure (b) left shows the estimated return times of shear stress events, where the vertical dashed line represents 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. Figure (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 days or more, or daily peak shear stress > 0.93 N/m2 and max wind speed between 21-35 ms-1 a total number of 30 events. Figure (c) shows the time series of 5-minute maximum shear stress used to classify extreme events. The black line shows the 0.93 N/m2 threshold used to classify events.

Resistance and resilience indices

The identified storms induced varying effects in the observed lake parameters which were divergent in their response to the storms (Figure 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 (Figure 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 towards the storms. Water temperature generally decreased with a mean of $\bar{x} = -0.5\ sd\ \pm 1.6$ with one storm decreasing temperature by -4 ˚C. Two of the storms resulted in no change in temperature, while 8 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 $\bar{x} = 0.33$ (Figure 5 and S.4). 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 a resistance mean of $\bar{x} = 0.90$, however, small changes in pH were moderately persistent in the system with a resilience mean of $\bar{x} = 0.49$ (Figure 5 and S.4). 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 (Figure 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 (Figure 5 and S.4). 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 ($R^2 = 0.48$, $F = (1, 23.6)$, $P < 0.001$).

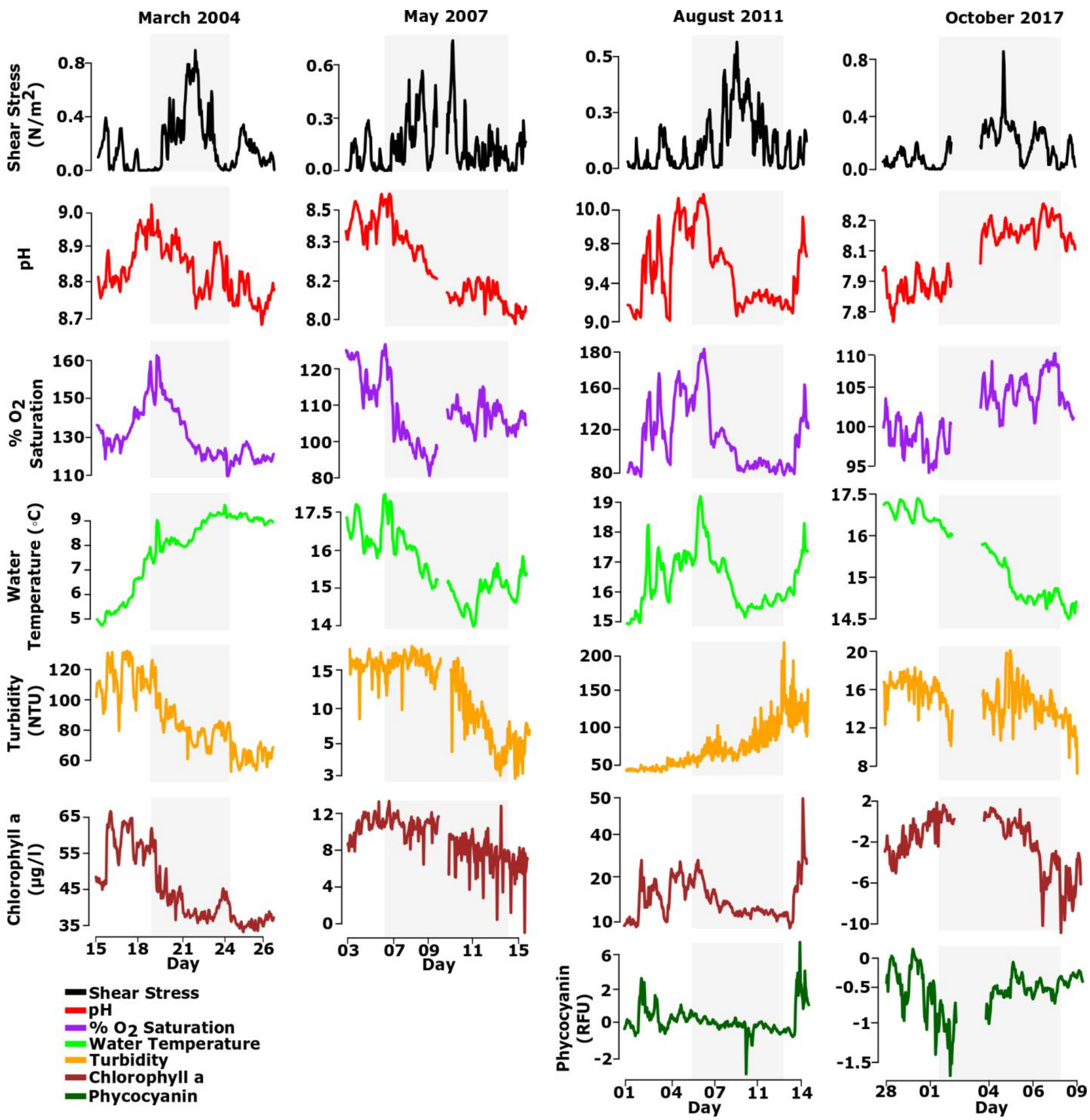

Figure 3: Four of the 25 analyzed shear stress events and the responses of lake ecosystem resistance and resilience. The figure provides an indication of the variability in storm events (i.e. shear stress = top row) and the responses of pH, % O_2 saturation, water temperature, turbidity, chlorophyll *a*, and phycocyanin (see legend). The grey 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.

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 (Figure 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 (Figure 3). Storms on average changed the turbidity conditions in the lake by ~ 87% with a resistance mean of $\bar{x} = 0.17$, with 8 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 (Figure 5 and S.4).

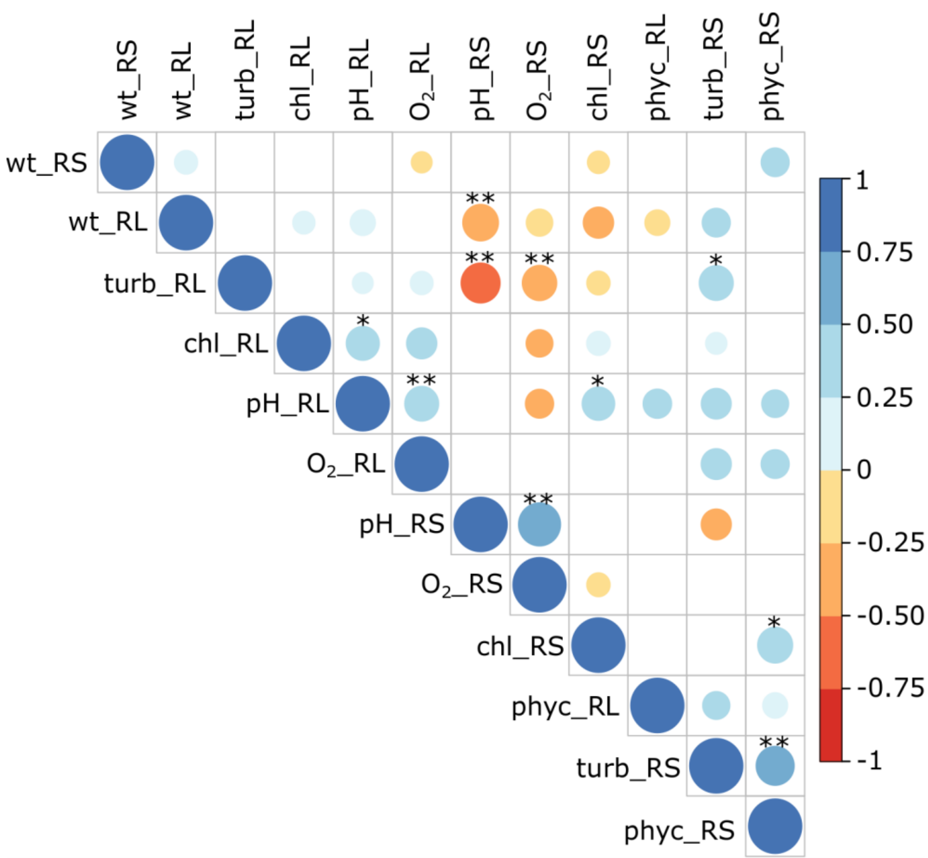

Figure 4: Hierarchical clustering of Spearman correlations between the varying resistance (RS) and resilience (RL) indices. Those relationships that have two stars above them were significant at $P \leq 0.05$ level, one star indicates a correlation at a $P \leq 0.10$ level. Blue circles represent positive 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.

In relation to chlorophyll *a*, the storms tended to change chlorophyll *a* concentration on average by 100% with a mean resistance of $\bar{x} = 0$, with 50% of storms causing more than 100%

change in chlorophyll *a* concentration (12 of 24 storms). Overall, chlorophyll *a* conditions tended to be moderately resilient with a mean of $\bar{x} = 0.55$ (Figure 5 and S.4). Chlorophyll *a* on average increased by 3.2 μg/l following storms (10 of 24 storms) and nearly equally decreased by -3.3 μg/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 (Figure 5 and S.4). Phycocyanin fluorescence 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 S.2).

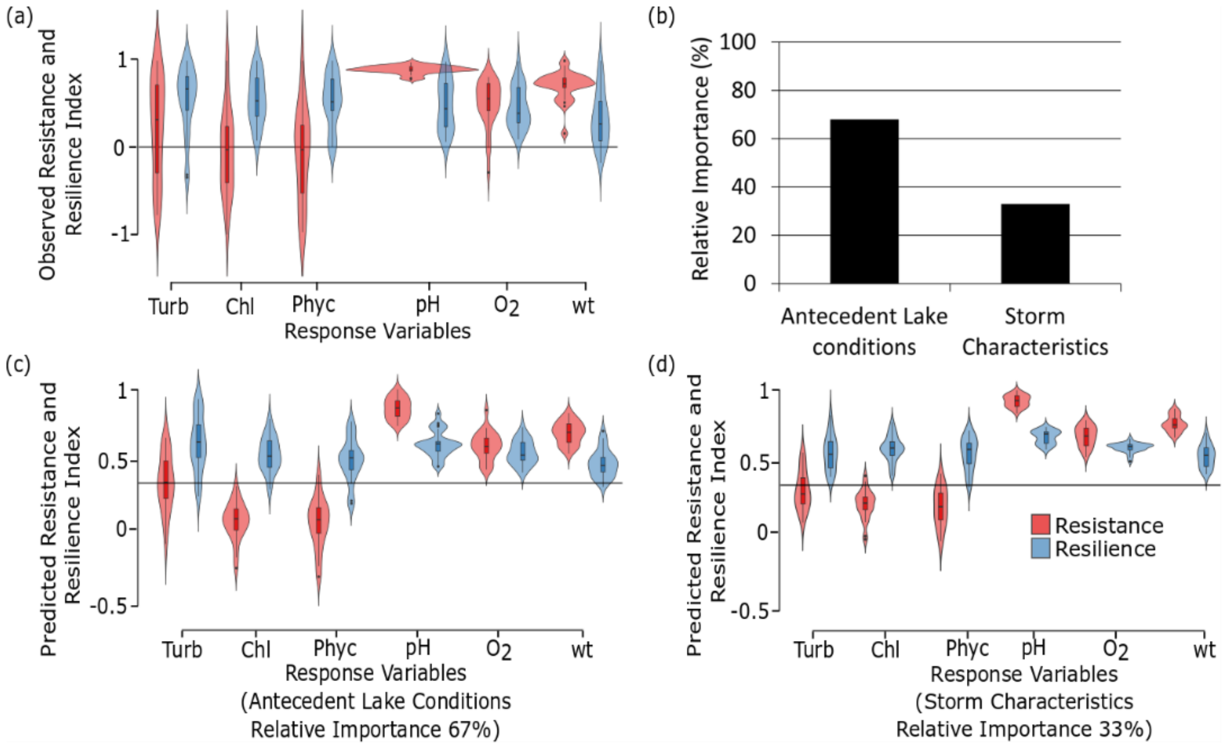

Figure 5: Observed lake ecosystem resistance and resilience is given in figure (a). Figure (b) gives the rescaled percent relative importance of antecedent conditions and storm characteristics, while the results from the antecedent lake condition predictions and storm characteristic predictions are given in figures (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. Figures (c) and (d) show 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 plots which give the probability distribution of resistance and resilience responses to 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 figure (a) shows at which point storms were causing more than 100% change/0% recovery, while in figures (b) and (c) it represents the median resistance and resilience across the individual predicted indices.

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 (Figure 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 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 (Figure 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 amongst 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%) (Figure 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 (Figure 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 (Figure 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%) (Figure 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 (Figure 6 and S.6). Lastly, storms occurring after 2012 increasingly had negative effects on the resistance and resilience of the lake (Figure 6 and 8).

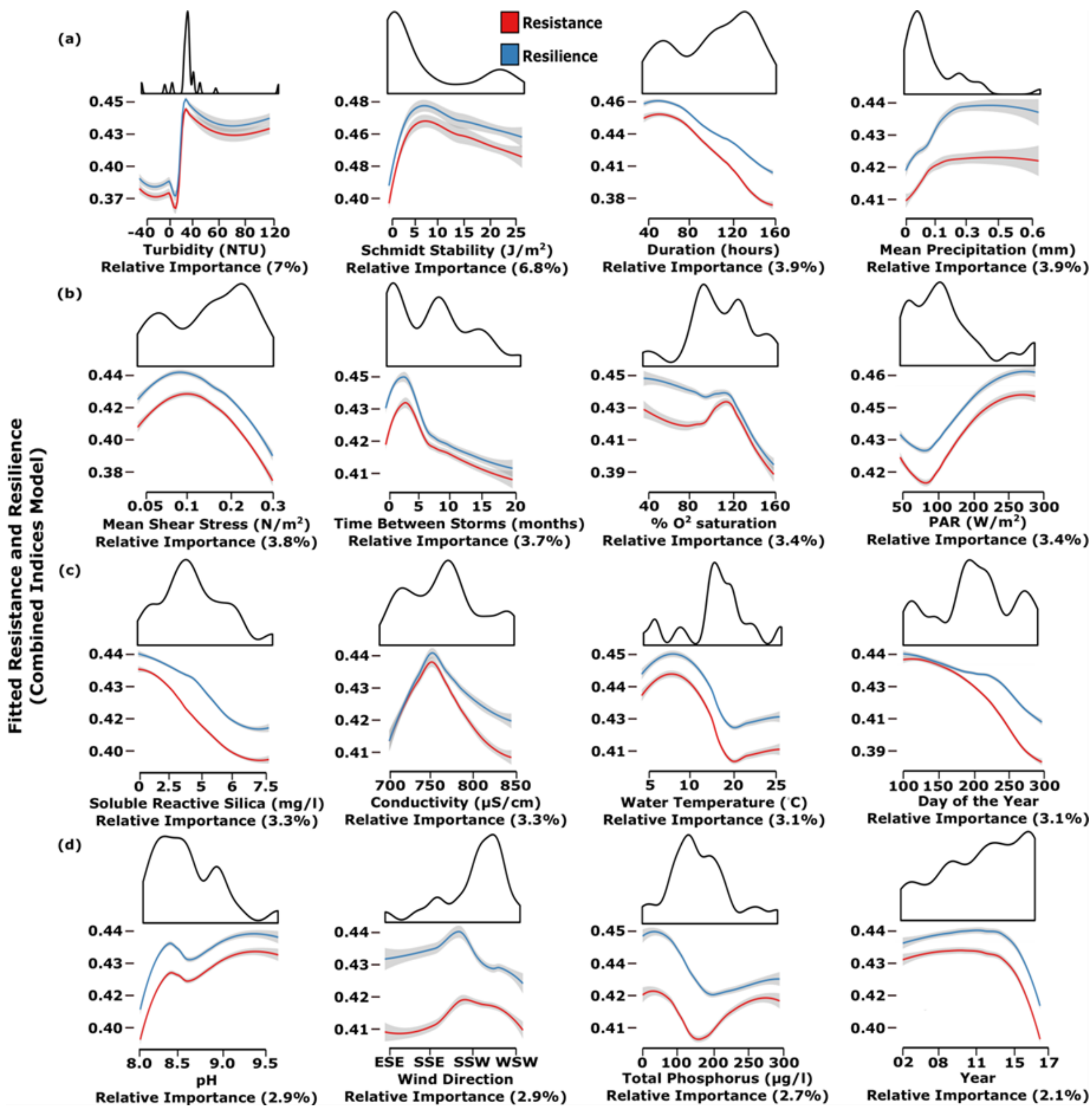

Figure 6: Line graphs show partial dependence of both the physiochemical and biological (i.e. combined indices model) resistance (RS = red line) and resilience (RL = blue line) (quantified on a standardized scale from -1 to 1), relative to antecedent lake conditions and storm characteristics. The graphs are in order of importance (see percentages) based on the variable on the x-axis. The grey 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%).

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

Modelling the two groups of variables separately provided insight into the non-linear 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 (Figure S.5). 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 non-linear dynamics we see in figure 6. Antagonistic effects on the resistance and resilience of the two 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 (Figure 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 increase the biological variables' (i.e. algal conditions) ability to recover from storm induced effects (Figure 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 (Figure S.6). Storm durations over 100 hours 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 (Figure 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 (Figure S.6). 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 (Figure 7) (see figure S.6 to see all antagonistic effects which are not shown in figure 7).

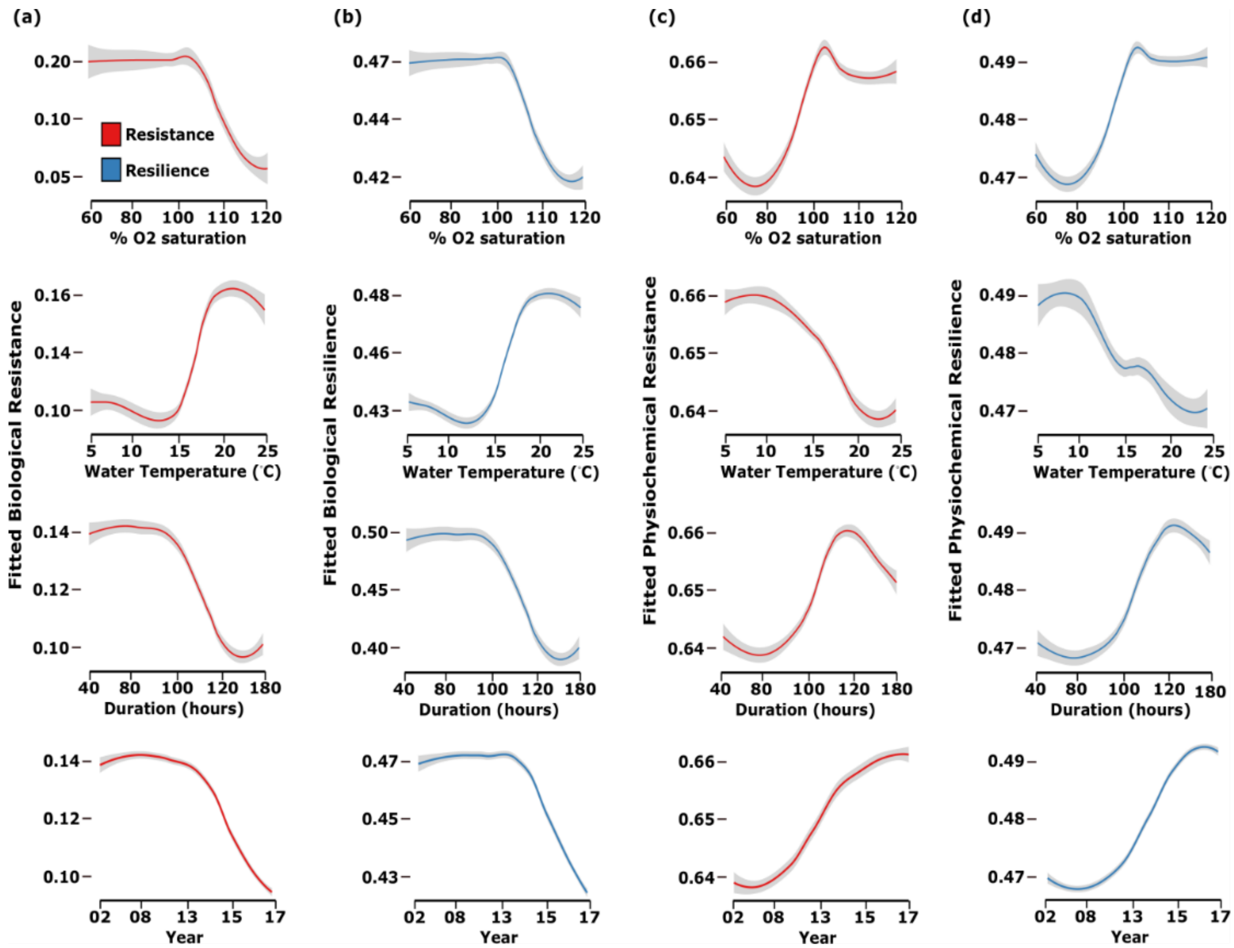

Figure 7: The partial dependency plots (quantified on a standardized scale from -1 to 1), in columns (a) and (b) show the marginal effects of antecedent lake conditions and storm characteristics on the resistance and resilience of the biological variables, while columns (c) and (d) show the marginal effects in relation to the physiochemical variables. In the figure we see the resulting effects of % O2 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, % O2 saturation above 100% increases resistance and resilience of the physiochemical variables, while the resistance and resilience of the biological variables decreases.

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 (Figure 8). Increasing antecedent total phosphorus led to increased resistance and decreased resilience, which when compared with the combined indices model suggests that the decreased resilience in the physiochemical environment is driving that pattern (Figure 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 (Figure 6 and 8). In relation to wind direction there is not any clear picture drawn from the combined indices model (Figure 6), but here we find that wind directions from less frequent directions decreased the resistance of the physiochemical variables and increased resilience (Figure 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 (Figure 8). However, it seems changes in wind direction are mostly driving lake resistance dynamics (Figure 6).

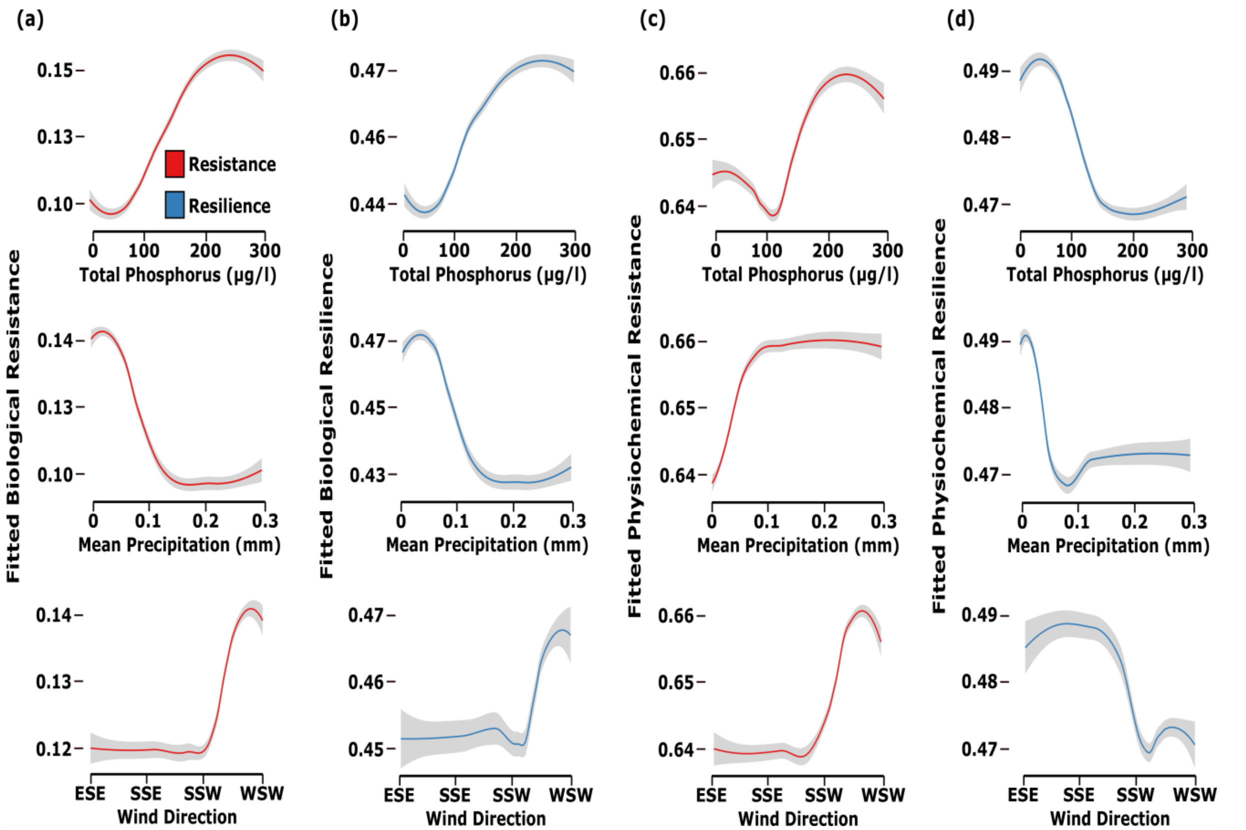

Figure 8: The partial dependency plots (quantified on a standardized scale from -1 to 1), in columns (a) and (b) show the marginal effects of antecedent lake conditions and storm characteristics on the resistance and resilience of the biological variables, while columns (c) and (d) show the marginal 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.

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 to determine if storm characteristics or antecedent lake conditions were more important in describing the lake's ability to resist and recover from the 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 (Figure 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 (Figure 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 (Figure 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 (Figure 6). This does not mean that resistance and resilience of the physiochemical and biological variables were always affected in the same direction (Figure 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 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 non-linear dynamics we see in the combined indices model (i.e. model combining both physiochemical and biological variables) (Figures 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 non-point 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 (Figure 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 (Figure 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 % (Figure 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% (Figure 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 (Figure 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 paleo-environmental 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 (Figure 7). However, silica concentrations had antagonistic effects on the biological and physiochemical variables respectively (Figure S.6). 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 (Figure S.6). 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 (Figure 6 and S.6). 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 (Figure 8 and S.6). 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 (Figure 5 and 6).

The resistance and resilience of the lake was partially shaped by antecedent conductivity and pH conditions (Figure 6 and S.5). Lake pH and conductivity dynamics are determined by similar factors such as hydrogeological processes, lake size relative to watershed size, point and non-point 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 (Figure 6 and S.5). 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 towards a clearer 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 (Figure 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 (Figure 2 and S.5). 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 resist and recover 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 was equally influenced by mean precipitation and storm frequency (Figure 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 (Figure 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 (Figure S.6). 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 Figure 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 (Figure 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 (Figure 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 forming 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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Chapter 2

Lake surface water temperature and oxygen saturation resistance and resilience following extreme storms: Chlorophyll a shapes resistance toward storms

by

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General Discussion

I have presented here a systematic, standardized and quantitative approach for describing mechanisms shaping lake ecosystem resistance and resilience following extreme storms. The expected increase in extreme storms as a result of climate warming, warrants the development of standardized approaches for understanding how extreme storms, and non-transitory watershed and lake characteristics come together to form transitory antecedent lake conditions responsible for shaping resistance and resilience of varying lakes (Figure 1a-d). In chapter one, we found in a shallow eutrophic lake, that seasonal clear and turbid phases were the primary drivers of resistance and resilience, highlighting the importance of transitory antecedent lake conditions in shaping storm responses in lakes (Figure 1d-e). In chapter two, we expanded the developed methodology to eight lakes of varying trophic status and found that increased dis-equilibrium from the atmosphere as a result of increased primary production and or changes in mixing status led to trade-offs between resistance and resilience. Consequently, showing oligotrophic lake processes optimize resistance towards storms, while eutrophic lake processes optimize resilience following storms (Figure 1f-h). Ultimately the way in which a storm impacts a single lake is a result of many direct and indirect effects (Figure 1-$P_{0\text{-}3}$) of both long- and short-term environmental dynamics. The methodology we have presented here is robust and broadly applicable to other systems, variables, and disturbance types and ready to be used to further our understanding of ecosystem resilience.

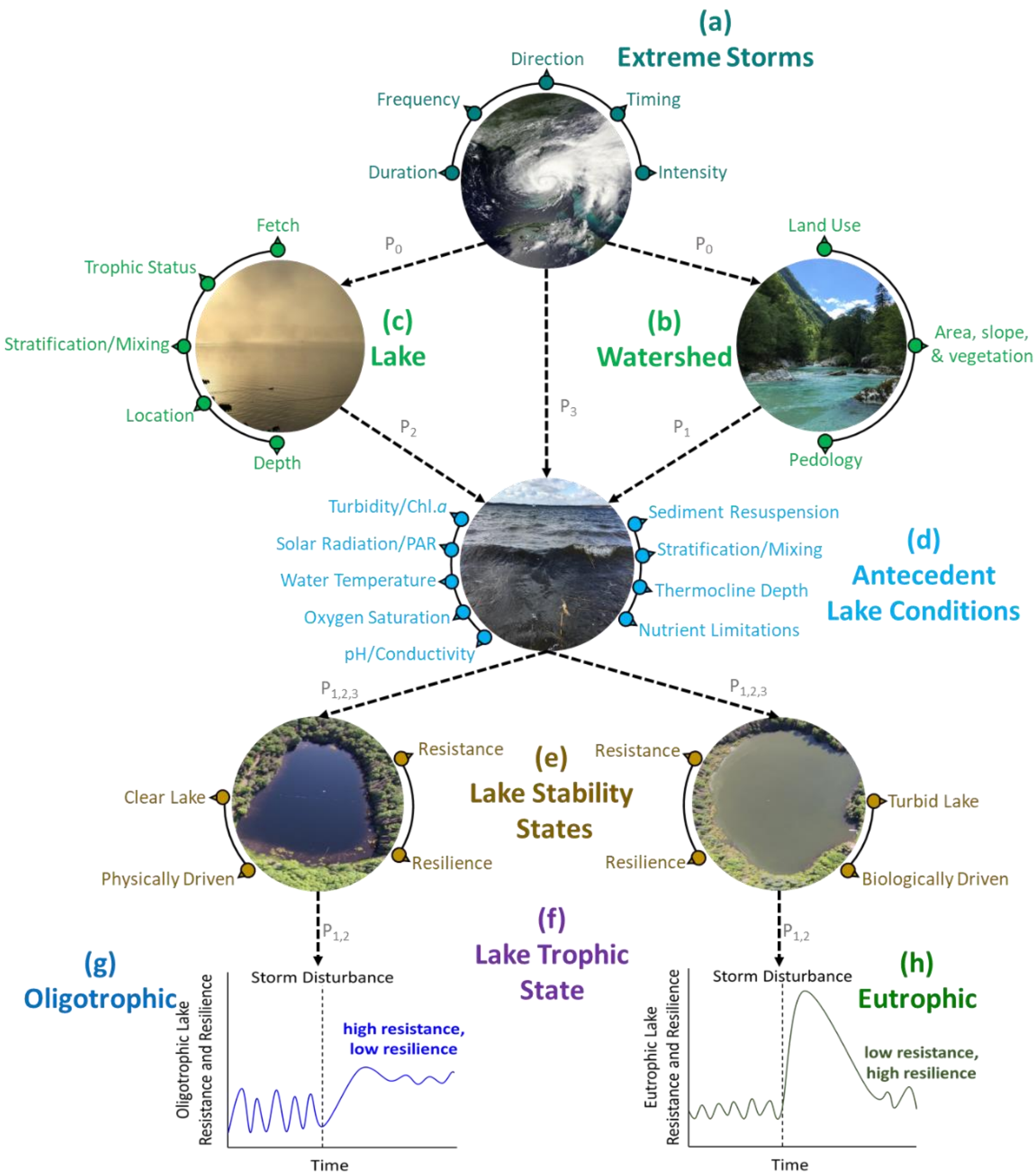

Figure 1 Shows a conceptual diagram of how extreme storms (a) have direct and indirect effects (black arrows) on non-transitory upstream watershed (b) and lake characteristics (c), which together form transitory antecedent lake conditions (d). In this study we first focused on a shallow lake which has seasonally clear and turbid stability states (e), which shape how resistant and resilient the lake was following a storm. The clear and turbid stable states are a result of indirect (P_0) and direct ($P_{1,2,3}$) effects of extreme storms, and upstream watershed and lake characteristics. Thus, the resistance and resilience of a single lake are being shaped by differing phenomena $P_{1,2,3}$ at various time scales, spatial extents, and interactions between a, b, and c. The degree to which a given lake experiences seasonally clear and turbid conditions is largely dependent on its trophic state (f), or whether it is oligotrophic (g), or eutrophic (h), which are shaped directly by longer term changes in pathways $P_{1\text{-}2}$. While a single lake can experience an array of transitory lake stable states over a single seasonal period, the trophic state of a lake, which is the primary determination of resistance and resilience following extreme storms, changes on the scale of decades. Overall, oligotrophic lake processes optimize resistance towards storms, while eutrophic lake processes optimize resilience following storms.

Extreme storm, watershed and lake characteristics (Pathways a-b-c-d)

Extreme wind and rain storms, and the effect they have on lakes is largely driven by the lake's antecedent lake characteristics, which are shaped by both transitory short-term and non-transitory long-term changes in watershed and lake characteristics (Figure 1a-d) (Perga et al. 2018; Thayne et al. 2022). In this dissertation we found that non-transitory lake characteristics trophic state and fetch were critical factors shaping resistance and resilience following extreme storms. Consequently, highlighting the importance of underlying pathways of primary production and the lakes physiographic location and orientation relative to predominant wind directions. However, while the fetch of a lake will mostly never change, other important transitory lake characteristics such as its nutrient concentrations and or stratification/mixing conditions can change over a season and or as a result of decadal shifts in climate and or changing watershed dynamics. Extreme storms can directly affect watershed characteristics via flooding, landslides, changes in sedimentation as result of shifting river corridors, and changes in vegetation coverage (Stockwell et al. 2020). While we have not focused on watershed characteristics directly, the indirect effects of watershed dynamics are captured in antecedent lake characteristics. For example, in chapter one we found that a shift in conductivity in Müggelsee as a result of old mine tailings seeping into the river spree was relatively important for determining and may have partially shaped resistance and resilience following storms. Taken as a whole, the way in which an extreme storm imparts change in a lake has less to do with its magnitude, and more to do with its timing and the lake's antecedent biophysical characteristics. For example, in Müggelsee a spring time storm is likely to drive change in light and nutrient conditions via sediment resuspension, while in mid-summer a similar storm is likely to drive changes in light and nutrient conditions via the enhancement and or breakdown of bloom conditions. Thus, storm driven changes in lake ecosystem resistance and resilience is generally shaped by whether physical or biological mechanisms are shaping antecedent lake characteristics at the time of storm exposure.

Lake stability and trophic states (Pathways a-d-e-f-g)

Lakes can display an array of characteristics throughout a single season. And depending on the timing of the storm, stratification and or bloom conditions, a given lakes response to an extreme storm is determined by its stability state (Figure 1d). Not to be conflated with alternative stable states which are typically non-transitory and generally related to ecologically relevant timescales. Stability states are transitory and shape the conditions in which we can measure resistance and resilience, which refers to an ecosystem and its components ability to return to pre-disturbance conditions and functions (Holling 1973; Pimm 1984; Worm and Duffy 2003; Shade et al. 2012). In lakes, stability states can be split into two generally described categories, whether the lake is in a clear or turbid state (Thayne et al. 2022). Subsequently, each stability state displays differing levels of resistance and resilience (i.e. trade-offs) depending on the underlying biological communities and physical processes being selected to optimize resistance and or resilience (Parker et al. 2022; Thayne et al. 2022).

In chapter one, we found in eutrophic Müggelsee that turbidity and or algal conditions were the most important characteristic determining how resistant and resilient the lake was following an extreme storm. Consequently, highlighting the importance of transitory antecedent algal conditions in shaping resistance and resilience following extreme storms. We determined that resistance and resilience of clear phases of the lake were primarily shaped by physical characteristics (i.e. cool mixed conditions vs. warm stratified conditions) and or the re-settling of sediment in the case of resuspension. An interesting finding in our research of Müggelsee was related to light and nutrient availability, where we found increased antecedent light availability and decreased soluble reactive silica led to enhanced resistance and resilience of the lake's physiochemical conditions. Thus, emphasizing how transient algal conditions not only effects the resistance and resilience of biological proxies chlorophyll *a*, phycocyanin, and turbidity, but also the resistance and resilience of physiochemical proxies pH, water temperature, and oxygen saturation. This result shows that the recovery of the physiochemical structure of Müggelsee is interconnected with the recovery of its algal conditions. And while not immediately clear why this would be the case, we can use an analogy from the terrestrial landscape to help clarify how phytoplankton is connected to the recovery of a lakes physiochemical structure following a storm.

We tend to look at lakes and see only water. But if we were to look across a terrestrial ecosystem we would see a biodiverse landscape dotted with varying plant and animal species. Now, imagine a grass landscape where the growth of the grass is partially dependent on the pH levels of the soil, but the pH levels are partially dependent on the presence and species of grass. The relationship is thus interdependent. If an intense fire burns through the grassland and subsequently wipes out large swaths of the grass, the pH of the soil is likely to change. If the pH of the soil is to recover following the extreme change in vegetation cover, the recovery of the vegetation is of utmost importance for pH levels to be resilient. We can apply this same analogy to lakes strongly driven by phytoplankton abundance. Phytoplankton growth is partially dependent on water temperature, and thus water temperature is partially dependent on phytoplankton abundance. The stronger the bloom conditions are at the surface of a lake, the stronger the interdependence between phytoplankton and physical properties such pH, light, and or water temperature become (Nõges et al. 2011; Shatwell et al. 2016; Thayne et al. 2022). Consequently, when a lake is under bloom conditions and is exposed to an extreme wind storm, the recovery of the bloom becomes an important factor for resilient pre-storm physiochemical conditions. And so, like terrestrial ecosystems, lakes are biophysically diverse, and phytoplankton structure and biovolumes vary depending on the trophic state of a lake (Eloranta 1986).

In chapter two, we found that eutrophic lakes, which tend to be more turbid and or phytoplankton driven, were less resistant, but more resilient than oligotrophic lakes (Figure 1f-h). Similar to Müggelsee resistance and resilience being partially dependent on whether the lake was in a clear or turbid phase, oligotrophic lake resistance and resilience are likely more driven by physical dynamics, and eutrophic lakes are likely more driven by biological dynamics. We found that in lakes which are more frequently drawn out of equilibrium with the atmosphere (i.e. $<$ or $>$ % O_2 saturation) either as a result of increased primary productivity and or changes in mixing status tended to show greater maximum displacement (i.e. diminished resistance) following the extreme storms. Consequently, highlighting the importance of longer-term changes in trophic status (i.e. phosphorus concentrations) and its effect on transitory antecedent lake characteristics in shaping resistance. Likewise, the observed trade-offs in resilience between oligotrophic and eutrophic lakes is likely similar to what we observed in Müggelsee. Such that storms were more likely to affect longer lasting change, or diminished resilience in physically dominated conditions during clear water phases (i.e. seasonal oligotrophy), and enhanced resilience during turbid phases (i.e. seasonal eutrophy). Trade-offs between resistance and resilience have been shown in previous studies, but never in conjunction with antecedent environmental and disturbance characteristics to help breakdown the mechanisms driving the trade-off. The importance of changing trophic state either as a result of more transitory changes in algal conditions, or as a result of more non-transitory physiographic characteristics such as phosphorus loading, both studies here highlight the importance of changes in sources and pathways of primary productivity, and the resistance and resilience of lake ecosystems following extreme storms. The methodology developed and results provide a systematic, standardized and quantitative approach for identifying critical processes shaping lake ecosystem resistance and resilience following extreme storms.

Research outlook

One of the primary benefits of quantifying storm responses of lakes into standardized indices of resistance and resilience, is the ability to continue to ask questions surrounding the topic using a single dataset. Furthermore, by using methods which allow the identification of hierarchal importance such as boosted regression trees, we are able to continually build a picture of what environmental conditions are of critical importance for building resistant and resilient lake ecosystems. Here, we briefly explore several avenues of further exploration using the resistance and resilience indices developed as a result of this work.

Antecedent climate and lake trends

While the work presented here focused on storm characteristics expected to be affected by climate change, exploring how antecedent climate conditions interact with antecedent lake conditions to shape resistance and resilience following extreme storms. One avenue of doing this could be to look at how long-term trends in antecedent climate and lake conditions drive storm responses in lakes. For example, one could take the long-term trend in climate and lake conditions leading into the first identified storm for a given lake. And there after measure the mean conditions 365 days prior to each of the following identified storms. Therefore, setting up a model which could explore how longer-term trends in climate and lake conditions are interacting with shorter term lake and storm characteristics to shape resistance and resilience following extreme storms. Such a model could perhaps start to give us an understanding of how climate change directly rather than indirectly effects the resistance and resilience of lake ecosystems.

Watershed and physiographic dynamics

Watershed characteristics play a central role in determining the antecedent lake characteristics shaping lake ecosystem resistance and resilience. However, as mentioned previously we have likely only captured indirect effects of such dynamics as land use by, for example, exploring the effects of trophic state on the resistance and resilience of lakes. An avenue for exploration could be including upstream watershed dynamics such as annual changes in river flow and morphology, number of damns, dominant vegetation, land use, and or the slope/area surrounding the lake. Combining this with the above described model could allow us to explore the relative importance of changing watershed dynamics and climate change in shaping the resistance and resilience of lake ecosystems following extreme storms.

Ecological resilience, thresholds and alternative stable states

To get at the heart of ecological resilience one would like to be able to identify critical thresholds between one stable state and another at ecologically relevant time scales. Having that ability would allow us the capability of predicting when one stable state is about to give way to another perhaps less desirable stable state as a result of crossing a threshold. Ecosystem responses to pressure tend to revolve around a prevailing framework that threshold levels of pressure exist and that when surpassed response magnitudes and their variance increase disproportionately (Hillebrand et al. 2020). Thresholds have been detected using a number of techniques in cyanobacterial and copepod populations in Müggelsee relative to shifts in nutrient concentrations, duration of stratification, and shifts in predator prey relationships (Wagner and Adrian 2009; Huber et al. 2011; Scharfenberger et al. 2013). However, Hillebrand et al. (2020) found that there is a lack of evidence of thresholds in ecosystems due to a lack of systematic quantitative evidence. I suggest that the methodology developed here maybe one avenue for exploring such topics. For example, in chapter two of this dissertation one could argue that we identified a cross-ecosystem threshold as a result of increasing phosphorus concentrations > ~30 µg/l. Where which, when a given lake surpasses annual loads of total phosphorus concentrations > ~30 µg/l, the magnitude in response towards storms increased (i.e. diminished resistance) as a result of increasing variability (e.g. increasing variance) in primary productivity (i.e. < or > % O_2 saturation) (Figure 2). This could be further explored by conducting simulation studies, whole lake manipulations, or mesocosm studies. However, better would be to use a lake such as Müggelsee where thresholds have been detected in underlying algal populations and has undergone a shift in clarity conditions as a result of nutrient reductions and the subsequent reappearance of submerged vegetation (Hilt et al. 2013, 2018). Nonetheless, the work developed here maybe useful for developing a systematic and quantitative approach for identifying thresholds between two alternative stable states in lakes and other ecosystem types.

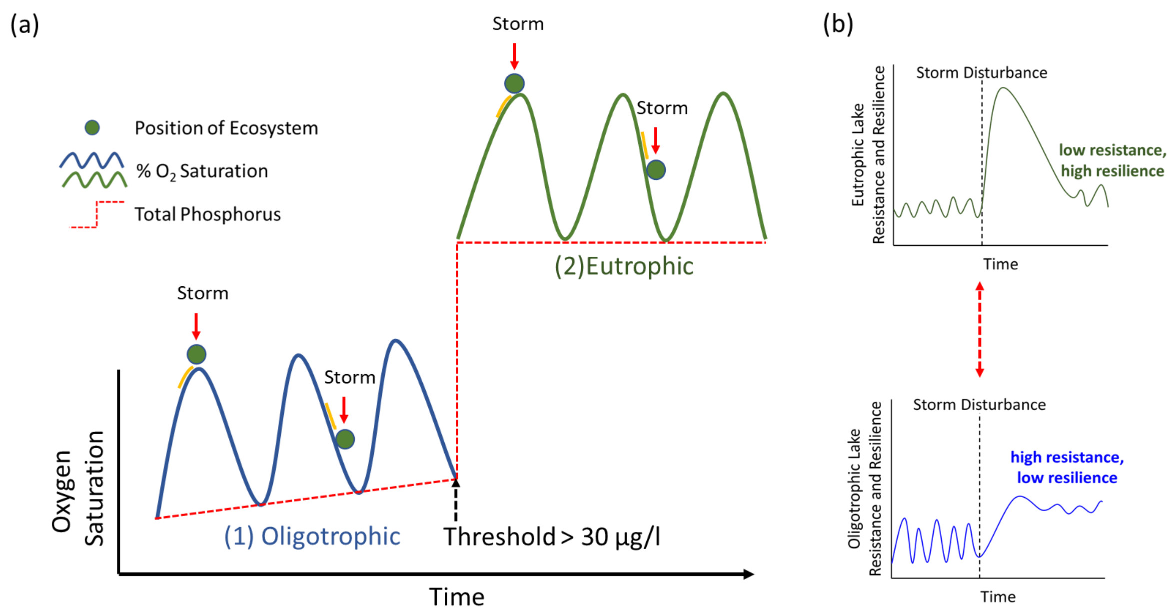

Figure 2: Shows a conceptual diagram of how the methodology presented in this dissertation maybe useful for identifying thresholds (black arrow) in lake ecosystems (green circles) as a result of a regime shift. For example, using the results from this work we could hypothesize a lake (Panel a) shifting from being (1) oligotrophic to (2) eutrophic as a result of increasing total phosphorus concentrations (red dashed line) and subsequent increasing variability in oxygen saturation above or below 100% (blue and green lines). The storms (red solid arrows) act as our perturbation of the system for quantifying resistance and resilience (i.e. proxies of stability state) (y-axis) through time (x-axis) relative to the changing antecedent saturation conditions (yellow lines) and shifting phosphorus concentrations. Using the results from chapter two, we could hypothesize that resistance and resilience following storms of the oligotrophic state of the lake would gradually diminish following storms with increasing levels of phosphorus. Or in other words, as the threshold in phosphorus concentrations is approached, the response magnitude of the oligotrophic lake state would gradually increase or become more sensitive towards storms (i.e. diminishing resistance), which would be accompanied by a decreased ability to recover following the storms (i.e. diminishing resilience). Once the 30 µg/l threshold is surpassed and remains so, we would expect resistance towards storms to remain diminished as a result of increased variability in oxygen saturation (i.e. primary productivity), however, we would expect enhanced resilience, or more complete recovery following the storms in the new eutrophic state. Thus, the subsequent trade-offs in resistance and resilience following storms (Panel b) provides us with a distinct pattern to identify when a threshold (red dashed double pointed arrow) has been crossed in either direction as a result of a regime shift, such that the lake diminishes in resistance, while resilience is enhanced following storms, or vice versa.

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Appendices

Appendix chapter 1: Supplementary tables and figures

Table S.1 Shows the year, month, duration, mean wind direction, 5 minute maximum wind speeds, mean shear stress, and peak shear stress for each of the 25 events identified for describing the lakes response to extreme and episodic events.

Year	Month	Duration (Hours)	Mean Wind Direction	Maximum Wind Speed (ms^{-1})	Mean Shear Stress (N/m^2)	Peak Shear Stress (N/m^2)
2002	Jul	98	SSE	24.5	0.2	0.5
2002	Oct	144	SW	28.5	0.3	0.9
2003	Jun	94	WSW	25.0	0.2	0.5
2004	Mar	138	SW	24.3	0.3	0.8
2005	Jul	112	WSW	31.8	0.1	0.4
2007	Jun	153	SW	25.2	0.3	0.7
2008	Mar	97	SSW	24.6	0.3	0.7
2008	Oct	96	SW	23.9	0.3	0.7
2009	May	121	SW	21.6	0.1	0.2
2009	Oct	117	SW	22.5	0.2	0.6
2011	Jun	73	SSW	25.6	0.1	0.4
2011	Jul	42	SSE	24.7	0.1	0.2
2011	Aug	122	SSW	25.5	0.1	0.5
2012	Oct	117	S	21.4	0.2	0.6
2013	Jun	101	ESE	27.9	0.2	0.7
2013	Aug	148	SE	30.2	0.1	0.5
2014	Apr	100	SW	21.8	0.2	0.5
2015	Jul	157	SW	22.2	0.4	0.7
2016	May	121	S	32.0	0.1	0.4
2016	Jul	73	SW	23.3	0.2	0.3
2017	Aug	122	SSW	25.6	0.1	0.4
2017	Aug	49	SSE	24.5	0.1	0.4
2017	Sep	127	SSW	25.3	0.3	0.6
2017	Oct	85	SW	32.3	0.2	0.5
2017	Oct	147	W	24.9	0.2	0.7

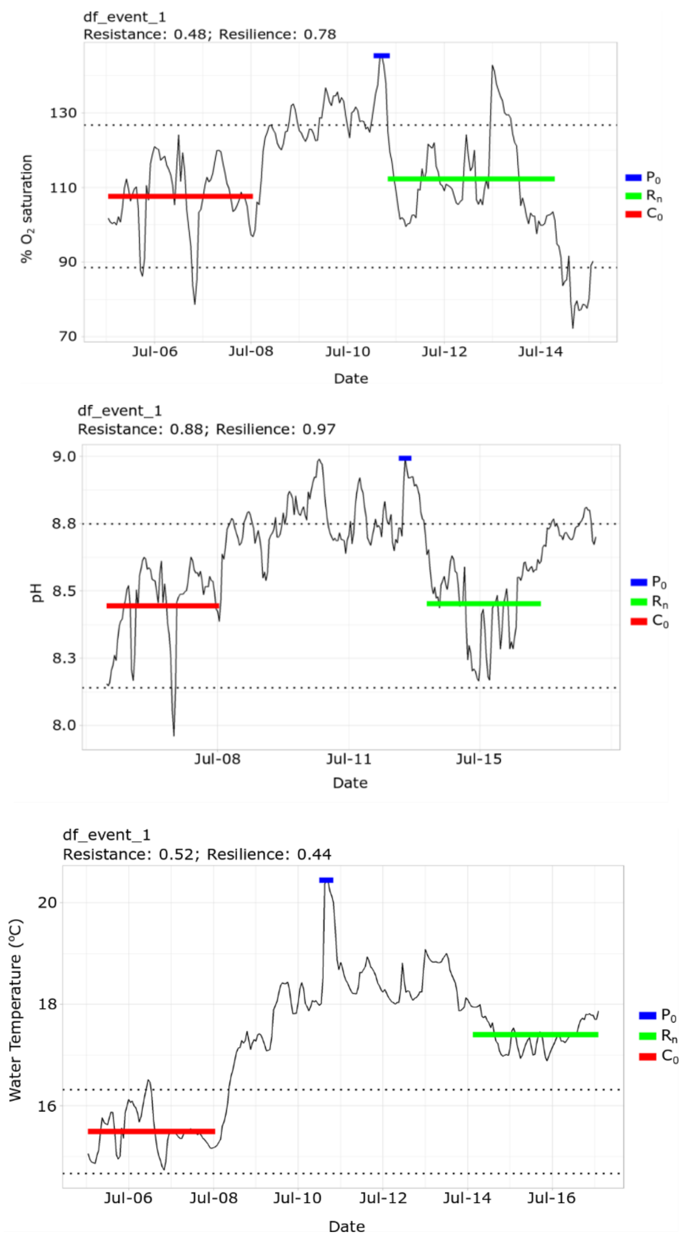

Figure S.1 Examples of resistance and resilience quantification during a storm in July 2002. The figures are those exported from the automated process. The red bar represents the antecedent conditions (C_0), the blue bar represents the peak response (P_0), and the green bar represents the 72 hour recovery window. The calculated resistance (RS) and resilience (RL) is given at the top right of each figure.

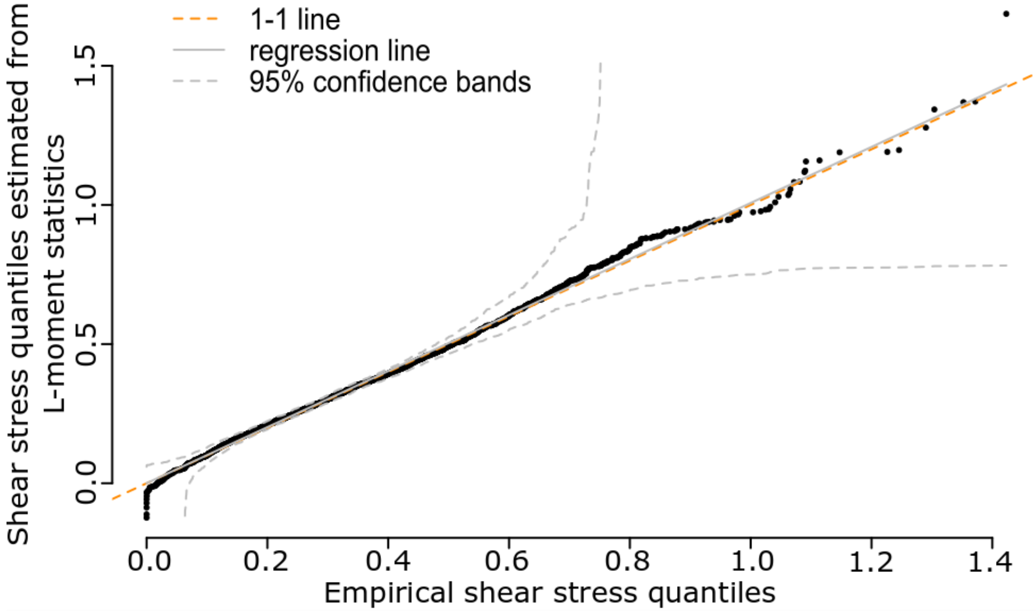

Figure S.2 Shows the empirical shear stress quantiles (x axis) compared to the shear stress quantiles estimated from L-moments statistics (y axis). The orange dashed line represents the one to one line between the empirical quantiles and the estimated quantiles. The grey solid line is the regression line which gives an idea for the goodness of fit which is bound by the 95% confidence interval (grey dashed lines). The estimated quantiles resulting from the L-moment statistics were found to be a good fit for calculating return periods for shear stress on the lake. The scale, location, and shape parameters were estimated to be 0.2526, 0.1558, and -0.0252 respectively, thus suggesting shear stress follow a Weibull distribution.

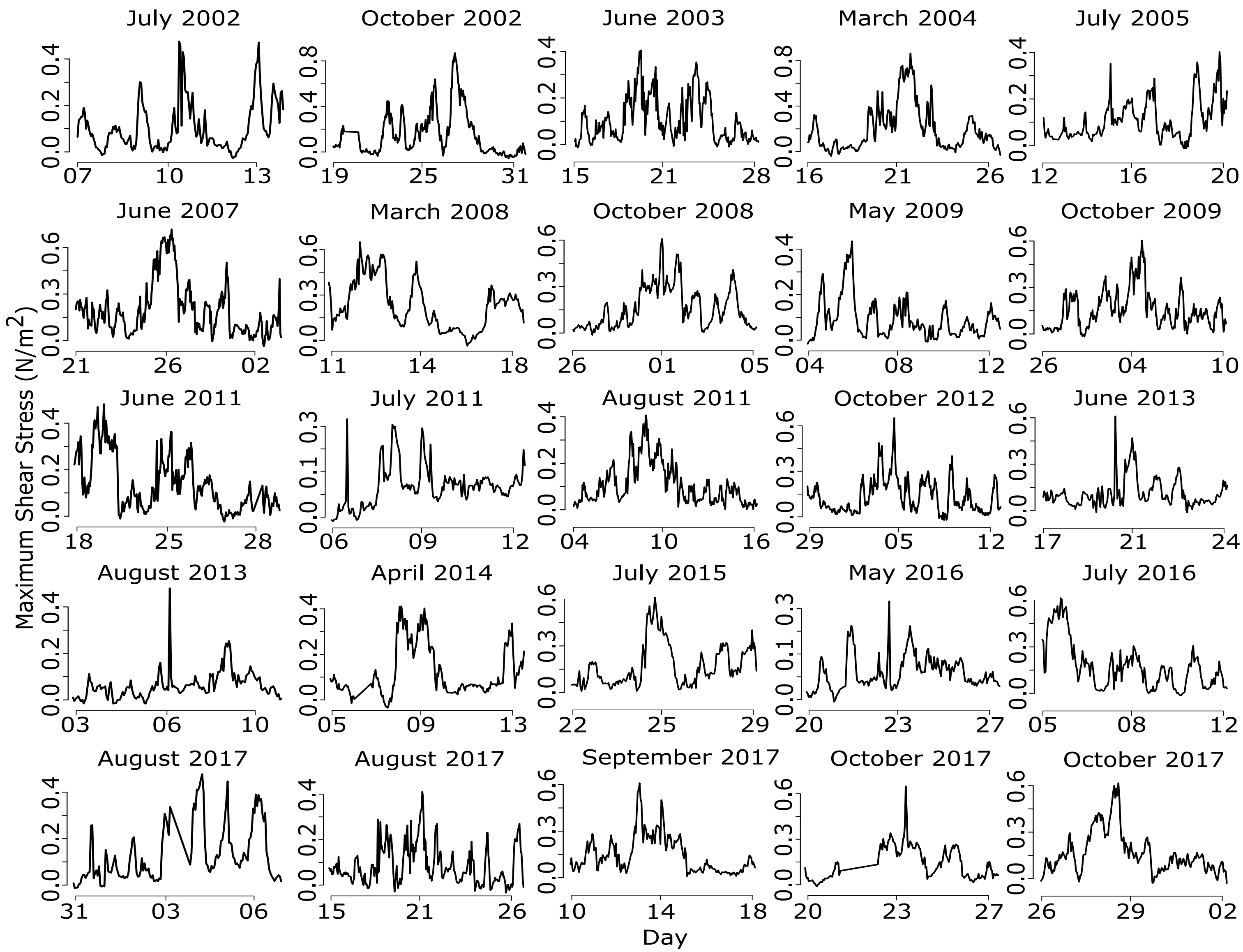

Figure S.3: The 25 shear stress events identified using general extreme value theory to estimate return periods. These events were generated from storms with maximum winds speed ranging between 22 and 35 (ms^{-1})

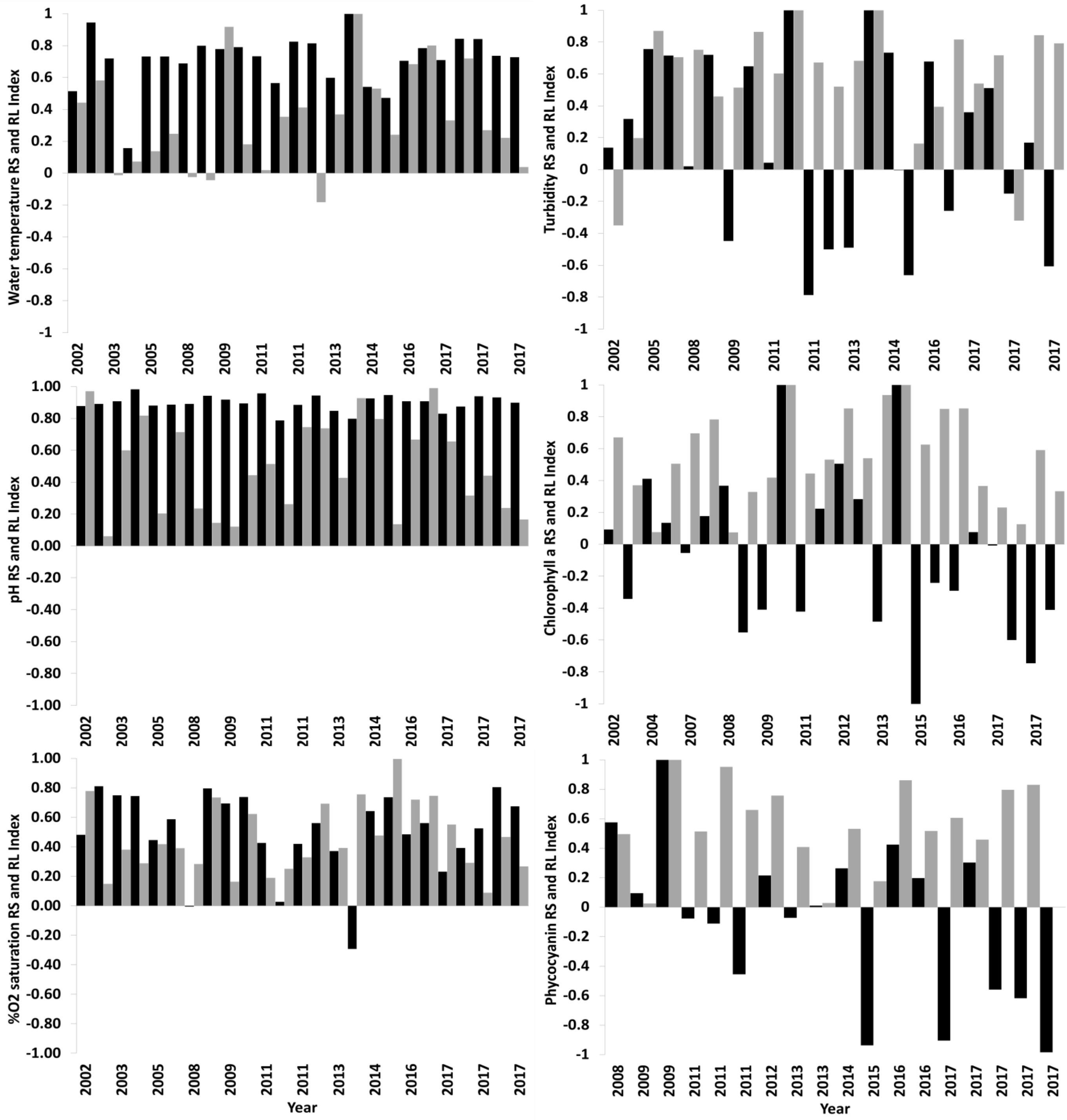

Figure S.4 Show the RS (black bars) and RL (grey bars) indices of each of the response variable analyzed. The bar charts are interpreted in terms of % change and % recovery. For example, the storm in 2002 caused nearly ~50% (RS = 0.50) change in water temperatures relative to antecedent conditions, and recovered ~40% (RL = 0.40) of antecedent water temperatures. In the case there were negative values of resilience (i.e. only present in turbidity conditions) suggest that the storms resulted in turbidity conditions that did not recover and in fact continued to move away from antecedent turbidity conditions.

Table S.2 Shows the final selected model relative to the varying tree complexities. The final model selected and used for analysis in this research is marked with a star.

Tree complexity	Number of trees	Learning rate	Mean deviance standard error	Cross validated mean	R^2
1	2100	0.0016	0.18	0.31	0.21
2	2800	0.0256	0.15	0.53	0.68
3	2200	0.0128	0.14	0.55	0.70
4	1600	0.0128	0.14	0.56	0.73
*5	1700	0.0128	0.14	0.56	0.76

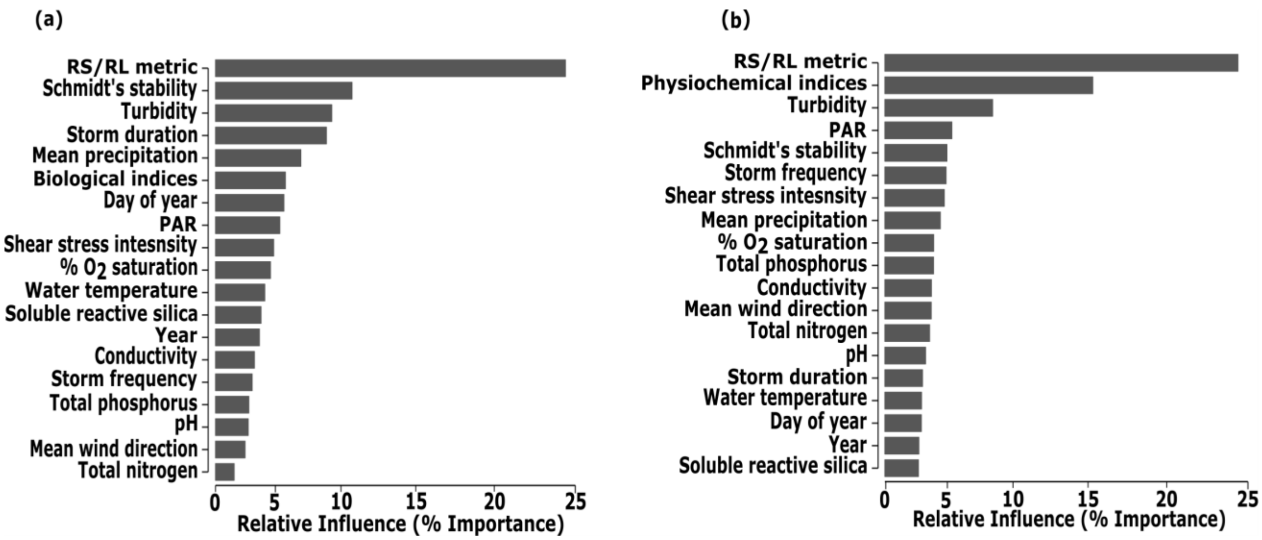

Figure S.5 The bar charts show the relative importance for each of the predictor variables in the biological model (figure a) and physiochemical model (figure b). While we find the same antecedent lake conditions and storm characteristics to important, the order in which they influence the two groups of variables varies. For example, storm duration is much more important for the biological variables, while storm frequency is more important for the physiochemical variables. This provides further insight into the patterns we see in the ecosystem model (figure 6).

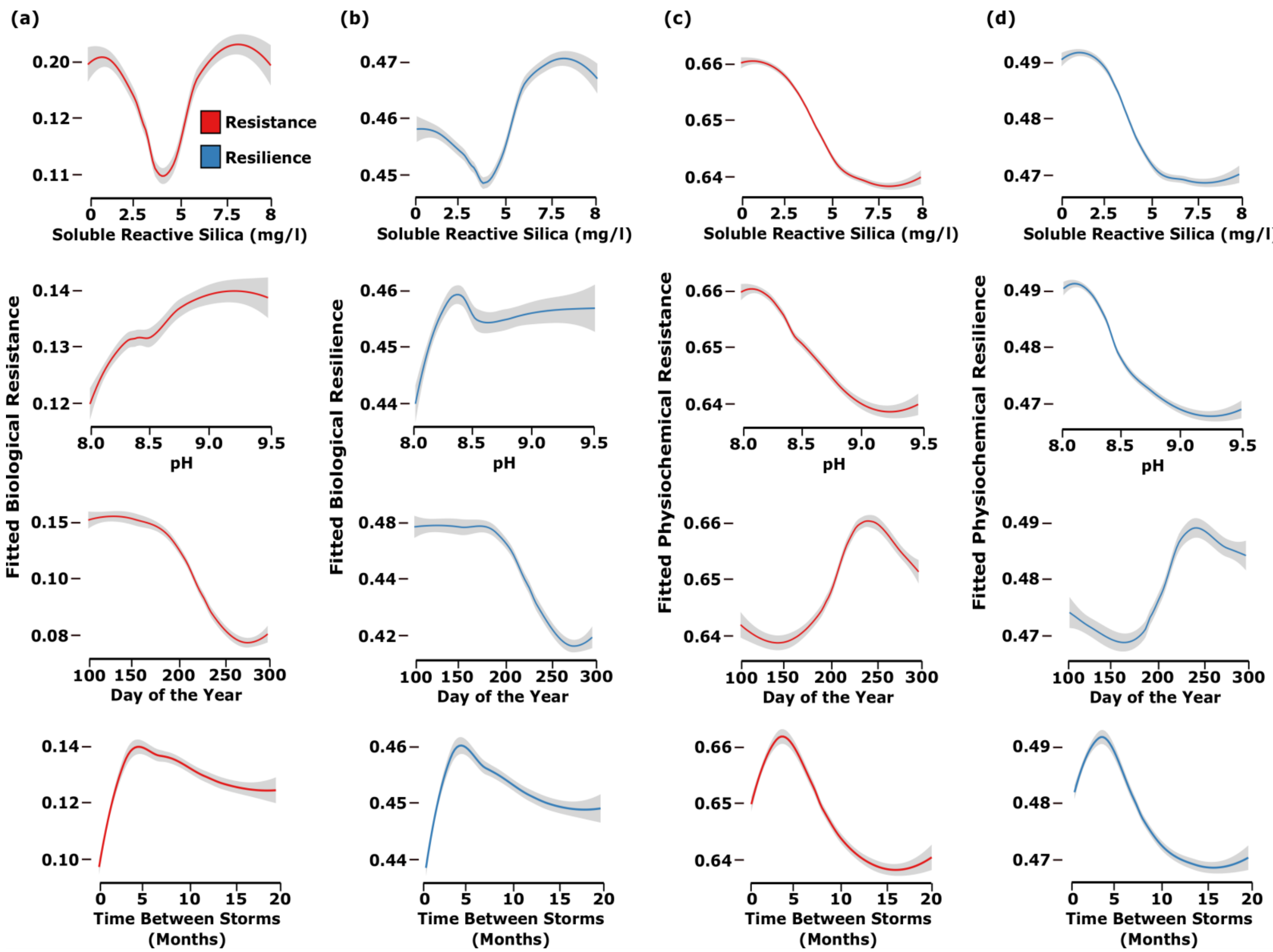

Figure S.6 The partial dependency plots (quantified on a standardized scale from -1 to 1), in columns (a) and (b) show the marginal effects of antecedent lake conditions and storm characteristics on the resistance and resilience of the biological variables, while columns (c) and (d) show the marginal effects in relation to the physiochemical variables. In the figure we see the resulting effects of soluble reactive silica, pH, and day of the 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.

Appendix chapter 1: Supplementary text

Bottom shear stress

A direct consequence of high wind speeds blowing over a lakes' surface is the generation of waves. The orbital motion of the wave is subsequently transferred through the water column towards the lake bottom. If the height of the wave (H) is sufficiently high when the water depth (h) is shallow, the orbital motion of the wave is converted into a back and forth oscillatory motion along the lake bottom (Laenen and LeTourneau 1996). Depending on sediment type, this oscillatory motion of water particles can create a shear force capable of re-suspending sediment. Shear forces capable of re-suspending sediment can be calculated as a function of wave length (L) and water depth, and generally resuspension will occur when water depth is less than one-half the wave length. For the purposes of this study, shear stress as a result of wave generation is considered the primary stressor resulting from extreme and episodic wind events.

Following methodology described by Rohweder et al. (2008) and Laenen and LeTourneau (1996) bottom shear was calculated for every given wind speed and direction as a function of lake depth. Maximum average wind speed (ms) data collected every 5 minutes between 2002 and 2017 was used to calculate shear stress. Because of ice formation on the lake, in some years there is data gaps in the months of December, January, and February. Because of these inconsistencies in winter and our intention to research extreme events during the more productive parts of the year, we used wind data collected between March and November. Prior to calculations all missing data, outliers, and duplicate time stamps for each independent wind speed and direction observation was removed from analysis. Because these data were collected above the lake surface there were no corrections conducted on these data.

To determine the effective fetch, or the unobstructed distance over which wind can travel over the lake surface, a polygon layer of Müggelsee was uploaded into QGIS (version 2.18.15). Using the polygon-to-lines algorithm, the shoreline of Müggelsee was generated and exported as a line shapefile. The regular points and clip algorithm was used to generate a regular grid of points every 100 m inside the lake space and then were exported as a point's shapefile. The grid of points, which are bounded by the shoreline, act as points for which effective fetch can be measured for any given wind direction across the lake. The resulting shapefiles were then imported into R studio using the readOGR function as part of the geospatial R package "rgdal" (Bivand et al. 2017). A list of coordinates was then extracted from the shoreline and in lake point's shapefiles and then converted into latitude and longitude coordinates using the project function as part of the R package "proj4" (Urbanek 2012). The respective lists of converted coordinates were then transformed into SpatialLines and SpatialPoints objects using the "rgdal" package for input into the effective fetch formula. Using the function fetch_len_multi from the R package "waver" (Marchand and Gill 2018) effective fetch was calculated for every possible wind direction. Inputs to the function are the shoreline, in lake points, a vector of wind directions, the maximum possible fetch length, and a vector which represents how many degrees around each primary wind direction should fetch be calculated which was ±10 degrees.

Bottom shear stress was then calculated for every given fetch and for Müggelsees' average lake depth of 5 m. This required the computation of the wave geometry, which includes calculating wave period (*T*), wave length in shallow water (*L*), and wave height (*H*). Calculations of wave geometry were conducted following wave forecasting equations for shallow waters (U.S. Army Corps of Engineers 1984).

$$T = 7.54\left(\frac{U_A}{g}\right)\tanh\left(0.833\left(\frac{gh}{U_A^2}\right)^{0.375}\right)\tanh\left(\frac{0.0379\left(\frac{gF}{U_A^2}\right)^{0.333}}{\tanh\left(0.833\left(\frac{gh}{U_A^2}\right)^{0.375}\right)}\right) \quad (1)$$

Where T is the wave period, U_A is the wind speed, g is acceleration of gravity (9.8), F is the effective fetch, and h is the water depth.

$$L = \left(\frac{gT^2}{2\pi}\right)\tanh\left(\frac{2\pi h}{\left(\frac{gT^2}{2\pi}\right)}\right) \quad (2)$$

Where L is the wave length in shallow water.

$$H = 0.283\left(\frac{U_A}{g}\right)\tanh\left(0.530\left(\frac{gh}{U_A^2}\right)^{0.75}\right)\tanh\left(\frac{0.00565\left(\frac{gF}{U_A^2}\right)^{0.5}}{\tanh\left(0.530\left(\frac{gh}{U_A^2}\right)^{0.75}\right)}\right) \quad (3)$$

Where H is the wave height. The elliptical orbital motion on the lake bottom was calculated from linear wave theory as follows (Komar et al. 1972):

$$u_m = \left(\frac{\pi H}{T \sinh\left(\frac{2\pi h}{L}\right)} \right) \quad (4)$$

Where u_m is the maximum orbital velocity on the lake bottom and H is the mean wave period which is 0.626 (U.S Army Coastal Engineering 1984). The shear stress (τ_w) caused by shallow water waves is then calculated as follows:

$$\tau_w = f_w \rho \frac{u_m^2}{2} \quad (5)$$

Where f_w is the friction factor caused by waves, which is 0.01, and ρ is the density of water. Shear stress was measured in Newtons/m^2 (N/m^2) which is equivalent to 1 pascal. Although there are more sophisticated models for calculating wave geometry, the above equations have been widely used to make inferences about the formulation of waves in fetch limited-shallow water bodies.

GEV R code for analysis

The following code can be used to calculate return periods based on generalized extreme value (GEV) distributions and L-moments summary statistics for parameter estimation of shear stress quantiles.

R > model_fit <- fevd(as.vector(daily.shear.stress.maxima), type = "GEV", method = "Lmoments", time.units = "days")

To estimate return periods for the estimated L-moment shear stress quantiles, we input the location, scale, and shape results (i.e. model_fit [["results"]]) from fitting the extreme distribution model into the return level function below. Model fit results can be found in supplemental figures.

R > return_period <- rlevd(period = 100, loc = 0.2526, scale = 0.1558, shape = -0.0252, type = "GEV")

Seasonal decomposition R code

The following code can be used to seasonally decompose lake variables. In the first line of code we create a data frame that includes a date column and the lake parameter being decomposed.

R > lake.parameter <- as.data.frame(df[,c("date","variable")])

We then transform the data frame into a multi-seasonal time series by inputting the seasonal periods being tested (i.e. daily, weekly, monthly, or annual).

R > seasonal.timeseries <- msts(lake.parameter, seasonal.periods = c(seasonal.components))

We then decompose the trend and seasonal components of the variable under scrutiny. The seasonal window aspect of the function is equal to the seasonal components being tested. The result is a seasonally decomposed mstl object.

R > seasonally.decomposed <- mstl(seasonal.timeseries [,2], s.window = c(seasonal.components))

We then subtract the identified seasonal component by using the seasadj function.

R > adjusted.lake.parameter <- as.vector(seasadj(seasonally.decomposed))

Appendix chapter 2: Pages 123-133 have been removed for copyright reasons.