The role of phytoplankton diversity in driving productivity in light of environmental control

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"In our obscurity, in all this vastness, there is no hint that help will come from elsewhere to save us from ourselves."

— Pale Blue Dot, *Carl Sagan*

Abstract

Accounting for about half the global photosynthetic activity and at least half of the oxygen production, phytoplankton are an incredibly diverse group of unicellular organisms with an important role in aquatic environments maintaining food webs and mediating global biogeochemical cycles. Fast-paced loss of biodiversity poses a threat to ecosystem functioning and its ability to provide services. Understanding the mechanisms driving biodiversity and ecosystem functioning (BEF) relationships is crucial for predicting ecosystem responses to environmental change. BEF theory predicts a positive linear relationship between diversity and productivity, with increasing diversity leading to higher ecosystem function via two main mechanisms: complementarity and selection effects. The extent to which these mechanisms drive phytoplankton productivity in natural ecosystems, however, is still under-explored. Using a combination of mechanistic and statistical modelling approaches, this thesis investigates the role of phytoplankton diversity, particularly taxonomic and size-structured diversity, in shaping ecosystem productivity. Going beyond species richness, we investigate the effects of phytoplankton diversity, as well as, which mechanisms are responsible for driving the relationship between biodiversity and ecosystem function. We used a long-term dataset from the San Francisco Bay, to evaluate how phytoplankton diversity, size structure, and environmental control influence several productivity proxies (e.g. biomass accumulation, resource use efficiency, Chl *a*). These findings challenge the widely accepted positive effect of richness on ecosystem function. In the San Francisco Bay system, diversity and productivity often exhibited a negative relationship, with species richness having a weak effect on ecosystem function. Instead, trait diversity, particularly related to size, emerged as a strong driver of productivity. Environmental control acted on productivity by modulating community composition and size structure. To further investigate the underlying mechanisms, nutrient–phytoplankton (NP) and a nutrient-phytoplankton-zooplankton (NPZ) model including multiple size classes were developed to separate the diversity effect from nutrient enrichment on productivity. Results from these models suggest that nutrient input was consistently the main driver of productivity, particularly at low diversity levels. Species richness plays a secondary role through its interaction with environmental conditions, i.e. nutrient levels. Notably, trophic interactions shift dominant biodiversity effects, which emphasizes the role of predator–prey dynamics in shaping productivity patterns. Finally, we developed a structural equation model (SEM) using both *in situ* and simulation results to quantify causal direct and indirect effects of the environment and diversity on productivity. Unlike traditional bivariate statistical approaches, SEM allows for the simultaneous estimation of multiple causal pathways. Here too, richness had a weak effect on phytoplankton productivity. Instead, environment and community size structure were the main drivers, jointly affecting levels of productivity, with richness playing a secondary role mainly through its indirect effects on size diversity and evenness. Overall, we demonstrate that phytoplankton diversity effects on productivity are strongly mediated by the environmental context and functional traits, rather than species richness alone. By integrating observational and modelling approaches, this work furthers our understanding of BEF dynamics in marine ecosystems and provides new insights into the ecological mechanisms that drive phytoplankton productivity under changing environmental conditions.

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Chapter 1

Introduction

1.1 What is Biodiversity?

Biodiversity is one of the most extraordinary features of our planet. It is also a multifaceted concept that, at its simplest, refers to the number of species in an area. At its more complex, biodiversity is a term used to describe the variety and variation of all life on Earth, encompassing genetic, species and ecosystem diversity. More formally, biodiversity includes the richness of genetically different types within a population, number of species in a given area as well as of ecosystem types, both managed and non-managed and their components (UN, 1992). The first usage of the term is independently attributed to three authors: Laura Tangley, in a report to the US Congress on how to conserve biological diversity in developing countries (Tangley, 1985), Walter G. Rosen, in a national forum on biodiversity in 1986, and to, Robert L. Peters in a comment to a global warming publication he previously co-authored (Peterson et al., 1986; Sarkar, 2021). Still, the term was first used in a book title by Thomas E. Lovejoy in 1988, and only formalized in 1992's Earth Summit in Rio de Janeiro, where the Convention on Biological Diversity (CBD) was proposed, signed and put into force in 1993. DeLong Jr (1996) review of definitions of the term 'biodiversity' highlights the challenge in unifying seemingly different aspects of biodiversity itself (Díaz and Malhi, 2022). Most notably, DeLong Jr (1996) exemplifies the many ways one can define a term, here biodiversity, and in the process create bias towards one's own interests. Either based on derivation of the word, by classification (i.e. attribute or measure), by listing characteristics (e.g. composition, structure, function), by comparison (realized meaning and limitations by contrasting with similar terms), by operation (e.g. how it works, what it does) and political interest. Thus, leading to a trade-off between broader meaning of the term 'biodiversity' and its lack of precision.

A formal unified definition of biodiversity has the power to convey the value and complexity of this concept, ultimately facilitating understanding, communication and management of natural resources. This, however, may come at the cost of compartmentalising biodiversity itself. The main goals of the CBD are related to conservation and sustainable use of biodiversity and its components, as well as fair and equitable sharing of benefits from genetic resources exemplifying the far-reaching potential of biodiversity and its value. However, the value of biodiversity lies beyond CBD's role in mediating interests, management, politics and environmentalism. Biodiversity is a result of 3.5 billion years of Earth's evolutionary processes, being one of the most remarkable features of the planet. According to Kellert (2009), it provides benefits to humanity that encompass direct economic use, scientific, aesthetic and symbolic, humanistic, mental and physical well-being, moralistic and naturalistic. Among these benefits, ecosystem functions (physicochemical and biological processes that maintain an ecosystem) and services (linked to human well-being that can have direct economic value) have a profound relationship with both humans and biodiversity. For a unified understanding of what biodiversity is, we need to be able to quantify, compare, and ultimately interpret its various dimensions.

Several metrics of biodiversity exist to capture the distribution, abundance, and functional roles of species within their respective ecosystems. The simplest measure is species richness, representing the number of species present in a given area. While it is a cornerstone metric of diversity, richness may not capture all ecological complexity of ecosystems (Hillebrand et al., 2018). Other metrics try to address this by including relative measures of species contributions to the community. Shannon's entropy is one of such metrics, where both species richness and their contribution in terms of abundance or biomass are used, with higher values suggesting higher diversity (Shannon, 1948). Evenness, a key component of this diversity, describes how equally individuals are distributed among species in a community. A high evenness value indicates that species are similarly contributing to the community, whereas low evenness reflects dominance by one or a few species. However, biodiversity extends beyond species count and evenness. To fully understand ecosystem functioning, it is essential to consider the functional traits of species. Functional traits are characteristics of species that influence ecosystem properties, or how species respond to their environment (Carmona et al., 2016). Species can be grouped according to these traits to understand general ecological mechanisms or simplify complex ecological interactions. Functional traits can be categorized into response and effect traits. Response traits determine how species respond to environmental changes and disturbances, while effect traits influence how species affect ecosystem properties (De Bello et al., 2010). This distinction is critical when considering biodiversity-ecosystem function (BEF) relationships, as the loss of particular functional traits may have greater consequences for ecosystem processes than species loss alone.

1.1.1 Consequences of biodiversity loss

Fast-paced loss of biodiversity poses a threat to ecosystem function and consequently, its ability to provide services. In the last 10,000 years, the increased rate of loss of species observed, largely due to habitat destruction, has led to a consensus that Earth is facing its sixth mass extinction (Chapin et al., 2000; Hooper et al., 2012; Tilman, 2000). Approximately 0.25% of remaining species are being lost annually. Such estimates are very conservative extrapolations, as the true number of species is unknown and thus, whether or not ecosystem functions and services would be particularly threatened by this is cause for concern. Ecosystem function is defined as all ecological processes that control energy, nutrient and organic matter fluxes in the environment, such as primary production (Cardinale et al., 2012). But, what does biodiversity loss mean to energy flows and biogeochemical cycles that are maintained by ecosystem functions and driven by diversity?

Real-world ecosystems are influenced by multiple interacting factors, such as environmental conditions, species interactions, and disturbances, which makes it challenging to isolate the effects of species richness and trait diversity. The loss of specific functional traits may have a more significant impact on productivity than the loss of species alone. The question of whether species richness or trait diversity is more important for ecosystem functioning remains somewhat unresolved outside controlled experimental settings, but it is not forgotten, and many studies have attempted to link trait diversity to ecosystem functioning in naturally assembled communities (Cadotte, 2017; Chen et al., 2019; De Bello et al., 2010; Hillebrand et al., 2022a; Lavorel et al., 2013; Le Bagousse-Pinguet et al., 2019; Maureaud et al., 2020; Spaak and De Laender, 2021; Sterk et al., 2013).

1.2 Biodiversity and Ecosystem Function

1.2.1 History of Biodiversity and Ecosystem Function research

Going beyond species richness, biodiversity and ecosystem function (BEF) research has a multifaceted view of diversity, focusing on understanding the mechanisms through which ecosystem function can be affected, and ultimately, how it will respond to a rapidly changing climate. Community ecology focuses mainly on explaining what drives and maintains species diversity and coexistence, whereas ecosystem ecology focuses on functional processes maintaining ecosystem functioning, but overlooks the role of ecological interactions among species in it (Loreau, 2010). To understand how ecosystems work, we must account for the feedback between community and ecosystem processes, as ecosystem flows affect community structure and composition, and in return, communities affect the flux of energy and nutrients.

BEF research emerged from the need to close this gap and better understand the relationship between diversity and ecosystem function, becoming a central issue in ecology in the last couple of decades (Cardinale et al., 2009; Tilman et al., 2014; van der Plas, 2019). Interest in the field gained renewed attention in the 90s, after the Earth's Summit in Rio de Janeiro, Brazil. BEF research then came to exist as a response to concerns regarding the increasing species loss and an old paradigm in ecology, the classic productivity-diversity view, where diversity is a consequence of environmental variation and ecosystem function, not a modulator (Hillebrand and Matthiessen, 2009; Loreau et al., 2001; van der Plas, 2019). This means that the BEF view sees diversity not just as an outcome of environmental conditions, but also as an active influence on how ecosystem processes function. By the mid-90s, several scientific articles on the topic were available, and BEF research had already manipulated species richness in experiments in the lab and field, observing links between ecosystem functions, such as biomass production and nutrient cycling, and biological diversity (Cardinale et al., 2006).

Instead of solely focusing on dominant species, the BEF approach recognizes that the combined influence of various species, with their unique traits and interactions, can collectively affect ecosystem functions. In 1994, Tilman and Downing (1994) put forth their seminal paper presenting evidence supporting this idea of a combined influence on ecosystem functioning. This paper was based on >200 grassland plots that differed in diversity and composition due to different rates of nitrogen addition and other disturbances. The authors saw that primary productivity of plots containing more species was more stable and resistant to drought. Naeem et al. (1994) also showed that a more diverse food web had greater primary productivity. Those experiments were designed under a scenario of random loss and gain of species, which allowed them to reach conclusions regarding the effects of species numbers, and to some extent identity, on community-level productivity. However, species loss and/or gains are rarely random in nature and the causality of BEF relations is complex and difficult to determine, with many hypothesised drivers (e.g. abiotic factors, species composition and diversity).

Historically, the BEF field is very experimental. Hundreds of experiments over the last decades have shown evidence linking species diversity with ecosystem functioning across several different taxa and habitat types (Hooper et al., 2005; Loreau et al., 2001; Tilman, 2001; Tilman et al., 2014). There is a general consensus that increasing diversity has a linear positive effect on ecosystem function, based on evidence derived from two main experiments run in the 90s that focused on grasslands. One was the Biodiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems (BIODEPTH) (Hector et al., 1999) that ran across eight countries in Europe and the Cedar Creek Ecosystem Science Reserve experiment in Minnesota, USA (Tilman et al., 1997a). BIODEPTH was a large-scale study conducted across different geographical, climatic and soil conditions with varying levels of species richness (Hector et al., 1999). Hector et al. (1999) provided robust evidence of the positive effect of increased diversity on ecosystem functioning, through means of niche differentiation and facilitation that lead to increased efficiency of nutrient utilisation. Cedar Creek's strengths, on the other hand, lies on its long-term approach.

Both experiments reached similar conclusions regarding productivity, nutrient cycling and stability. A reported log-linear increase of productivity with increasing diversity across different sites that became stronger with time, as well as less variability of function across years. The results of these experiments added to the discussion around methodological concerns, interpretation of results, and the broader implications for ecological theory and conservation policy in the real-world. Criticisms were particularly focused on random species addition and/or removal and other processes that alter community assembly, that may lead to unrealistic communities. Particularly, a 'sampling effect', where the observed increase of productivity of the community is simply due to the increased probability of a highly-productive species to be present with increasing species richness and not an effect of diversity *per se* (Huston, 1997). These experiments were designed to isolate the effects of species richness from other factors such as climate, nutrient availability and presence of certain functional types. Yet, these factors can also alter ecosystem function (Jochum et al., 2020). As such, the relevance of these conclusions are questioned when thinking about real-world ecosystems (Huston, 1997; Wardle, 2016). Despite not fully capturing the complexity of natural environments, researchers argue that these experiments still provide valuable insights into the mechanisms driving the relationship between biodiversity and productivity whilst still acknowledging the importance of environmental control (Duffy et al., 2017; Loreau, 2010; Loreau and Hector, 2001; Tilman et al., 1997a).

1.2.2 Selection and Complementarity effects

As Loreau (2010) shrewdly remarked, empirical and theoretical research are usually disconnected in Ecology, and BEF experiments outpaced theory, with no theoretical framework to work upon. But soon theory caught up with empirical research, and two main classes of mechanisms were proposed to clarify the effects of biodiversity on productivity. This new approach termed the *additive partitioning* of biodiversity effects and, analogous to the Price equation in evolutionary genetics, separates the effects of diversity into two: i) complementarity and ii) selection effects, which then allowed researchers to assess the contribution of these mechanisms in previously run experiments (Loreau and Hector, 2001). Price's equation describes how changes of community properties occur in a population under selective pressure from one generation to another (Price, 1970). Loreau and Hector (2001) adapted this framework to separate and quantify diversity effects on productivity via selection and complementarity. This approach made clear that diversity affects ecosystem function by means of species' individual traits and interactions related to the function being observed. In other words, if the addition of new species does not increase trait diversity, the effects of increasing species richness might not be important. In addition, the partitioning helped demonstrate that the 'sampling effect' is just an extreme case of the selection effect, which is in turn an analogue of the evolutionary process of selection, and not a mere statistical artifact. Finally, many subsequent studies have built upon these ideas and have demonstrated that the results observed in experimental conditions are indeed relevant for real-world environments (Duffy et al., 2017).

After much debate, a general consensus was reached, at least for terrestrial ecology, from both theory and experiments that form the foundation of the BEF field of research (Cardinale et al., 2012). First, biodiversity loss can reduce resource use efficiency and biomass production in communities. This appears to be consistent and although the mechanisms involved are not fully resolved, the loss of species has an effect on ecosystem functioning across taxa, trophic levels and habitats (Cardinale et al., 2006; Chapin et al., 1997; Tilman et al., 2014). Secondly, biodiversity increases stability of functions with time - here diversity allows for more resilient communities, with a larger range of traits and consequently, resource capture strategies and biomass production under disturbances (Loreau et al., 2001; Naeem et al., 1994). This interacts with the fact that effects of biodiversity on ecosystem function are non-linear, saturate with time and changes accelerate with increasing diversity loss; with a more resilient, therefore, stable community being more capable of buffering any negative compound effects of species loss. Diverse communities produce more because they have key species with larger influence on productivity (i.e. selection effects) and the differences in traits among these organisms increase resource use efficiency (i.e. complementarity effects). In this thesis, the role of species richness *per se* in driving productivity is questioned. However, it has been made clear that both the identity and the diversity of organisms jointly control the functioning of ecosystems (up to 50% of the net biodiversity effect) (Cardinale et al., 2011). Loss of diversity across trophic levels may have an even stronger effect on function than within levels. Food web interactions are key mediators in ecosystem functioning and loss of higher consumers can cascade through the web (Duffy et al., 2017). Finally, loss of functional traits in a community can have a much larger impact on ecosystem function, with magnitude of function change being highly dependent on which traits are lost (Hooper et al., 2005). These effects are variable, ranging from reduction of efficiency of the ecosystem to increased productivity and stability, highlighting the complex feedback between community and ecosystem.

Complementarity effects generally have a positive effect on ecosystem function, that arises from and helps maintain diversity and can be predicted by species' traits. Conversely, selection helps to reduce diversity, at least in static environments. Selection effects are more variable too (positive and negative) and more dependent on focal systems, organisms, spatial and temporal scales and spatial heterogeneity. For example, harvesting, as opposed to random losses, may drive key species to extinction. As such, the performance of species and the order of species loss can be highly variable and have strong effects on ecosystem function. The 'sampling effect' can then be broken down into two independent parts. A probabilistic sampling, which increases the likelihood of including diverse traits, and a deterministic selection part, where the most productive species is favoured by competition and dominates to the point of excluding its competitors (Loreau and Hector, 2001). These effects then should not be disregarded as an artefact. Instead, they represent biologically significant processes that parallel how natural selection operates in evolution. The selection of competitive species may be particularly important on fluctuating environments for long-term composition and productivity.

By this partition and interpretation, complete dominance of a single species (i.e monoculture) is not required for positive selection effects to be observed. This more flexible interpretation reconciles both complementarity and selection effects and it shows that the presence of a few key species can disproportionately affect ecosystem functioning, without complete exclusion of species. Thus, both (i) and (ii) effects are not mutually exclusive and can work synchronously, with diversity being responsible for creating a range of traits that these effects can act upon (Cadotte, 2017; Loreau, 1996, 2010; Loreau et al., 2001).

1.2.3 Phytoplankton diversity and its role on ecosystem function

Phytoplankton are an incredibly diverse group of unicellular organisms, taxonomically and phylogenetically, with around 4,300 species described and likely many more still to be discovered (Falkowski et al., 2003; Righetti et al., 2020). Accounting for about half of global photosynthetic activity and at least half of global oxygen production, phytoplankton have an important role in aquatic environments, despite contributing to only 1% of the global photosynthetic biomass (Falkowski, 2012; Field et al., 1998). They are a key link between the surface ocean and higher trophic levels, helping sequester carbon dioxide as well as feeding a huge portion of the food webs, due to their fast turnover rates (days as opposed to decades like trees) and distribution over a large surface area (the oceans). As such, they are paramount in maintaining aquatic food webs and in modulating global biogeochemical cycles and climate, surpassing the contribution of all terrestrial plants combined (Behrenfeld et al., 2001; Falkowski, 2012). Temperature, light, nutrient and CO_2 all affect phytoplankton physiology and stoichiometry and therefore, ability to grow and maintain ecosystem function and services (Moreno et al., 2018). With that, phytoplankton have an important role on Earth's biological pump as well, while also contributing to the microbial loop via remineralisation (Azam and Malfatti, 2007).

Although oceans cover over 70% of the Earth's surface, the links between phytoplankton diversity, environmental parameters, and productivity pose a challenge on BEF studies (Duffy et al., 2017; Otero et al., 2020; Ptacnik et al., 2008; van der Plas, 2019). For instance, pelagic ecosystems do not abide to the same geographical constraints as terrestrial systems, being an unstructured fluid environment. This open and highly-mixed environment imposes interesting limitations on the structuring of planktonic communities, which have led to 'Paradox of the Plankton' problem (Hutchinson, 1961). Hutchinson's paradox relates to the controversial observations of high diversity of plankton in nature, in contrast to the expectations of the competitive exclusion principle.

First described by Volterra (1928) but since then explored, the principle states that *n* species cannot coexist under a regime with fewer than *n* resources and/or niches, at least in static environments (Armstrong and McGehee, 1980; Hardin, 1960). As such, under the homogenized nutrient conditions found in the oceans, diversity of phytoplankton should be low, as one species would out-compete all others and become dominant. This clash between theoretical expectation and *in situ* observations gave rise to numerous attempts to understand what mechanisms allow for the coexistence of species. Finding 'solutions' to the paradox became particularly important for studies that model phytoplankton diversity, where competitive exclusion is a common behaviour (Armstrong and McGehee, 1980; Record et al., 2014).

Several mechanisms have been put forward to explain this paradox, relating to trophic, temporal and spatial differences that can be classified as either stabilizing, i.e. processes that increase negative within-species interactions relative to across-species interactions; or equalizing, i.e. processes that reduce fitness differences (Chesson, 2000; Wilson, 2011). Sampling techniques used also underestimate microbial diversity in the oceans (Cermeño et al., 2013). The relative lack of barriers leads to greater resource transport and homogenization rates, greater organisms' dispersal capabilities, fast turnover rates, and higher response rates to large-scale environmental variation and stronger competition among species. So, high diversity of phytoplankton communities coupled with sampling biases hinders accurate BEF assessments (Chao et al., 2014).

Most literature focuses on terrestrial plants and the Global North. As such, studies of BEF in natural aquatic communities are still scarce, making general conclusions difficult (Hooper et al., 2005; van der Plas, 2019). In both freshwater and marine environments, phytoplankton diversity has been linked to increased ecosystem productivity and stability (Cardinale et al., 2011; Gamfeldt et al., 2015; White et al., 2020). Unlike terrestrial systems, in which both selection and complementarity equally drive diversity effects, mechanisms described driving this relationship in aquatic environments often involve mostly niche complementarity, where different species utilise resources in slightly different ways (Cardinale et al., 2011; Loreau et al., 2001). Aquatic environments in general are less structured, with quick population turnover rates and strong vertical gradients of abiotic factors (e.g. temperature, light, salinity, nutrient), vast spatial coverage and fluid nature (e.g. currents, mixing processes) and large temporal variability of disturbances. Furthermore, marine communities are more sensitive to changes in nutrient input and to its environment, with greater connectivity between populations as opposed to terrestrial systems with their 2D-structure and more distinct boundaries (Carr et al., 2003).

Marine ecosystems are also more functionally, phylogenetically and taxonomically diverse than land habitats, with pelagic primary producers spanning several kingdoms and widespread across all oceans (Carr et al., 2003). This leads to increased redundancy of traits and consequently, to an increased buffering capacity against species loss (i.e. higher resilience, Gamfeldt et al. (2015)). Functional traits are usually overlooked when addressing this question and it may be an important aspect of diversity to help us elucidate the trade-offs involved in the BEF relationship in the oceans (Cadotte, 2017; Edwards et al., 2013). Adaptive capacity of a phytoplankton community is increased under frequent and intense disturbances at the cost of higher productivity in the long-term where conditions may be more stable. That way, environmental conditions will select functional types (i.e. increased size diversity) that more likely will endure rapidly changing conditions in the short-run, but will grow slowly when compared to less diverse communities in periods of infrequent disturbance (Smith et al., 2016). The effect of diversity on productivity under environmental disturbance across larger temporal and spatial scales, increased range and level of diversity (e.g. functional, genetic, phylogenetic) and also its effect on ecosystem multi-functionality remains to be more deeply explored. Levels of optimal diversity for maximizing productivity will be determined by the frequency and intensity of environmental disturbance. Temporal and spatial scales by themselves do not govern diversity effects, but rather environmental variability co-varying with space and time. Which can lead to erroneous conclusions based on spurious correlations (Cardinale et al., 2011; Cardinale et al., 2006; Gamfeldt et al., 2015).

1.2.4 Functional diversity as a way forward

Trait-based approaches provide valuable tools for linking diversity to ecosystem function, especially through mechanisms such as niche complementarity and functional redundancy (i.e., multiple species with similar traits) (De Bello et al., 2010; Hillebrand et al., 2022a; Vallina et al., 2017). Functional diversity can be broken down into three main components:*functional richness, functional evenness, and functional divergence*, which can be assessed at various scales (Mason et al., 2005). However, defining and quantifying functional groups and diversity within a community can be challenging due to arbitrary decisions about groupings and the dependence on the specific ecosystem function under consideration (Hooper et al., 2005; Mlambo, 2014). Most BEF studies focus on effect traits, with response traits providing insights into potential changes in species distributions. To fully understand how ecosystems will respond to rapid climate change, it is essential to integrate both concepts.

Despite its potential, using functional traits are not always straightforward and requires careful consideration of context and measurement. How loss of diversity will affect ecosystem function and services might be scale-dependent (both spatial and temporal), but might also depend on what facet of biodiversity research is focused on. A key challenge is disentangling the relative roles of functional diversity and environmental drivers in shaping these relationships, as this is essential for making robust predictions about ecosystem health and function.

Cell size is considered to be a ‘master’-trait, being crucial for several ecophysiological processes such as metabolism and sinking rates (Brown et al., 2004; Hillebrand et al., 2022a). Size of cells can also potentially mediate trade-offs between traits that affect competitive abilities for resource acquisition, growth rates and even grazer resistance, and ultimately, organism’s fitness (i.e. its reproductive success) (Belgrano et al., 2002; Brose et al., 2006; Enquist et al., 1998). The role of phytoplankton on the ecosystems is directly related to their community composition, due to many species-specific strategies for nutrient acquisition, carbon sequestration, defence and even edibility to potential predators (Capone and Carpenter, 1982; Smayda, 1997; Smetacek, 1999; Sterner and Hessen, 1994). Further, they are highly abundant, with fast turnover rates with sizes ranging from 1μ up to several millimetres, making phytoplankton a great tool to study fundamental ecological questions.

Understanding how functional diversity, particularly size-structured diversity, influences phytoplankton productivity is critical for predicting ecosystem responses to environmental change. Moving forward, a more mechanistic understanding of how trait-based trade-offs influence biodiversity–ecosystem function relationships will be key to improving models of marine primary production and biogeochemical cycles.

1.2.5 Modelling vs empirical approaches

One of the major criticisms towards experimental studies in the BEF field concerns the validity of their observations when extrapolating results to non-controlled natural settings (Balvanera et al., 2006). When dealing with phytoplankton, very few studies have directly manipulated species richness and its effect on productivity. While both terrestrial and marine ecosystems exhibit important BEF relationships, the marine environment imposes unique challenges.

Most empirical approaches focused on terrestrial habitats, where modelling approaches cannot fully capture their complexities (Cardinale et al., 2012; Isbell et al., 2018; Jochum et al., 2020; Tilman et al., 2014). Models allow us to simplify systems and test theories that can then be extracted into mechanisms that eventually can be used on large-scale predictions. Similar to experimental studies, models often predict that higher diversity is associated with higher productivity, albeit from different approaches when compared to experiments (Cardinale et al., 2004; Tilman et al., 1997b). Models often introduce diversity by means of manipulating the temperature-, nutrient and/or light-axis; and how species' functional diversity within those axis affects productivity (Chen et al., 2019; Goebel et al., 2014; Vallina et al., 2017; Vallina et al., 2014). Due to tractability of results, modelling studies tend to be less complex than empirical ones. This is a powerful advantage, where we can bypass several shortcomings usually found in empirical studies (e.g. duration of experiments, high diversity in the oceans). On the other hand, models often require strict assumptions about species interactions and environmental responses that may not fully reflect real-world complexities.

Numerical models can give us the opportunity to isolate and quantify specific levels of diversity effects on ecosystem productivity with a high level of mechanistic understanding, while also being able to control environmental heterogeneity and disturbance to a certain level (Chen et al., 2019; Vallina et al., 2014; Vallina et al., 2023). Caution is warranted when scaling up conclusions, as some studies report contrasting findings hinting at how variable this relationship can be depending on scale, environmental context and species interactions (Barry et al., 2021; Tao et al., 2024). Still, some consensus was reached based on both model and empirical results, such as higher species richness leading to overall higher functionality, namely a strong positive effect on biomass, nutrient cycling and resource use efficiency in freshwater and marine systems (Otero et al., 2020; Ptacnik et al., 2008; Tilman, 2001), as well as increased ecosystem stability, resistance and decreased variability in productivity over time in the face of environmental changes (Isbell et al., 2011; Isbell et al., 2018; Vallina et al., 2017). Both approaches can be seen as complementary to each other and their integration can improve our understanding of how phytoplankton diversity affects ecosystems.

1.3 Thesis Aims

This study is focused on developing a causal understanding of BEF relationships in natural and simulated phytoplankton communities. I want to understand how their role in the oceans will be affected, by means of determining what drives phytoplankton productivity across different spatial and temporal scales, diversity levels and environmental changes. Specifically, by using available data of naturally assembled phytoplankton communities and statistical and mechanistic models, I want to:

1. investigate the mechanisms (i.e. complementarity vs selection effects) driving the relationship between biodiversity and ecosystem function, going beyond species richness and exploring how phytoplankton diversity affects ecosystem functions such as biomass accumulation, Chl *a* and resource use efficiency
2. understand ecosystem function responses to diversity and environmental changes by analysing long-term *in situ* data from the San Francisco Bay estuary region, focusing on the role of environmental drivers (e.g. light, nutrient) and diversity (i.e. size structure) shape phytoplankton community-level functioning
3. fill key gaps in our understanding of BEF in marine ecosystems, providing insight particularly into which aspect of diversity (e.g. richness, size diversity, evenness, trait) influences ecosystem function in light of environmental control

1.4 Thesis Structure

The thesis is divided into in five chapters, each addressing different aspects of the relationship between biodiversity and ecosystem functioning (BEF) in marine ecosystems, with a particular focus on phytoplankton communities. Each chapter follows a 'journal article' style, with an introduction specific to its objectives, methodology, results, main discussion and conclusions. **Chapter 1** refers to the introduction to the field and its main findings to date, what kind of methods were used and its main drawbacks, the representation of aquatic ecosystems and the role of empirical vs modelling approaches. **Chapter 2** is a description of the data used for the entire thesis, its main features, advantages and disadvantages, as well as a description of the main methods used to transform and analyse the dataset. In **Chapter 3** I focus on the relationship between diversity and productivity in a naturally assembled community and its drivers, based on bivariate and multivariate analyses, in order to understand the specific roles of diversity and the environment in driving community-level productivity. **Chapter 4** summarises the results of nutrient-phytoplankton (NP) and nutrient-phytoplankton-zooplankton (NPZ) models, investigating the effect of diversity on productivity under varying nutrient and diversity levels, driving mechanisms and effects across trophic levels. **Chapter 5** comprises the results of a structural equation model (SEM) that was parametrised on both *in situ* and simulation data to assess both direct and indirect effects of the environment, diversity and different scales on productivity. Finally, I end the thesis with the main conclusions and outlook of the field.

Chapter 2

Data description

2.1 Rationale

The aim of this chapter is to describe all relevant information from the data set used in this thesis, its sources and how to access it, as well as all data processing performed, and potential limitations. I present results of data distribution across time and spatial scales, focusing on general trends. In addition, the San Francisco Bay (SFB) region long-term monitoring has resulted in a high quality data set with a large spatial and time coverage, detailed information regarding phytoplankton taxonomy, as well as nutrient and abiotic parameters. This makes the SFB system a great setting to investigate the effects of environmental control on ecosystem productivity.

2.2 Data collection and source

The *Water Quality of San Francisco Bay project* is a long-term monitoring study of the San Francisco Bay delta-system run by the U.S. Geological Survey (USGS), with the primary goal of water quality management. All detailed information can be found in Schraga and Cloern (2017) and on the project's website (https://sfbay.wr.usgs.gov/water-quality-database/).

Water-quality measurements of near-surface sampling stations along a 150 km transect were taken from 1969 to present day across the four subregions: the South, Central, North and Suisin bays (Figure 2.1) (Cloern et al., 2017). The database consists environmental parameters, such as chlorophyll *a*, suspended particulate matter (SPM), dissolved oxygen, and dissolved inorganic nutrients (nitrite, nitrate + nitrite, ammonium, phosphate and silicate) measured from discrete water samples and shipboard sensor-derived parameters: depth, calculated chlorophyll *a*, dissolved oxygen, oxygen saturation, calculated SPM, extinction coefficient, salinity, temperature, and sigma-t. Furthermore, phytoplankton composition and abundance (cells mL^{-1}) were obtained via analyses of samples collected between 1992-2021 using light microscopy. Cell volume and biovolume of each phytoplankton taxa were subsequently calculated. All measurements are regularly calibrated. Details on methods and data validation are available online (Cloern et al., 2017; Schraga and Cloern, 2017) and data sets can be downloaded via the website for phytoplankton, here (https://www.sciencebase.gov/catalog/item/5908f489e4 b0 fc4e448ffff1) and for water quality measurements, here (https://www.sciencebase .gov/catalog/item/5966abe6e4b0d1f9f05cf551) (Schraga and Cloern, 2017). The specific data used in this thesis, can also be found in Appendix A.

2.3 San Francisco Bay

The San Francisco Bay (SFB) is located in northern California (USA) and the area has been an object of investigation by the US Geological Survey (USGS) for over five decades (1969-present). The bay area comprises two geographically and hydrologically distinct estuaries within a salinity gradient: the North and South Bays (Conomos et al., 1985). The North Bay includes the Suisun and San Pablo Bays and receives primarily freshwater input, being the estuary of the Sacramento and San Joaquin rivers. South Bay is a shallow marine lagoon subject to tidal processes situated in the urban area. These estuaries are connected by the Central Bay, under the influence of the Pacific Ocean's coast tidal processes and wind-driven coastal upwelling (Cloern,

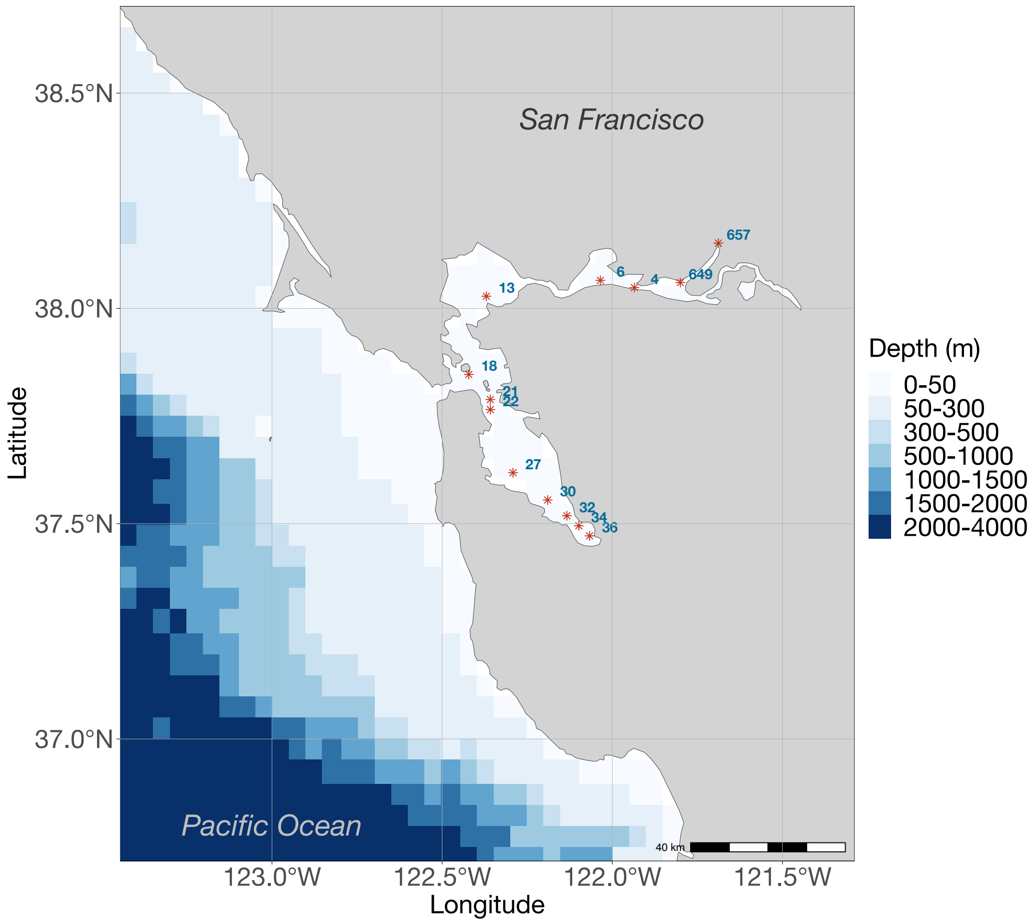

Figure 2.1: **Map of study area.** San Francisco Bay stations sampled by the USGS used in this study located on the Pacific coast. North (Stations 657, 6, 13), Central (18, 22) and South bays (27, 32, 34, 36) were used in the analyses.

2018; Cloern et al., 2017; Cloern et al., 2020; Raimonet and Cloern, 2016). Through its connection between land and ocean, estuarine ecosystems such as the SFB area, are under the effect of river discharge, urban and agricultural run-off, nutrient and environmental variability (Cloern et al., 2017; Raimonet and Cloern, 2016).

2.3.1 Environmental and phytoplankton data

Samples (n = 677) were defined based on unique sampling location, date and depth. Prior to that, I cross-checked phytoplankton taxonomic data with the AlgaeBase and World Register of Marine Species (WoRMS) databases, aiming to retrieve all missing information regarding Phylum, Class, Order, Family, Genus and Species as well as update any non-accepted taxonomic details. Any samples with missing phytoplankton information were removed from the dataset.

Mean temperature, salinity, dissolved inorganic nutrient (DIN), phosphate, silicate and chlorophyll *a* (Chl *a*) values were calculated for each sample. Due to missing light availability information, I used imputation to predict values of interest by using Chl *a*, latitute and longitude coupled with available extinction coefficient (Ext$_{coeff}$) and surface photosynthetic active radiation (PAR) values to estimate PAR for each sample, assuming a mixed layer depth (MLD) of 2 m [Equation 2.1]. Size of each species was estimated as the log-transformed equivalent spherical diameter (ESD, µm) using cell volume [Eq. 2.2]. Cell volume (V, µm^3 cell^{-1}) was transformed into cell carbon content (pg C cell^{-1}), following Menden-Deuer and Lessard (2000) [Eq. 2.3], with different scaling constants for diatoms and other phytoplankton types. Biomass was then estimated as the amount of carbon per sample (µg mL^{-1}) based on species' relative abundances. Resource use efficiency (RUE) was calculated as the natural logarithm of the ratio of phytoplankton carbon biomass to nutrient concentration (DIN). Environmental variables used can be found in Table 2.1.

$$PAR = \frac{PAR_s}{Ext_{coeff} \times MLD}(1 - e^{Ext_{coeff} \times MLD}) \tag{2.1}$$

$$ESD = (6\frac{V}{\pi})^{1/3} \tag{2.2}$$

$$C_{cell} = aV^b \tag{2.3}$$

2.3.2 Size and Taxonomic Diversity

Community weighted mean size (CWM$_{size}$) was estimated in each sample using natural log-transformed ESD (lnESD) values and the proportion of phytoplankton biomass (p_i) of n number of taxa, following De Bello et al. (2021) [Eq. 2.4]. Size diversity (σ^2) was then determined as the biomass-weighted variance of individual phytoplankton sizes around the CWM$_{size}$ [Eq. 2.5].

$$CWM_{size} = \sum_{i=1}^{n} \ln\mathrm{ESD}_i \times p_i \tag{2.4}$$

$$\sigma^2 = \sum_{i=1}^{n} p_i \times (\ln\mathrm{ESD}_i - CWM_{size})^2 \tag{2.5}$$

Species richness (R) and the Shannon's entropy [Eq.2.6] were used as estimates of taxonomic diversity. Richness is the easiest measure to obtain, consisting of the number of species present in the community. However, in practice, species' richness may be subject to sampling bias with richness increasing with sampling effort. Here, ^1D, as the effective number of species, accounts not only for presence, but also for commonness and rarity of species in a community, where R is the total number of species and p_i is the proportion of individuals' abundance or biomass that contributes to the entire sample (Jost, 2006). ^1D can be estimated as the exponential of Shannon's entropy. Finally, evenness was estimated as Hill's evenness [Eq. 2.7]. Values range between 0 and 1, for low and high evenness respectively. Furthermore, a total of 43 samples with $R = 1$ were removed from analyses. Diversity metrics used can be found in Table 2.1.

$$H = -\sum_{i=1}^{R} p_i \times \ln p_i \tag{2.6}$$

$$Evenness = \frac{^1D}{R} \tag{2.7}$$

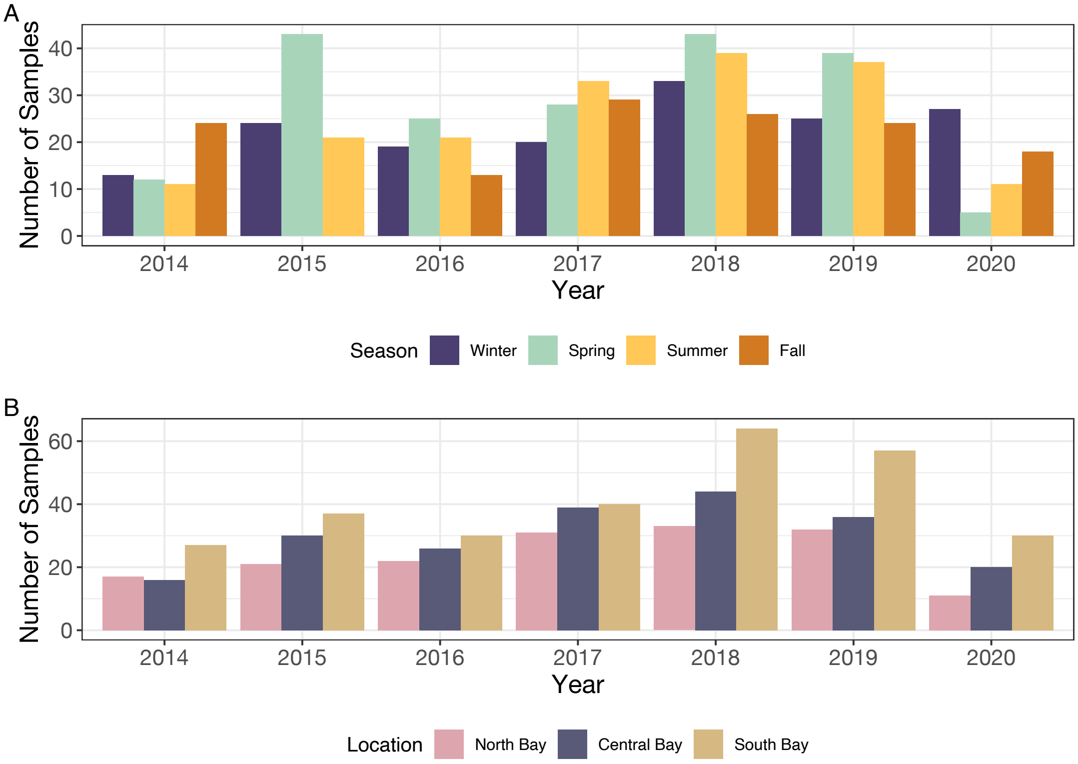

Figure 2.2: **Number of samples per season and region over time.** Samples are more frequent during spring (n = 195), followed by summer (n = 173), winter (n = 161) and fall (n = 134). South bay is more represented (n = 285), then Central (n = 211) and North bays (n = 167).

2.4 Results

2.4.1 Environmental and diversity data

Samples were more frequent at the South Bay (n = 285), followed by the Central (n = 211) and North Bays (n = 167). Regarding seasonal representation, most sampling in the dataset relates to spring (n = 195), summer (n = 173), winter (n = 161) and fall (n = 134) (Fig. 2.2).

Biomass, chlorophyll *a* (Chl *a*) and resource use efficiency (RUE) distributions are right-skewed, indicating that while most stations exhibit low to moderate values, there are occasional high concentration events usually in springtime (Figs. 2.3-2.4). Further, biomass and DIN are decreasing over time, whereas RUE seems to be in-

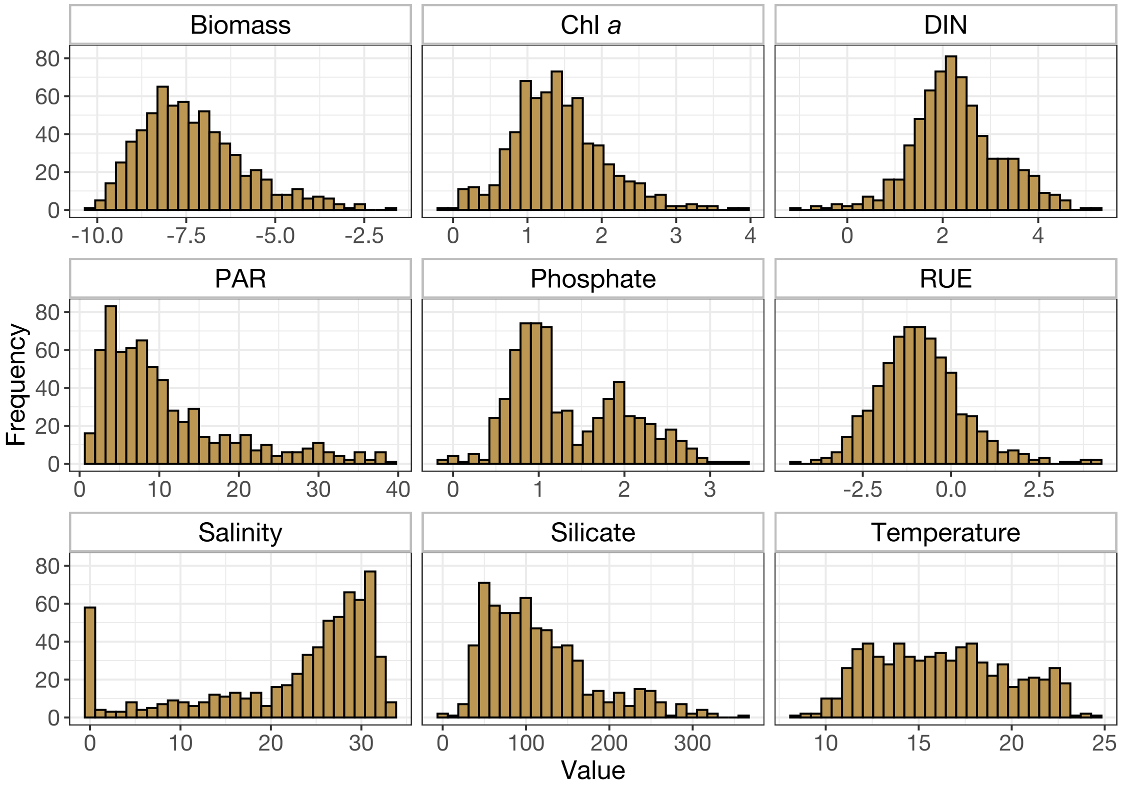

Figure 2.3: **Histograms with data distribution of productivity proxies (biomass, Chl *a*, RUE) and environmental variables.** Biomass (ln μg mL^{-1}), Chl *a* (ln mgL^{-1}), DIN (μM), phosphate (μM) and RUE are log-transformed. All other variables are in raw units: silicate (μM), PAR (μmol $m^{-2}s^{-1}$) and temperature (°C).

creasing. PAR distribution suggests a low light availability most of the time (Fig. 2.3), with variability also associated with seasonality (Fig. 2.4).

Nutrient measurements do not reflect actual fluxes, and therefore the phytoplankton community uptake. Phosphate showed a bimodal distribution likely also associated with seasonality effects and spatial scale (i.e. North vs South bay regions) (Figs. 2.3,2.4). DIN, on the other hand, is subject to a stronger seasonal and inter-annual variability, with a sharp decrease between 2015 and 2016, but varying less spatially (Figs. 2.3, 2.4, 2.7). Silicate levels were considerably high in the dataset, as such, I did not include it in further analyses. However, this nutrient showed an increase with time, but no clear seasonal and/or spatial patterns, likely due to urban run-off leading to eutrophic conditions and low phytoplankton uptake (Figs. 2.4, 2.7, 2.3).

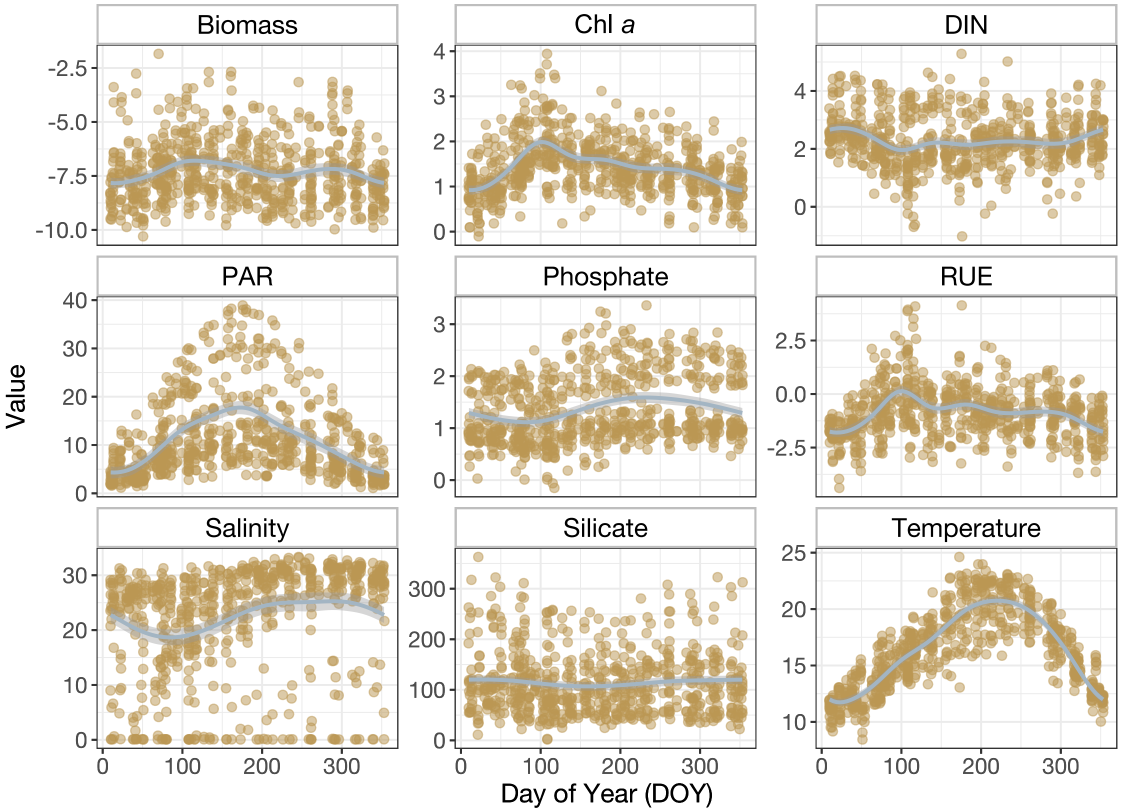

Figure 2.4: **Seasonal variation of productivity proxies and environment-related variables.** Seasonal trends were smoothed using a generalized additive model (GAM) with cyclic splines, illustrating the variability for each variable. Note that y-axis are different. Biomass (ln μg mL^{-1}), Chl *a* (ln mgL^{-1}), DIN (μM), phosphate (μM) and RUE are log-transformed. All other variables are in raw units: silicate (μM), PAR (μmol $m^{-2}s^{-1}$) and temperature (°C).

Temperature and salinity reflect the observed gradients in the San Francisco Bay. Salinity is strongly influenced by the spatial distribution of the stations (i.e. high freshwater input in the North Bay vs saline intrusions in the South region) (Fig. 2.7) as well as by levels of precipitation and river discharge throughout the year (Fig. 2.4); (Cloern et al., 1985; Cloern et al., 2017). Temperature is also under a strong seasonal influence (Fig. 2.4) with warmer temperatures during the dry season (summer and fall), with inter-annual but not strong spatial variations (Fig. 2.7).

Diversity-related metrics were also transformed, aiming for a normal distribution approximation. Evenness was slightly left-skewed, suggesting that most values were

Table 2.1: **Diversity metrics and environmental variables used and their units.**

Variable	**Unit**
Temperature	$^{\circ}C$
Salinity	-
PAR	μmol $m^{-2}s^{-1}$
CWM$_{size}$	ln μm^3
Size Diversity (σ^2)	(ln $\mu m^3)^2$
exp Shannon (^1D)	-
Richness	-
Genus Richness	-
Hill's evenness	-
Phosphate	μM
Silicate	μM
DIN	μM
Biomass	ln μg mL^{-1}
Chlorophyll *a*	ln mgL^{-1}

intermediate to high, and therefore more even communities were present (Fig. 2.5). Diversity indices were all spatially, seasonally and inter-annually affected at varying degrees. Apart from evenness and size diversity, all other proxies display a long-term decrease (Fig. 2.8, 2.6). Higher richness was observed at the northernmost stations, decreasing towards the south (Fig. 2.8).

Some gaps can be seen across species and genus richness distributions (Fig. 2.5). I believe this is likely due to predation, as a small bloom of *Protoperidinium* sp. was observed in the data and the gap seen in the size distribution is reasonably within their prey range. Low taxonomic resolution of samples may also have lead to their removal from analyses, and thus, gaps in the size spectra. The seemingly weak seasonal signal observed for exponential Shannon (^1D) may reflect the species composition and dominance, and therefore, evenness component of the community. Evenness is strongly affected by the spatial component, with generally higher evenness southwards, and the seasonal component, with a decrease during spring. Size diversity also decreases around springtime, suggesting that seasonal environmental changes may create conditions that favour a few dominant species or size classes, leading to lower overall size diversity and evenness. Thus, size structure seems to be an impor-

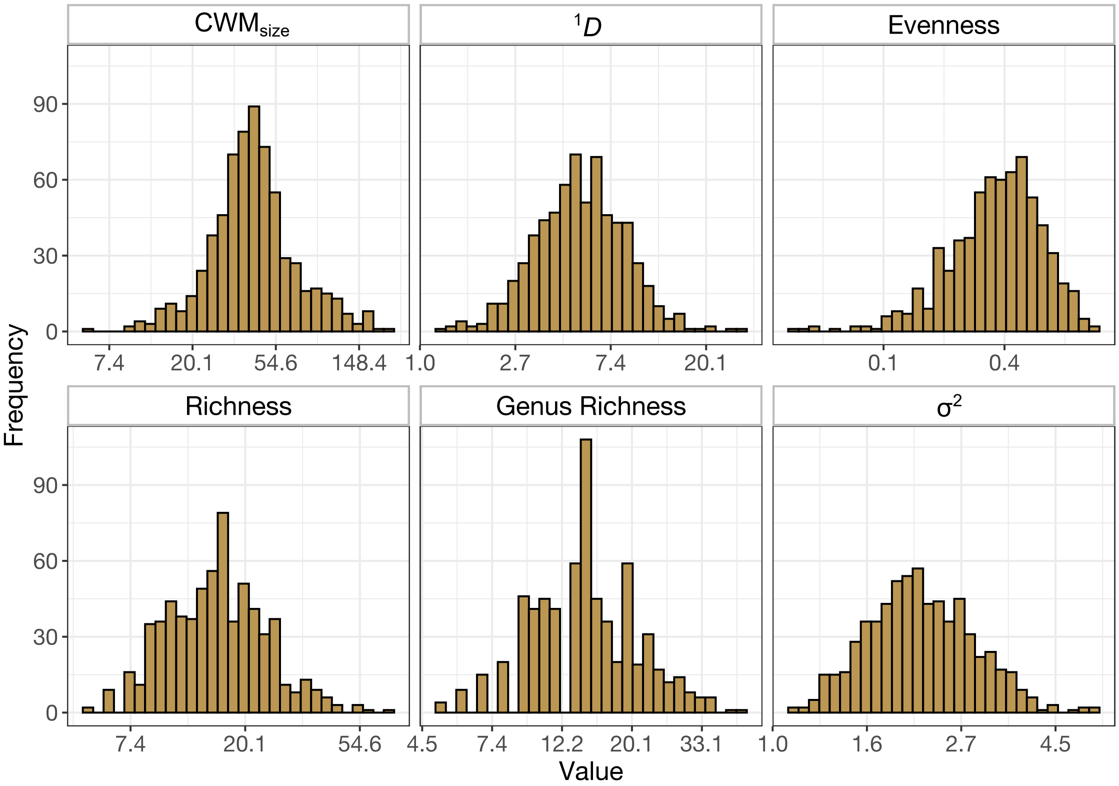

Figure 2.5: **Histograms with data distribution of diversity indices.** Diversity proxies relate to size (CWM$_{size}$: community weighted mean size, σ^2: size diversity) and taxonomic identity (^1D: exp Shannon, species and genus richness) of organisms. All variables are in their raw units.

tant factor in shaping community evenness, instead of richness, alongside temporal and spatial drivers. Community weighted mean size also peaks during spring and late fall, with variability across stations (Fig. 2.8, 2.6) that could also reflect this shift in size composition of the community.

2.4.2 Phytoplankton community structure and composition

In total, 583 species across 247 genera and 127 families were observed in the San Francisco Bay (SFB) system between 2014 and 2020. Only ten species were found in more than 50% of all samples, with *Eucapsis microscopica* being the most common species (Table 2.3). Individual cell volumes ranged between 0.18 μm^{3}cell^{-1} and 1.05 x 10^8μm^{3}cell^{-1}. Cell sizes ranged between 0.7 and 534 μm, with *E. microscopica* and

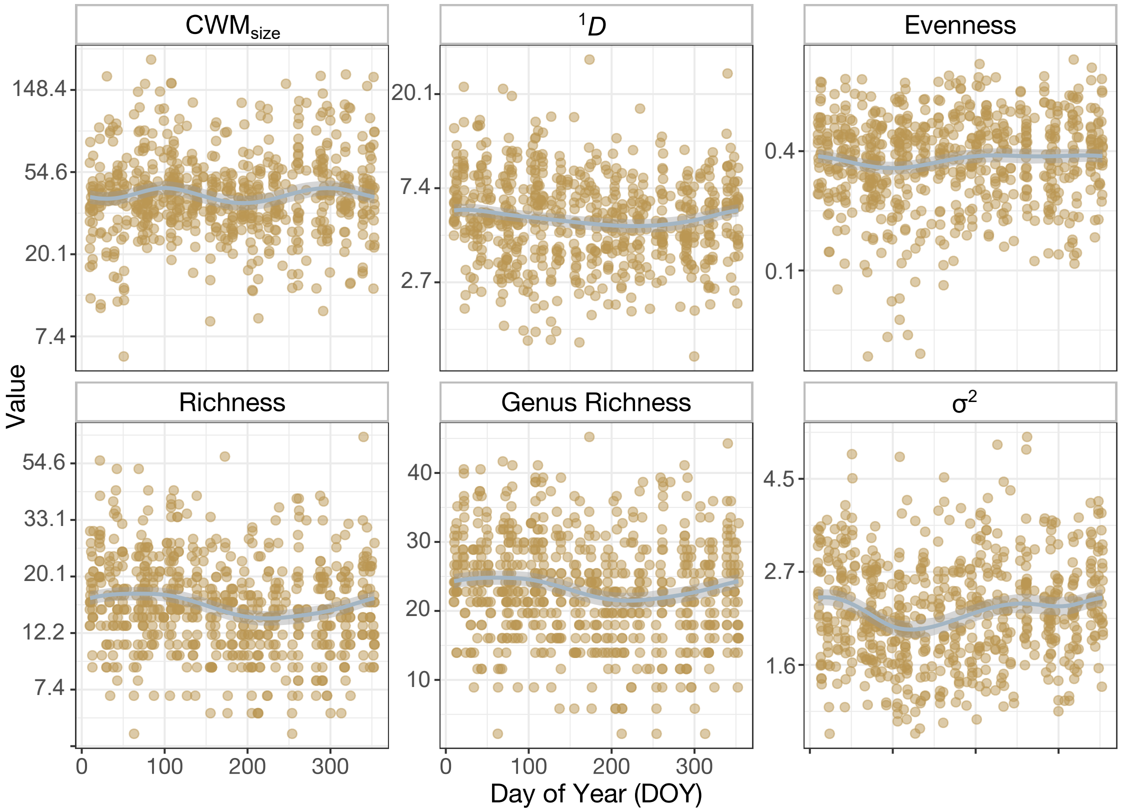

Figure 2.6: **Seasonal variation of diversity metrics.** Seasonal trends of size-related (CWM$_{size}$: community weighted mean size, σ^2: size diversity) and taxonomic (^1D: exp Shannon, species and genus richness) diversity proxies were smoothed using a generalized additive model (GAM) with cyclic splines. Note that y-axis are different. All y-axis are log-transformed.

Coscinodiscus sp. being the smallest and largest cells, respectively.

Across all samples (n = 677), four phytoplankton groups contributed to 95% of all biomass, with diatoms being the most important one (60%), followed by cryptophytes (19%) and dinoflagellates (14%). Other groups such as green algae (2%), cyanobacteria (1%), euglenophytes (1%), silicoflagellates (1%), chrysophytes (<1%), raphidophytes (<1%), haptophytes (<1%) xanthophytes (<1%) and charophytes (<1%) contributed to the remaining biomass (Table 2.2; Figs. 2.11, 2.10). Among diatoms, despite their richness (Fig. 2.9), only three species contributed with more than five percent to the group's total biomass across all samples. They are *Entomoneis* sp., *Ditylum brightwelli* and *Coscinodiscus* sp. For cryptophytes only one species had

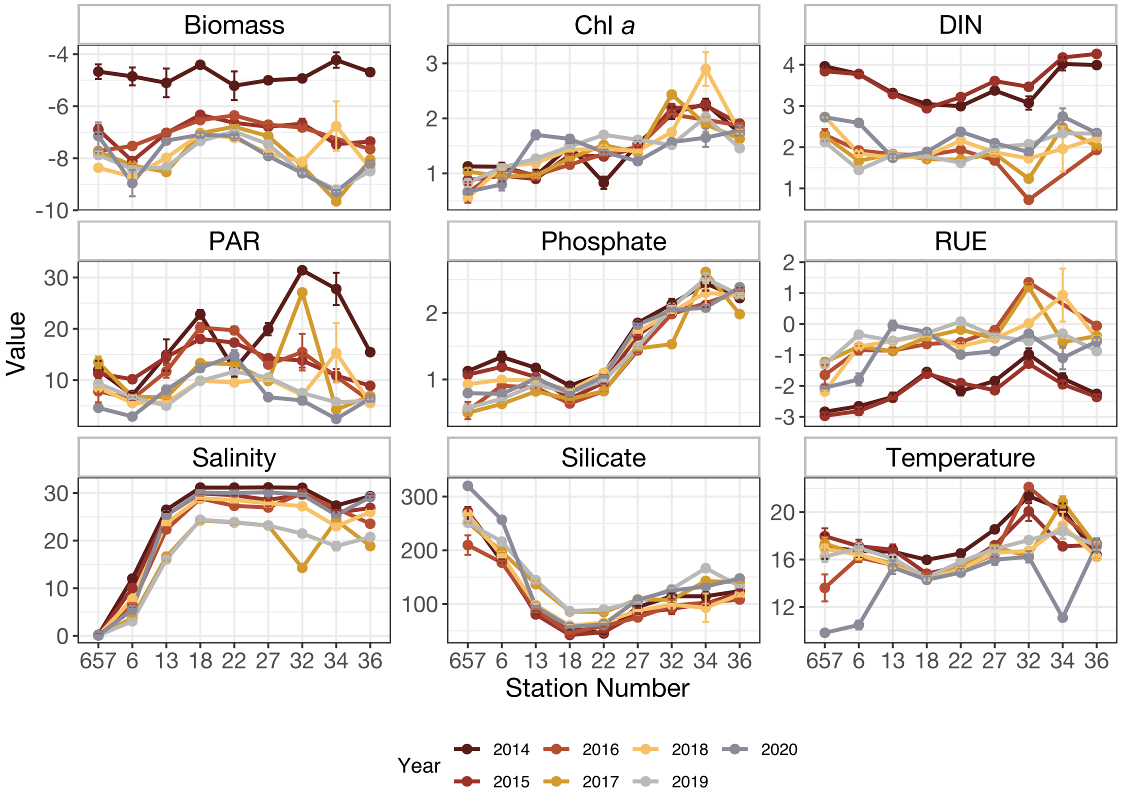

Figure 2.7: **Productivity proxies and environment-related variables across stations over time.** Plot shows mean and standard deviation values of productivity proxies and environmental variables across stations over time in the San Francisco Bay. Stations are sorted from the northernmost (657, 6, 13) to southernmost regions (27, 32, 34, 36) with stations 18 and 22 representing the transitional zone of Central Bay. Note that y-axis labels differ. Biomass (ln μg mL^{-1}), Chl *a* (ln mgL^{-1}), DIN (μM), phosphate (μM) and RUE are log-transformed. All other variables are in raw units: silicate (μM), PAR (μmol $m^{-2}s^{-1}$) and temperature (°C).

a large contribution (*Teleaulax* sp.). As for dinoflagellates, only two species contributed with more than five percent of biomass (*Akashiwo sanguinea* and *Tripos lineatus*). Regarding abundance, cyanobacteria alone contributed with 98%, with each remaining group contributing to less than 1% to total abundance, and with *Eucapsis microscopica* being the largest contributor.

Unlike community weighted mean size (CWM$_{size}$), the equivalent spherical diameter (ESD) was not weighted according to the biomass contribution of each species, and therefore is the average size of all species present in a sample. Overall, ESD dis-

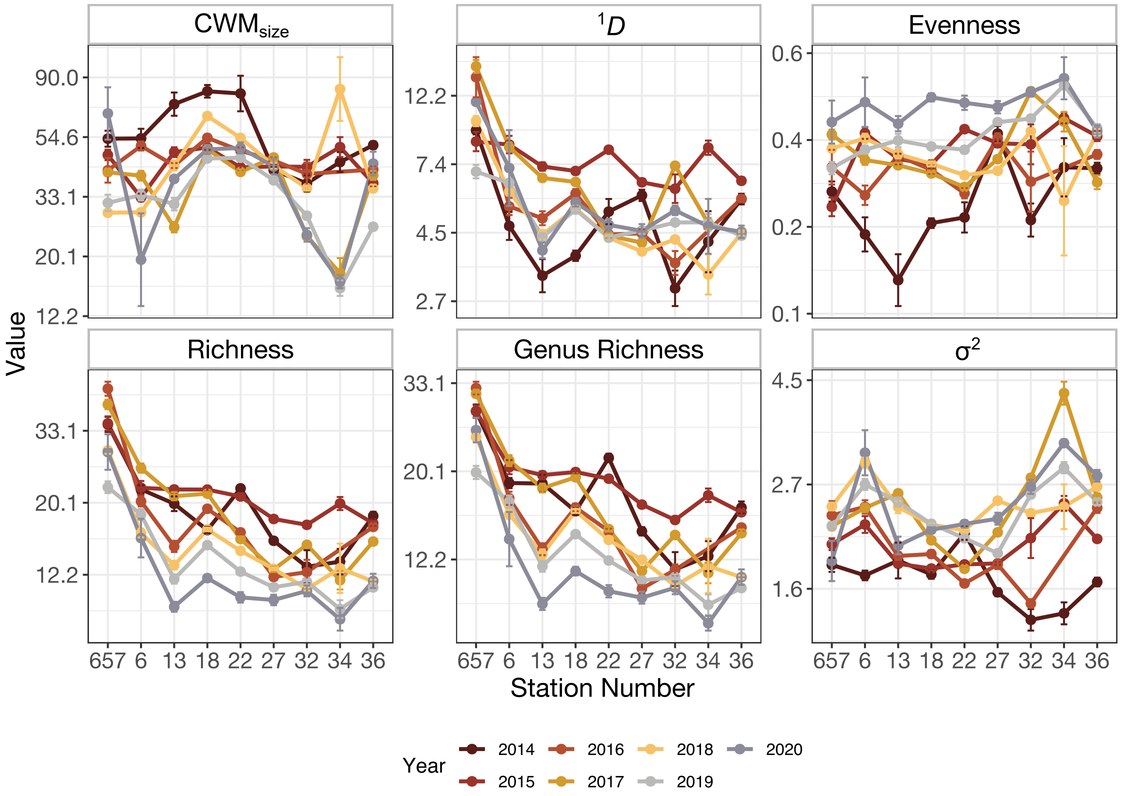

Figure 2.8: **Community weighted mean size (CWM$_{size}$) and diversity indices across stations over time.** Plot shows the mean and standard deviation values of size and taxonomic diversity-related variables across years in the San Francisco Bay. Stations are sorted from the northernmost (657, 6, 13) to southernmost regions (27, 32, 34, 36) with stations 18 and 22 representing the transitional zone of Central Bay. Note that y-axis labels differ and they are all in raw units. ^{1}D: exponential Shannon, σ^2: size diversity.

tribution is right-skewed, due to the presence of larger-sized cells. Small-sized organisms were also very abundant (i.e. Cyanobacteria, Table 2.3, Figs. 2.12, 2.11). On average, silico-flagellates had one of the largest mean cell sizes observed in the San Francisco Bay area, even though they were not present in most of the North Bay region, with cell sizes generally decreasing towards the south (Fig. 2.12, 2.13). Largest variability can be seen for dinoflagellates, with sizes increasing towards the Central Bay followed by a decrease at the South Bay region. This general pattern of increasing mean cell size towards the Central Bay followed by a decrease southwards can be observed for green algae as well, and to a lesser extent to diatoms. Diatoms' commu-

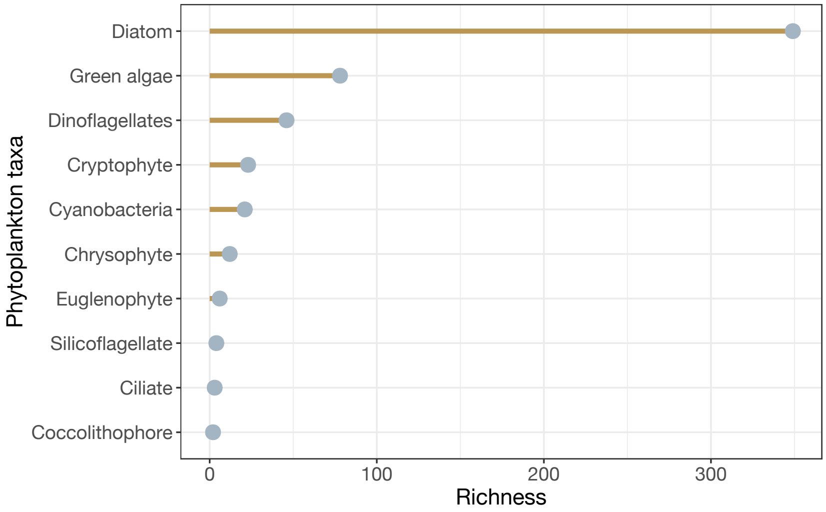

Figure 2.9: **Richness of each phytoplankton group.** Number of species for each phytoplankton taxa across all samples in the San Francisco Bay.

nities had large cells, but in general they were less variable. Euglenophytes also had a community of mainly large cells, generally decreasing southwards, followed by an increase in the South region. I also observe that most cells are relatively uniform in size within Cyanobacteria, albeit the data seems to be left-skewed indicating the presence of many small cells when compared to the rest of the community intermediate to larger sizes (i.e. *Planktothrix* sp, Table 2.3, Fig. 2.13). Cryptophytes also display a consistent mean size, but they exhibit some variability of size ranges, being mostly dominated by larger cells being reflected in their biomass contribution (Figs. 2.12, 2.13; Tables 2.3, 2.2). For chrysophytes and raphidophytes a lot of variability in sizes can be seen, which may contribute to size diversity across samples, even though their abundance and biomass contributions were very low.

2.5 Limitations

Although the dataset covers multiple stations throughout the San Francisco Bay (SFB), certain regions may be insufficiently represented, especially areas with complex bathymetry or those further away from the main sampling points. Sampling fre-

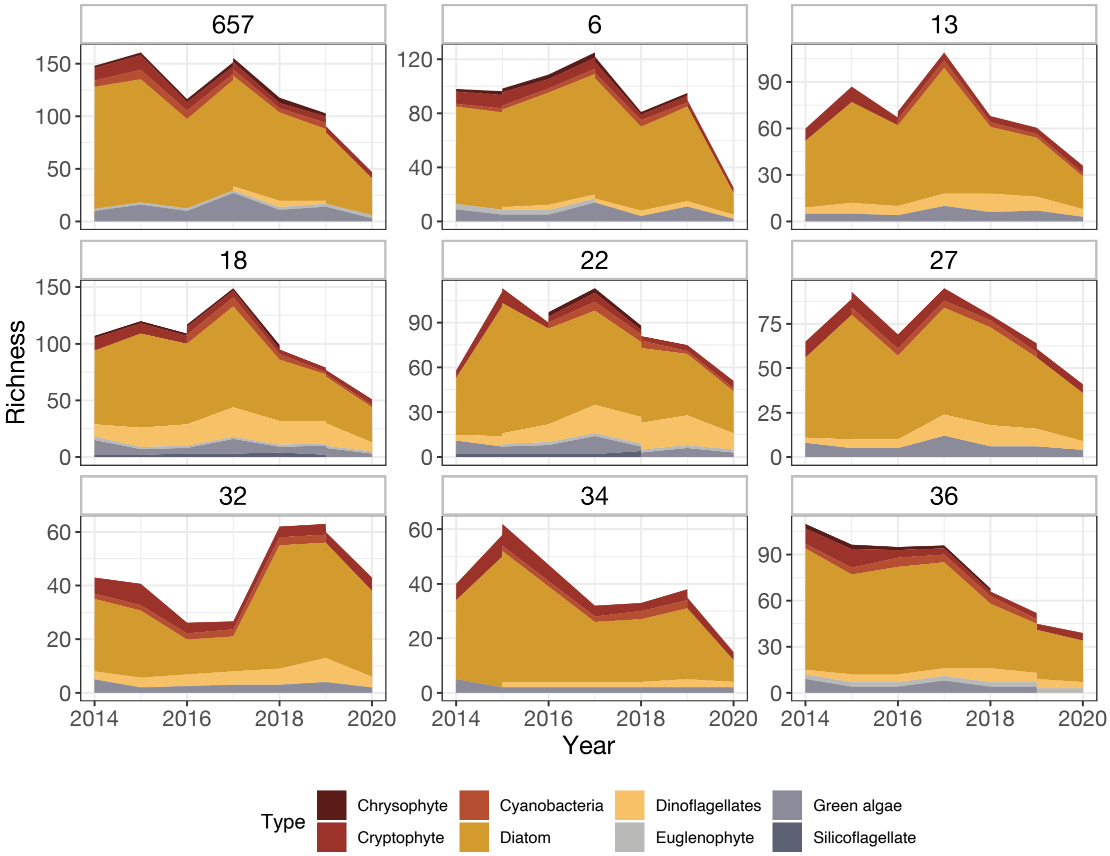

Figure 2.10: **Richness across years in each station.** Area plot with the number of species within each main phytoplankton group across years in each station. Stations are sorted from the northernmost (657, 6, 13) to southernmost regions (27, 32, 34, 36) with stations 18 and 22 representing the transitional zone of Central Bay. Note that y-axis labels differ.

quency has varied over time. In some periods, data was missing or collected less frequently (e.g., monthly or bi-monthly; Fig. 2.2), which may limit our ability to resolve short-term events. Data prior to 1992 were removed from the analyses due to missing phytoplankton information and to the program's sampling strategy focusing on bloom conditions (<2014) and standard monitoring (>2014). Consequently, analyses were performed on the data spanning across 2014-2020 only, reducing temporal and spatial coverage. However, stations still span across several years and across all three bays. While Chl *a* can be used as a proxy for phytoplankton biomass, the dataset does not provide primary productivity (PP) rates or information on functional traits. For

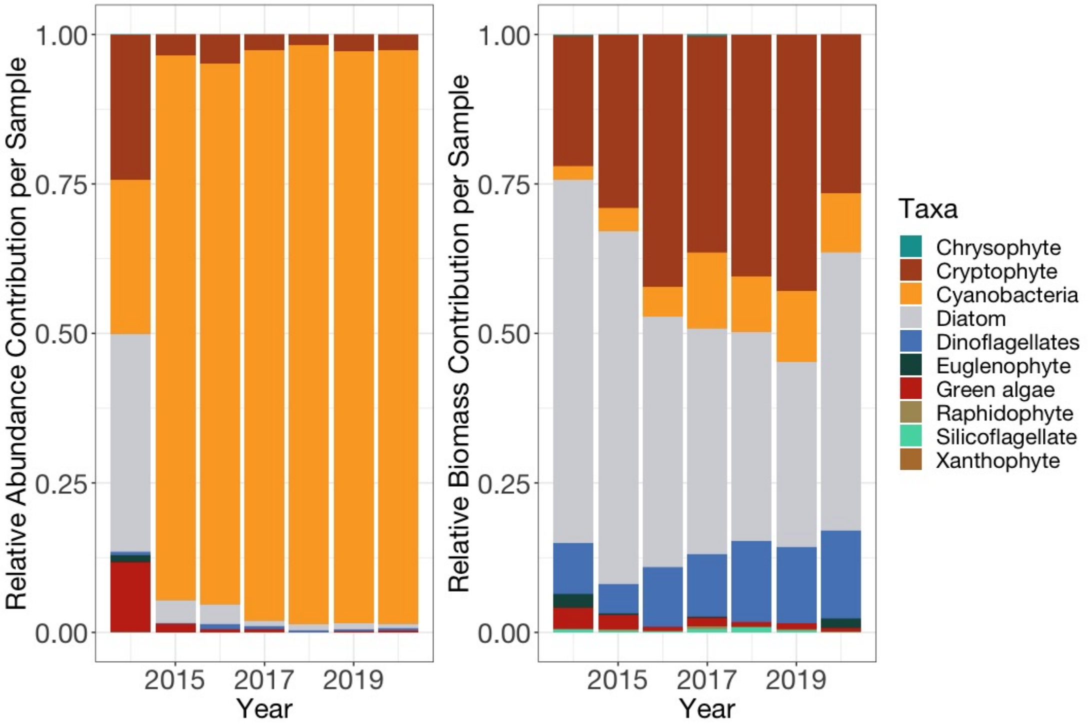

Figure 2.11: **Relative abundance and biomass contribution across all samples.** Phytoplankton groups contribution (%) to abundance and biomass across all samples between 2014 and 2020.

Table 2.2: **Main phytoplankton groups in the San Francisco Bay system.** Relative biomass (%) and abundance (%) contributions of observed groups across all samples.

Type	Biomass	Abundance
	%	%
Diatom	60	1
Cryptophyte	19	1
Dinoflagellate	14	<1
Green algae	2	<1
Cyanobacteria	1	98
Euglenophyte	1	<0.01
Silicoflagellate	1	<0.01
Raphidophyte	<0.1	<0.01
Chrysophyte	<0.1	<0.01
Haptophyte	<0.01	<0.01
Xanthophyte	<0.01	<0.01

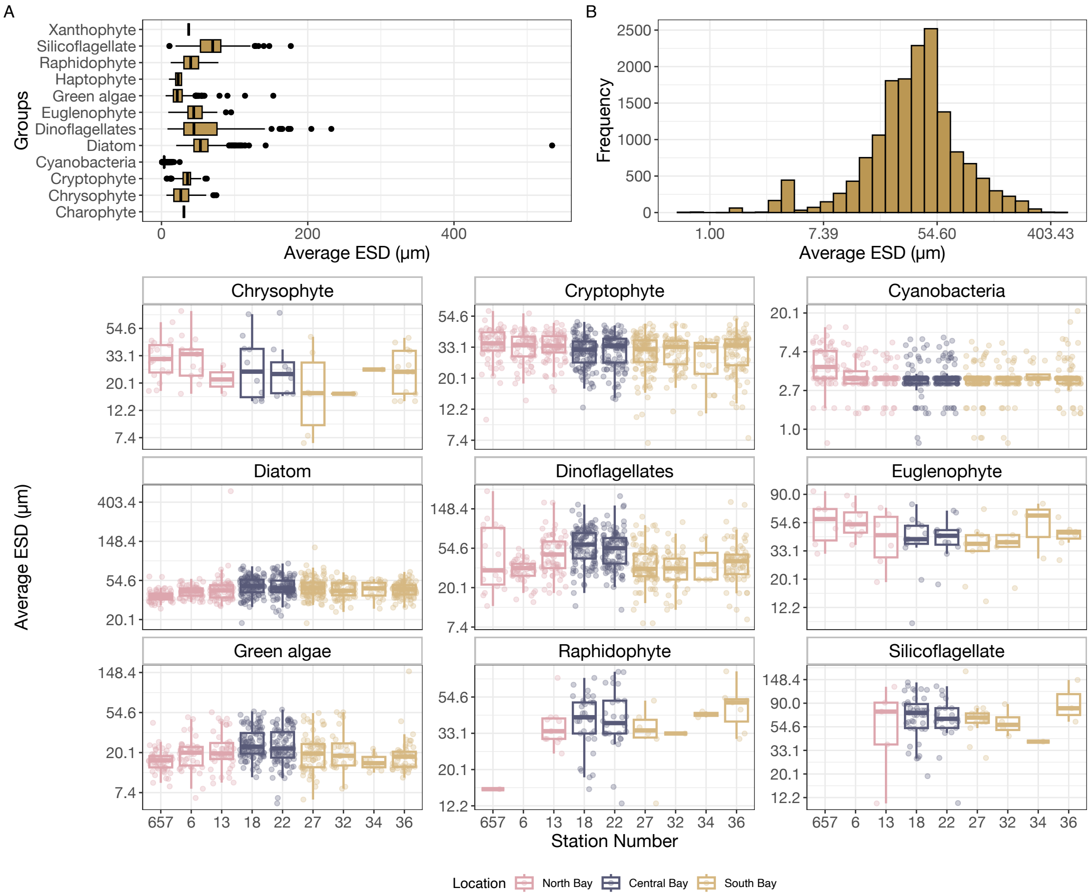

Figure 2.12: **Size distribution of phytoplankton taxa.** Boxplots (A, lower panel) and histogram (B) of average equivalent spherical diameter (ESD) in μm of phytoplankton groups observed in the San Francisco Bay and in each station. Stations are sorted from the northernmost (657, 6, 13) to southernmost regions (27, 32, 34, 36) with stations 18 and 22 representing the transitional zone of Central Bay. Note that y-axis are not logged and labels differ. All y-axis are in raw units.

PP estimates, a simple relationship between phytoplankton growth rate and biomass was assumed. Details can be found in Chapter 4. Size is a 'master'-trait in ecology and, as such, the functional description of the communities are all size-related (e.g. community weighted mean size, size diversity). Finally, the dataset does not contain information regarding zooplankton community, and as such, I could not analyse predator-prey dynamics. Known mixotrophs and heterotrophic taxa were present in the dataset. I removed these records as productivity proxies (biomass, Chl *a* and re-

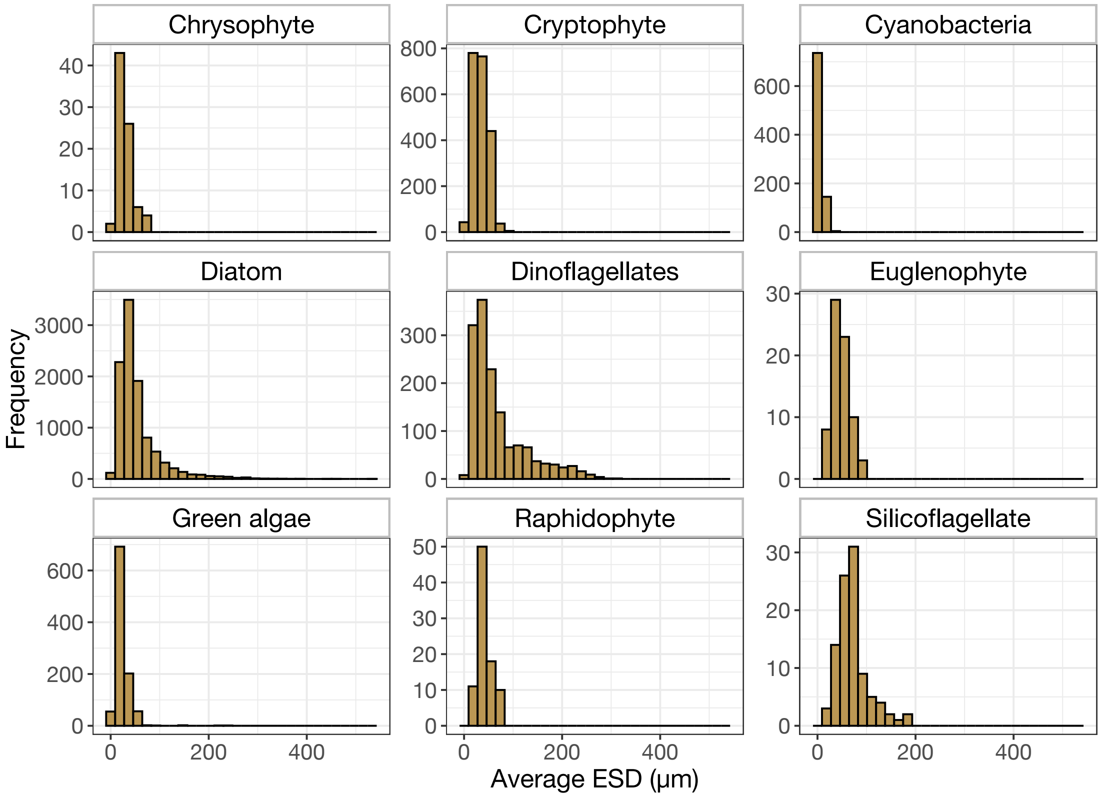

Figure 2.13: **Histograms of average ESD distribution of phytoplankton taxa.** Distribution of mean cell equivalent spherical diameter (ESD) in μm across samples of each phytoplankton group found in the San Francisco Bay.

source use efficiency) were all based on autotrophs contribution and therefore, the presence of heterotrophs and/or mixotrophs would bias these estimates. In Chapter 4, I simulated zooplankton communities based on a 10:1 size relationship to phytoplankton. Although this is a crude simplification, this allowed us to quantify diversity effects of more than one trophic level and observe effects on the prey biomass accumulation. Another important limitation of this dataset comes from the fact that the SFB is an eutrophic system, which could make it difficult to separate diversity effects from the environment and even to generalize results to more nutrient-limited systems.

Despite its limitations, this dataset is a valuable resource for understanding the dynamics of the San Francisco Bay estuarine region and to gain a general mechanistic understanding of the biodiversity-ecosystem function relationship in natural aquatic communities. With its dynamic environmental settings, the dataset is very useful as a tool to help understand the effects of phytoplankton diversity and environmental drivers on productivity. As such, I use this dataset throughout the thesis to: i) perform statistical analyses focusing on understanding the biodiversity-ecosystem function relationship under non-controlled conditions and its potential drivers; ii) to inform a nutrient-phytoplankton (NP) and a nutrient-phytoplankton-zooplankton (NPZ) model based on sizes observed in the community; and iii) as input in a structural equation model (SEM) focusing on causal drivers of productivity comparing both natural and simulated data. The findings can be found in the following chapters.

Table 2.3: **Most common taxa across all samples in the San Francisco Bay system.** Number of occurrences and relative presence (%), minimum and maximum sizes observed per species (ESD; μm), relative biomass (%) and abundance (%) contribution to all samples, ordered from highest number of occurrences to lowest.

Type	**Species**	**No. of occurrences**	**Presence**	ESD$_{min}$	ESD$_{max}$	**Biomass**	**Abundance**
Cyanobacteria	*Eucapsis microscopica*	677	92	0.7	4.2	1	98
Diatom	*Thalassiosira* spp.	676	92	6.6	334.6	15	<1
Cryptophyte	*Plagioselmis prolonga*	635	87	4.6	42.2	4	1
Diatom	*Nitzschia* spp.	609	83	5.3	190.1	1	<0.1
Cryptophyte	*Teleaulax* sp.	556	76	8.7	76.7	8	<1
Diatom	*Paralia sulcata*	518	71	7.8	95.2	2	<0.1
Dinoflagellate	*Heterocaspa rotundata*	447	61	5.8	46.4	1	<0.1
Diatom	*Skeletonema* sp.	396	54	4.2	87.1	1	<0.01
Diatom	*Cyclotella* sp.	374	51	7.8	176.8	1	<0.1
Diatom	*Actinoptychus senarius* sp.	371	51	9.6	206.1	1	<0.1
Diatom	*Navicula* spp.	260	36	7.6	178.5	<1	<0.01
Cryptophyte	*Cryptomonas* spp.	243	33	10.1	98.2	<1	<0.1
Cryptophyte	*Plagioselmis nannoplanctica*	221	30	9.9	58.1	3	1
Green algae	*Pyramimonas* spp.	218	30	6.1	58.8	<1	<0.01
Diatom	*Thalassionema* sp.	180	25	8.8	87.9	<1	<0.1
Diatom	*Aulacoseira* sp.	178	24	9.3	146.9	1	<0.01
Diatom	*Thalassiosira eccentrica*	161	22	12.1	320.9	3	<0.01
Diatom	*Cocconeis* sp.	158	22	15.2	85.1	<0.1	<0.01
Green algae	*Pseudoscourfieldia marina*	156	21	4.5	27.8	<1	<0.1
Diatom	*Thalassiosira angulata*	140	19	11.4	91.1	<1	<0.1
Dinoflagellates	*Heterocapsa* sp.	132	18	7.3	82.6	<1	<0.01
Dinoflagellates	*Heterocaspa triquetra*	131	18	17.6	102.1	1	<0.01
Diatom	*Achnanthidium minutissimum*	128	18	5.3	34.3	<0.1	<0.01
Diatom	*Odontella aurita*	116	16	25.1	181.6	<1	<0.01
Diatom	*Chaetoceros* spp.	106	15	6.0	70.3	<1	<0.1
Cryptophyte	*Hemiselmis* sp.	105	14	4.9	31.9	<1	<0.1
Diatom	*Eunotogramma dubium*	102	14	8.8	50.5	<1	<0.1
Diatom	*Cocconeis placentula*	99	14	13.8	68.9	<1	<0.01
Green algae	*Pyramimonas longicauda*	96	13	8.2	62.6	<1	<0.01
Diatom	*Coscinodiscus* sp.	93	13	17.3	534.2	6	<0.01
Raphidophyte	*Heterosigma akashiwo*	88	12	12.6	77.3	<0.1	<0.01
Diatom	*Fragilaria brevistriata*	86	12	9.7	47.6	<1	<0.01
Diatom	*Pseudo-nitzschia* sp.	86	12	4.1	89.9	<0.1	<0.01
Diatom	*Thalassionema nitzschioides*	85	12	7.4	91.1	<0.1	<0.01
Diatom	*Ditylum brightwellii* sp.	84	11	46.5	328.6	6	<0.01
Diatom	*Entomoneis* sp.	83	11	19.4	290.4	5	<0.01
Diatom	*Navicula* sp.	83	11	15.3	214.0	<0.1	<0.01
Diatom	*Pleurosigma* sp.	83	11	13.1	467.0	<1	<0.01
Diatom	*Amphora* sp.	81	11	4.7	83.7	<0.1	<0.01
Diatom	*Diploneis* sp.	80	11	14.4	141.2	<1	<0.01
Diatom	*Gyrosigma* sp.	80	11	15.0	221.3	<1	<0.01
Dinoflagellates	*Karlodinium veneficum*	79	11	9.6	61.9	<0.1	<0.01
Dinoflagellates	*Gymnodinium* sp.	78	11	7.6	176.4	<1	<0.01

Chapter 3

Biodiversity-ecosystem function in natural aquatic ecosystems

3.1 Diversity as a driver of productivity: a long-standing discussion

The effect of ecosystem function on diversity, or productivity and diversity relationship (PDR), has long been debated. The debate came to be primarily as a way to understand species diversity distribution and coexistence in a scenario of increasing rates of species' loss. Although there might be a scale-dependence between diversity and productivity (Chase and Leibold, 2002; Dodson et al., 2000), a 'hump-shaped' pattern is argued to be the most commonly found pattern in both terrestrial and aquatic ecosystems (Irigoien et al., 2004; Mittelbach et al., 2001; Vallina et al., 2014). This 'hump-shaped' pattern is observed when diversity (usually species richness) peaks at intermediate levels of productivity. In this scenario, diversity is the dependent variable and, as such, subject to environmental fluctuations and community dynamics. However, positive linear relationships between diversity and productivity are equally plausible and have been reported (Bai et al., 2007; Mittelbach et al., 2001), as well as no relationships (Adler et al., 2011). This classic PDR view represents an old paradigm, where diversity is a consequence of environmental variation and ecosystem function (Hillebrand and Matthiessen, 2009; van der Plas, 2019).

The 1992 Earth Summit in Rio de Janeiro (UN, 1992) renewed interest regarding how changes in biodiversity and species loss interact to affect ecosystem function. Soon after, the first related scientific papers started to appear (Hector et al., 1999; Naeem et al., 1994; Tilman and Downing, 1994). This represented a completely new way of approaching the matter, and now diversity is seen by many as a potential driving factor of function, not merely a consequence of it, leading to the emergence of the biodiversity-ecosystem function (BEF) field around 25 years ago (Loreau et al., 2001; Tilman and Downing, 1994).

In general terms, two main approaches were chosen to disentangle the relationship between species diversity and ecosystem function. Initially, experiments with manipulated diversity dominated. Usual responses observed were biomass production, decomposition rates, carbon sequestration, trophic interactions and pollination (van der Plas, 2019 and references therein). Most biodiversity experiments have been designed to determine the consequences of random gains or losses of species, which has allowed these experiments to tease apart the effects of species addition or removal, and maybe composition (Hector et al., 1999). However, species loss is rarely random in nature. Determining the shape of this relationship helps identify the mechanisms behind, and ultimately lead to causal drivers of ecosystem function.

Coupling experiments with theoretical frameworks, this topic of research has become a central issue in modern ecology and environmental sciences ever since (Loreau, 2010). Even though several experiments have been conducted, for several taxa, habitat and ecosystem functions, the majority were focused on grasslands and terrestrial manipulated ecosystems, with a lot of variation in the response being observed (Hooper et al., 2005; van der Plas, 2019). In 1994, Tilman and Downing (1994) seminal article presented evidence that supported the biodiversity and ecosystem functioning hypothesis. This paper was based on >200 grassland plots that differed in diversity and composition due to different rates of nitrogen addition. Naeem et al.

(1994) also showed that an experimentally assembled diverse food-web had greater primary productivity rates. The role of species composition was already acknowledged (Hooper and Vitousek, 1997), yet the effect of diversity *per se* was not. Notably, these experiments were usually designed to test the effects of diversity on ecosystem function independent of species identity and any other factor that may drive biodiversity changes.

In order to remove the effect of identity and environmental factors, experiments (e.g. BIODEPTH and Jena in Europe; Hector et al., 1999, Cedar Creek in the US; Tilman, 2001) were made with replicated communities at each diversity level. These communities were assembled by drawing species at random from a common local species pool and growing them under identical conditions in a given site. This can be understood as the classic BEF approach. Two main mechanisms driving the BEF relationship were described then by Loreau et al. (2001): i) complementarity effect and ii) selection effect. In both cases, biodiversity allows for a range of trait variation where these mechanisms can act upon; where in (i) productivity is collectively enhanced by a diverse set of traits in the community and (ii), particular traits are selected and become dominant increasing overall productivity (Loreau and Hector, 2001). This raised the question of whether richness itself is the causal predictor or not, since phenotypic trait variation seems to drive productivity by means of complementarity and/or selection effects.

In the BEF approach, diversity is seen as one of the modulators of ecosystem processes. Therefore, diversity is not just an outcome of environmental conditions, but actively influences how ecosystem processes function, recognizing that the combined influence of various species (with their unique traits and interactions) can collectively affect ecosystem functions. The two approaches, PDR and BEF, are not contradictory. They can be reconciled by taking into account that large spatial patterns usually observed in the PDR studies reveal correlations between diversity and productivity, driven by the environment (Loreau, 2010). Meanwhile, the small-scale experiments typically used in the BEF focus on the effects of species traits and richness on ecosystem functions after controlling for the environmental factors. By 2006, over 100 experiments had shown that species diversity had a repeatable and consistent effect on productivity (Cardinale et al., 2006; Hooper et al., 2005; Loreau, 2010; Tilman, 2001), at least for terrestrial ecosystems. Several questions remained regarding trait identity, number of species, type of diversity (e.g. taxonomic, functional, phylogenetic), time and spatial scale, to name a few. Nevertheless, across the years some general consensus was reached regarding the effect of diversity on productivity. For example, biodiversity has a consistently positive effect on productivity, many species are needed to maintain stability and ecosystem functioning in changing environments (Loreau, 2010), functional redundancy and complementarity are important to increase stability and productivity (Vallina et al., 2017), and rare species can indeed have strong impacts on ecosystem function (Hooper et al., 2005). Finally, these effects tend to get stronger with time (Cardinale et al., 2012; Hillebrand and Matthiessen, 2009; van der Plas, 2019).

Despite the considerable number of experiments and publications, there is still a lot of debate regarding the generality of these findings as these studies may lack biotic and abiotic complexity. Furthermore, the effects on productivity tend to accelerate with increasing diversity loss, with the magnitude of function change being heavily dependent on which functional traits are being considered, and if they relate to the function being observed (Cardinale et al., 2012; Hooper et al., 2012; Ye et al., 2019). Several issues are also important to keep in mind, regarding the validity of these observations from experiments when applied to natural data and consequently, BEF's relevance. These include experimental conditions (e.g. short runtime of experiments, number of ecosystem functions used, lack of immigration, non-random loss of biodiversity), bias towards terrestrial and temperate ecosystems, effect size of resource supply, competition and predators' diversity in natural settings and methodological/analytical choices. Even so, the field of BEF is slowly evolving and addressing these problems aiming at identifying causal drivers of ecosystem function, namely productivity, and conclusions drawn from these studies can be relied upon (Duffy et al., 2017). The most recent synthesis acknowledges that both diversity and the environmental factors can not only drive and reduce variability, and increase stability of ecosystem functions, but also covary with productivity (van der Plas, 2019). In spite of these advances, a lot of unanswered questions remain to be addressed and the aquatic environment is under-represented.

3.2 Phytoplankton diversity and productivity in the oceans

As loss of species increased globally (Chapin et al., 1997), so did the efforts to try to understand the relationship between species richness and productivity. The idea that ecosystem productivity affects species richness can be dated as far back as the 60s (Leigh Jr, 1965), but the shape of the relationship, and consequently, the mechanisms behind it, have been widely debated (Waide et al., 1999). The majority of studies found an unimodal pattern, with maximum richness at intermediate levels of productivity, in both terrestrial and aquatic ecosystems (Irigoien et al., 2004; Vallina et al., 2014). Other patterns have been reported as well as a scale-dependency (Chase and Leibold, 2002; Mitchell-Olds and Shaw, 1987). Unlike terrestrial ecosystems, pelagic oceans are vast and dynamic environments, with fast turnover rates and nutrient cycling with complex ecological interactions, making these habitats more resilient to climate disturbances in the short-term. Under these homogenized conditions found in the oceans, phytoplankton diversity should be low, as few species would have competitive advantage and become dominant. This, however, is not observed in natural communities where high diversity is usually the norm. Hutchinson's paradox, also known as, 'the Paradox of the Plankton' relates to the violation of the competitive exclusion principle that allows for species coexistence and thus, the observed high richness (Armstrong and McGehee, 1980; Hutchinson, 1961).

Most promising ideas to explain the classic productivity-diversity relationship (PDR) patterns are rooted in the pursuit of understanding what mechanisms allow for species coexistence (Armstrong and McGehee, 1980). According to the competitive exclusion principle, two species cannot coexist indefinitely if they are competing for fewer than two resources (Hardin, 1960; Volterra, 1928). Thus, species coexistence is only possible due to violations of the principle (Palmer, 1994). For instance, for 'complete' competitive exclusion to take place, i.e. a single species becomes dominant, enough time has to have passed, and, insufficient time for exclusion to occur could allow species to coexist. The degree of niche overlap can affect competition, coexistence and ultimately, productivity. Moderate niche overlap can allow for increased productivity and coexistence, unless other factors come into play (e.g. disturbances, predation). Mass-ratio hypothesis relates to species contribution to ecosystem function not being equal, and to how that drives productivity via the traits of the most dominant species (Grime, 1998). This could lead to a positive linear relationship between diversity and productivity, even if long-term coexistence is not possible. However, negative and even neutral relationships between diversity and productivity can be observed if the dominant trait is not causally linked to the function as well as according to spatial scale in question (Chase and Leibold, 2002; Chen et al., 2019; Waide et al., 1999).

Niche differentiation then becomes relevant. Species' different requirements reduce competition and increase resource use efficiency by the community. Levels of disturbance (e.g. predation pressure, temperature, nutrient availability, light) can also allow for higher richness and possibly enhanced productivity via complementarity. Intermediate disturbance and keystone-predation hypotheses relate to these kind of disturbances. The intermediate disturbance hypothesis argues that moderate levels of disturbance delay competitive exclusion (maintaining high diversity) while preventing species' extinction in non-equilibrium conditions via niche complementarity. At high disturbance levels, few species can persist, again reducing productivity. At low disturbance levels, competitive exclusion by dominant species reduces diversity and potentially limits productivity. This results in a unimodal diversity-productivity relationship, where species richness peaks at intermediate disturbance levels (Irigoien et al., 2004). Meanwhile, the keystone-predation hypothesis argues that competitive exclusion can be slowed down by predators selectively consuming dominant species, reducing their competitive advantage and maintaining a diverse community in the process. In this case, moderate predation pressure supports both high diversity and higher productivity. Both cases rely on moderate levels of disturbance to explain the coexistence patterns observed in the oceans and how these shapes the PDR curve, with nutrient competition and selective grazing being the mechanisms behind the unimodal curve (Vallina et al., 2014). Thus, there are numerous ways in which the competitive exclusion principle can, in theory, be avoided.

Competing theories regarding the classic PDR focus on species richness and are fundamentally linked with how species interact within ecosystems and therefore, with their productivity. Biodiversity-Ecosystem function (BEF) theory extends on these ideas by exploring how diversity then modulates multiple ecosystem functions, including productivity, nutrient cycling, carbon sequestration, and resilience to environmental changes. BEF also argues that in addition to niche complementarity, selection effects are also responsible for driving ecosystem productivity (Loreau and Hector, 2001). Going beyond species richness itself, BEF theory incorporates species' traits and their functional diversity, as community properties with direct effect on ecosystem processes. Given the high diversity of phytoplankton in the oceans, taking into account functional diversity is a great approach to the subject.

Unlike the 'universal' unimodal PDR curve, BEF theory predicts a general positive linear relationship between diversity and productivity in the oceans, with increasing biodiversity (not just species richness) leading to enhanced overall ecosystem function via complementarity and selection effects. In diverse communities, species' niches complement each other by utilising resources more efficiently than in monocultures (i.e. species grown alone). On the other hand, increasing diversity also increases the likelihood that highly productive or functionally important species will be dominant in the community, leading to enhanced ecosystem function via selection effects. These two mechanisms can act together at different temporal scales, which would explain the monotonic positive curve reported in BEF studies. However, studies have reported negative and even neutral relationships (Adler et al., 2011; Chen et al., 2019; Smith et al., 2016), relating to different scales of diversity under consideration. Coupled with the fact that most BEF studies have been conducted under controlled (experimental or modelled) short-term settings, this hints at a more variable relationship in the oceans, with no universal pattern.

The objective of this chapter is to address a few of these open questions in a naturally occurring phytoplankton community, specifically in the San Francisco Bay (SFB) system. As a pivotal study site, SFB gives us an opportunity to delve into the dynamics between biodiversity and ecosystem function within a nutrient rich estuarine environment.

3.2.1 Research questions

The emergence of a 'hump-shaped' pattern between diversity and productivity can relate to environmental heterogeneity (under low and high productivity levels, lack of resource and habitat diversity), disturbance, resource supply and competition, predation and species sorting. Two main mechanisms have been argued to consistently explain the unimodal pattern between diversity and productivity observed in the oceans: selective grazing and competition for nutrients at high and low productivity levels, respectively (Irigoien et al., 2004; Vallina et al., 2014). However, to explore the question of the role of phytoplankton diversity on productivity in a natural environment, I focused on: i) the direction of the biodiversity-ecosystem function relationship; ii) the variability of resources and its effect on productivity and; iii) comparing several diversity indices and productivity proxies. The main question was: what shape does the relationship between diversity and productivity (biomass) have in the San Francisco Bay system? (e.g. unimodal, monotonically increasing or decreasing?). The following hypotheses were tested:

- *H0*: Productivity should increase linearly with richness as predicted by BEF theory.

- *H1*: Community size structure, rather than species richness, is a better predictor of productivity in the San Francisco Bay area.
- *H2*: Environmental control changes how diversity affects productivity.

3.3 Methodology

3.3.1 Data Analyses

Prior to analyses, all data were transformed using the BoxCox method, aiming for the best approximation of a normal distribution of each variable. Correlation tests were run between variables of interest using Spearman's (ρ) method, followed by simple linear regression to examine the bivariate relationship between productivity (here biomass, chlorophyll *a* and resource use efficiency [RUE] as proxies), diversity indices and environmental variables. Models with the best fit were selected based on adjusted R^2, Akaike Information Criterion (AIC) and normality of residuals. All analyses were performed in the R software (v4.2.1, R Core Team, 2021).

The hypothesis that the relationship between diversity as a predictor of productivity is unimodal was tested using the two-line test (TLT) after Simonsohn (2018). The test assumes no functional form of the relationship between x and y, and uses interrupted regression to test whether the effect of x on y changes sign for low versus high x values. This method provides a better way to assess if the relationship is indeed unimodal ('hump'-shaped) as opposed to simply interpreting quadratic regressions, even with additional tests (Mitchell-Olds and Shaw, 1987; Mittelbach et al., 2001).

Multiple linear regression analyses were also employed to further investigate the factors likely driving productivity in this area. Variables were characterized as environmental (E; salinity, temperature, DIN, phosphate, PAR), diversity (D; R, ${}^{1}D$, evenness, σ^2), trait (Tr; CWM_{size}) and temporal (T; Year, cosine (xc) and sine of x (xs) to capture cyclical nature of seasonality), for each productivity proxy (biomass, Chl *a*, RUE). As such, the model has several predictors and can be specified by the general form:

$$\text{Productivity} = \beta_0 + \text{Environment} + \text{Diversity} + \text{Trait} + \text{Temporal} + \epsilon \qquad (3.1)$$

Where β_0 is the intercept and ϵ is the error term. Second-degree polynomials were included when necessary in order to account for non-linearity in the data. For more details on model specification, please see Table 3.2. Selection of best predictor variables in the model was guided not only by ecological considerations, aiming to determine the effect of environmental and diversity factors on productivity, but also using metrics commonly found in the literature, followed by a step-selection procedure. Variables that were either highly correlated or displayed no significant correlation with the response were removed from the models. In addition, the variance was partitioned among predictors using redundancy analyses. The analyses models the relationship between a response matrix (i.e. biomass) and one or more explanatory matrices (e.g. environment, diversity, temporal, trait) in order to determine importance of each explanatory variable and/or group of variables to the overall response, in order to ultimately identify drivers.

3.4 Results

3.4.1 Productivity ~ Diversity

In the San Francisco Bay system, the majority of diversity effects observed were negative and likely monotonic for all productivity proxies used, with only one unimodal relationship observed (Fig. 3.1). Even when looking at the classic diversity-productivity relationship, where diversity is hypothesised to be driven by productivity, monotonically decreasing curves were more common than unimodal and increasing ones. This suggests no significant sign changes were observed between low and high values of x. When the TLT test (Supplementary fig. A.1) is used to check for

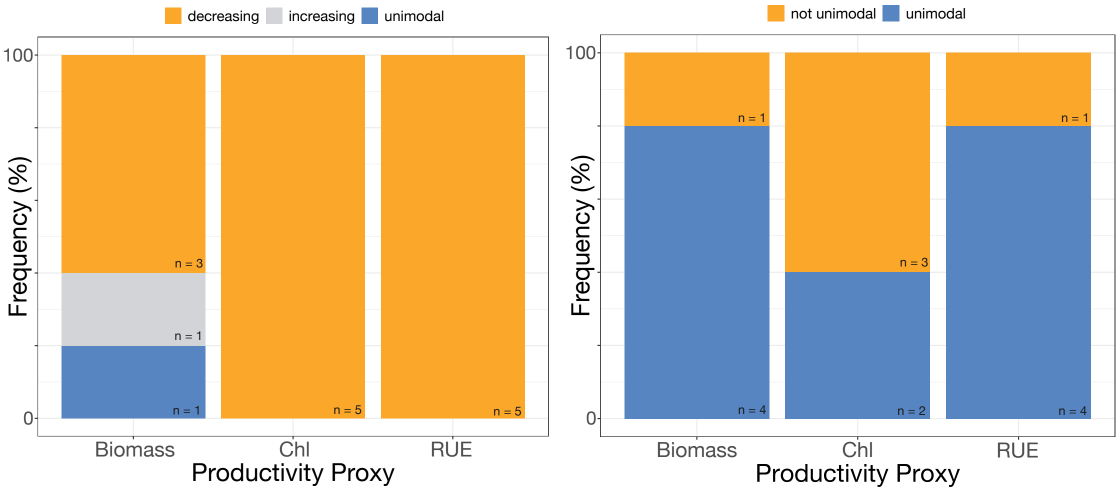

Figure 3.1: **Frequency of relationship shapes observed between biodiversity and ecosystem function with different methods of analyses: (a) two-line-test (TLT) and (b) classic quadratic regression.** This graph exemplifies the variability of observed relationships according to metrics used and method of assessment used. Most commonly found relationships were monotonically negative and/or positive, with only a few unimodal.

the evidence of a ‘hump’, only one true unimodal curve is observed. Whereas, when using a significant quadratic term to determine the existence of a ‘hump’-shaped relationship, unimodal curves were the most commonly found pattern, with some variation when changing productivity proxies. Thus, I would like to raise the question of subjectivity of method selection for determining the shape of this relationship and the universal aspect of this unimodal pattern.

3.4.1.1 Biomass

Nutrients were negatively correlated with biomass, with the exception of DIN (Si; ρ = -0.5; DIN; ρ = 0.12; P; ρ = -0.20; all p-values <0.001). Salinity was positively correlated with biomass (ρ = 0.25) and weakly correlated to temperature (ρ = 0.08). Community weighted mean size (CWM$_{size}$) had a strong positive relationship with biomass (ρ = 0.66) (Fig. 3.2). CWM$_{size}$ was a relatively good predictor of biomass with R^2_{adj} of 0.38.

Biomass decreased linearly with all diversity metrics, with the exception of rich-

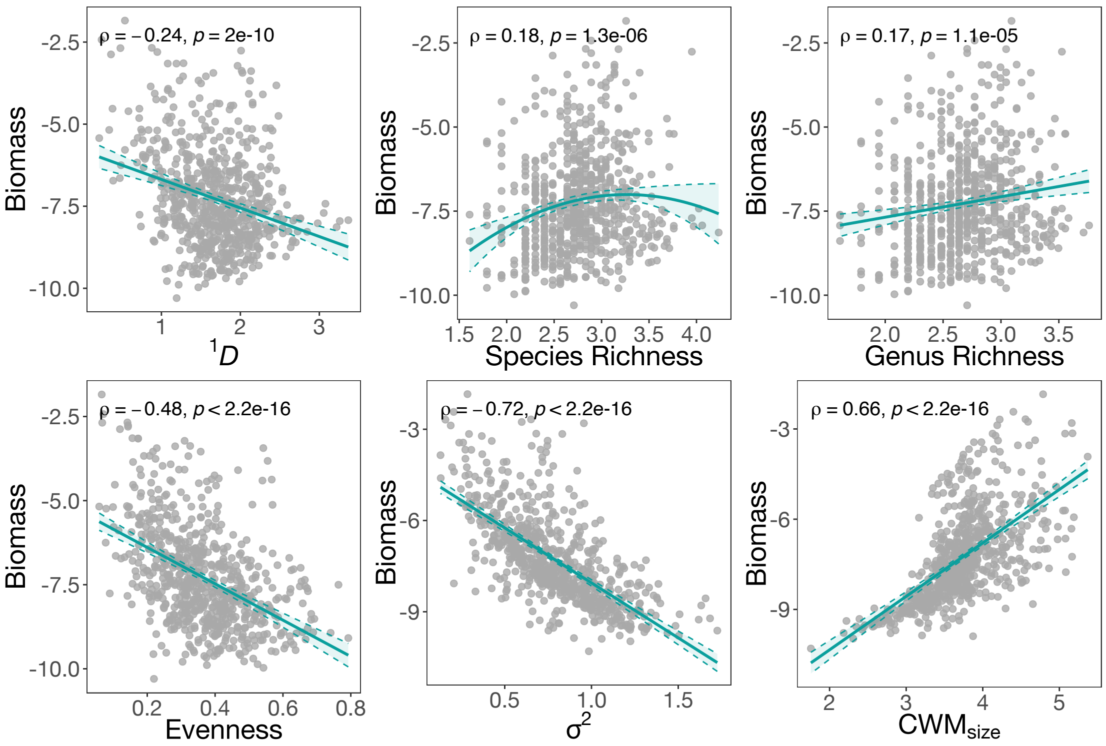

Figure 3.2: **Scatterplots of biomass and diversity metrics.** Plots display the bidirectional relationship between diversity metrics and biomass as a productivity proxy. Spearman's correlation (ρ) and p-values can be seen at the top left of each plot. All axis are natural log-transformed. ^1D: exponential Shannon; σ^2: size diversity.

ness and genus richness (Fig. 3.2, Table 3.1). Size diversity (σ^2) was highly negatively correlated with biomass (ρ = -0.72). For taxonomic diversity, negatively correlated (ρ = -0.48). Richness and genus richness were positively correlated with biomass (ρ= 0.18 and 0.17, resp.). Among the diversity indices, the best predictor was size diversity (R^2_{adj}= 0.48), followed by evenness (R^2_{adj}= 0.25, Table 3.1). All other indices explained less than 10% of the variance found.

When looking at the multiple regression models, size related variables were again the best predictors, followed by evenness, with an overall R^2_{adj}= 0.84. Biomass trends were non-linear across years, decreasing up until 2018 where afterwards, it appears to be increasing, with seasonal peaks around springtime (Fig. 3.3, A-B). Additionally, non-linear trends of biomass were also observed for DIN (Fig. 3.3, H), scaling positively with CWM_{size} and PAR and negatively with size diversity, evenness, salin-

Table 3.1: **Summary of selected simple linear models between productivity and diversity.** Model coefficients (x and x^2, Spearman's ρ, adjusted R^2 (R^2_{adj})) and shape of relationship, ordered by largest variance explained to lowest. Chl *a*: chlorophyll *a*, *RUE*: resource use efficiency, ^1D: exponential Shannon, σ^2: size diversity, TLT: two-line test. The TLT test checks whether there is a significant change in sign between small and large x values, if so, the relationship can be viewed as unimodal.

Response	**Predictor**	**Spearman's ρ**	**R^2_{adj}**	**Coefficients**		**TLT**
Biomass				**x(se)**	**x^2(se)**	
	σ^2	**-0.72**	0.48	**-26.51** (1.07)	**5.11** (1.07)	decreasing
	Hill's Evenness	**-0.47**	0.25	**-1.87** (0.12)	-	decreasing
	^1D	**-0.24**	0.12	**-10.87** (1.40)	**7.94** (1.40)	decreasing
	Richness	**0.18**	0.03	**6.20** (1.47)	**-4.13** (1.47)	unimodal
	Genus Richness	**0.16**	0.02	**0.60** (0.15)	-	increasing
Chl *a*						
	^1D	**-0.23**	0.08	**-0.38** (0.05)	-	decreasing
	Genus Richness	**-0.22**	0.06	**-3.26** (0.60)	**-2.53** (0.60)	decreasing
	Richness	**-0.20**	0.06	**-3.28** (0.60)	**-2.46** (0.61)	decreasing
	σ^2	**-0.21**	0.05	**-3.20** (0.61)	**2.16** (0.61)	decreasing
	Hill's Evenness	-0.04	0.06	**-2.33** (0.61)	**3.42** (0.61)	decreasing
RUE						
	σ^2	**-0.61**	0.37	**-24.90** (1.25)	**4.90** (1.25)	decreasing
	Hill's Evenness	**-0.44**	0.23	**-1.88** (0.13)	-	decreasing
	^1D	**-0.33**	0.17	**-15.61** (1.44)	**7.43** (1.44)	decreasing
	Richness	0.04	0.01	0.84 (1.58)	**-4.05** (1.58)	decreasing

ity and temperature (Fig. 3.3, C-G). CWM$_{size}$ alone explained 11% of the partitioned variance (Tr; Fig. 3.8, A), followed by diversity (D; 10%, Fig. 3.8, A), where size diversity explained the largest amount of variance within diversity metrics used (31%).

3.4.1.2 Chlorophyll *a*

When chlorophyll *a* (Chl *a*) was used as a proxy for productivity, nutrients had a more variable relationship (DIN: ρ = -0.22; P: ρ = 0.22), whereas Si was negatively correlated (ρ = -0.21). Salinity and temperature were positively correlated with Chl *a* (ρ = 0.13 and 0.23, respec.). All size related variables were positively correlated with Chl *a*, albeit not very strongly (CWM$_{size}$ = 0.14) (Fig. 3.4). All independent variables did not explain >1% of the variance. All p-values associated with these models were <0.001.

Table 3.2: **Summary of selected multiple regression models.** Model coefficients (standard errors), p-values and adjusted R^2 (R^2_{adj}) for each productivity proxy. Chl *a*: chlorophyll *a*, RUE: resource use efficiency, xc: cosine of x, xs: sine of x. Variable^2 represents second-degree polynomials.

	Biomass		**Chl *a***		**RUE**	
β_0	-7.26 (0.02)	<0.001	0.49 (0.13)	<0.001	-8.34 (0.16)	<0.001
R^2_{adj}	0.84		0.49		0.66	
	Estimate (se)	**p-value**	**Estimate (se)**	**p-value**	**Estimate (se)**	**p-value**
Temporal						
xs	-0.1 (0.04)	0.01	0.3 (0.01)	<0.001		
xc	-	-	-	-	-0.2 (0.07)	0.01
Year	-8.9 (0.94)	<0.001	0.03 (0.03)	0.02	0.07 (0.02)	<0.001
Year^2	8.4 (0.78)	<0.001	-	-	-	-
Diversity						
Size diversity	-13.1 (0.88)	<0.001	-1.3 (0.68)	0.01	-1.9 (0.18)	<0.001
Size diversity^2	3.9 (0.66)	<0.001	1.01 (0.49)	0.01	-	-
Hill's evenness	-2.3 (0.85)	<0.01	0.004 (0.66)	0.99	-5.9 (1.30)	<0.001
Hill's evenness^2	0.6 (0.64)	0.34	1.7 (0.48)	0.12	2.4 (0.96)	0.01
Richness	-	-	0.32 (0.74)	0.66	-5.3 (0.51)	<0.001
Richness^2	-	-	-1.5 (0.51)	<0.001	-0.95 (1.05)	0.36
Trait						
CWM$_{size}$	14.8 (0.78)	<0.001	2.9 (0.58)	<0.001	14.5 (1.20)	<0.001
CWM$_{size}{}^2$	2.2 (0.72)	0.002	1.08 (0.53)	0.04	1.6 (1.10)	0.13
Environment						
Temperature	-3.3 (0.89)	<0.001	1.7 (0.77)	0.03	3.3 (1.36)	0.01
Temperature^2	0.1 (0.68)	0.84	-	-	-1.2 (1.04)	0.25
Salinity	-0.8 (0.71)	0.08	1.6 (0.69)	0.02	0.43 (1.38)	0.75
Salinity^2	-1.14 (0.72)	0.11	-0.06 (0.57)	0.90	-2.3 (1.38)	0.03
DIN	-1.9 (0.89)	0.02	-5.1 (0.62)	<0.001	-	-
DIN^2	1.6 (0.70)	0.02	3.6 (0.51)	<0.001	-	-
Phosphate	-	-	0.32 (0.04)	<0.001	-8.9 (1.34)	<0.001
Phosphate^2	-	-	-	-	2.4 (0.97)	0.01
PAR	10.7 (0.96)	<0.001	0.15 (0.03)	<0.001	8.7 (1.44)	<0.001
PAR^2	1.9 (0.67)	0.008	-	-	2.7 (1.0)	0.01

Taxonomic diversity indices were negatively correlated with Chl *a*: ^1D (ρ = -0.22), evenness (ρ = -0.04, not significant) and size diversity (ρ = -0.21). Finally, richness (ρ = -0.2) and genus richness (ρ = -0.22) both showed a negative correlation with Chl *a* (Fig. 3.4). For diversity, all predictors also explained <1% of the variance in the data.

In general, multiple predictors did not explain a lot of the variance observed when using Chl *a* as a productivity proxy (R^2_{adj}= 0.50), with environmental (14%) and other (12%) variables related to temporal variation explaining more of the variance ob-

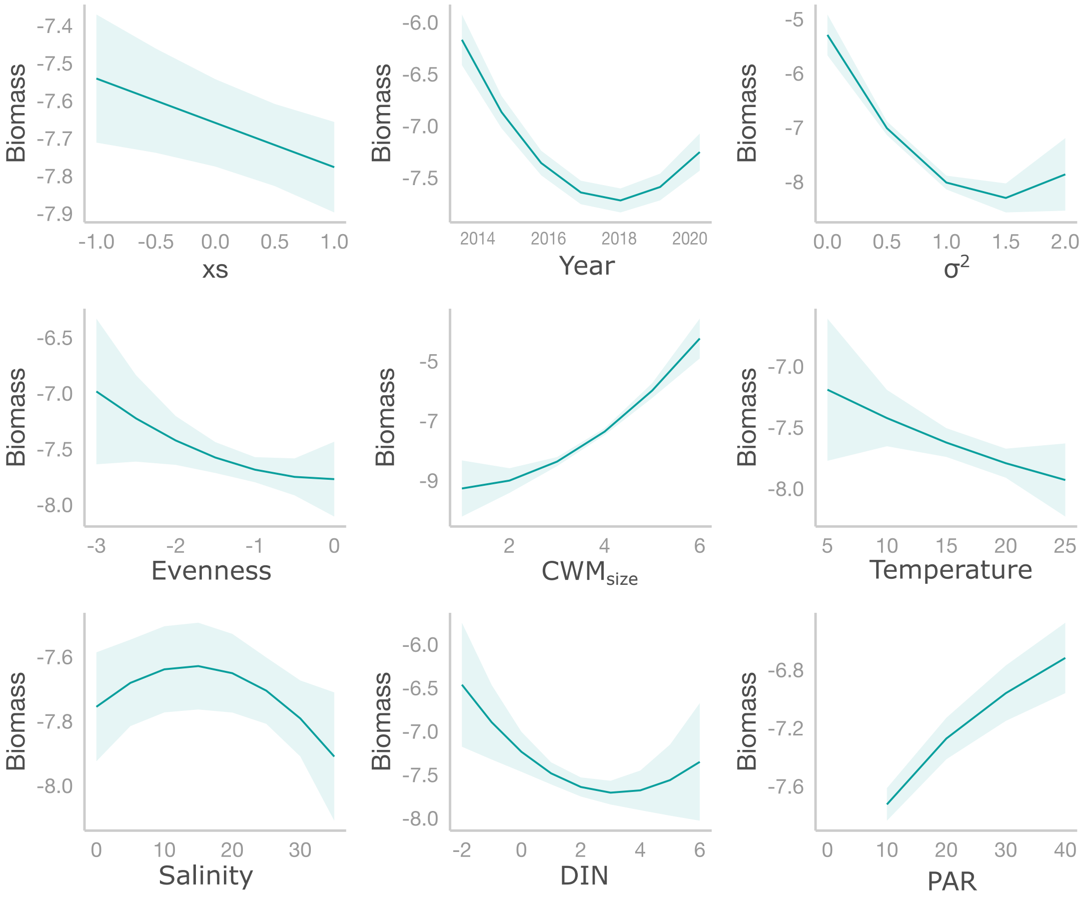

Figure 3.3: **Partial-effect plots from multiple regression model with biomass as response for the San Francisco Bay system.** Changes in biomass according to seasonal and annual trends are shown, as well as size diversity (σ^2), evenness, CWM$_{size}$, temperature, salinity, dissolved inorganic nutrient (DIN) and PAR.

served (Fig. 3.8, B). With the exception of phosphate (Fig. 3.5, J), predictor variables were non-linearly related to the response. Chl *a* displayed an unimodal relationship with richness (concave down), size diversity (concave up), CWM$_{size}$ (concave up), evenness (concave up) and temperature (concave down). Whereas, PAR and DIN that had seemingly saturating relationships with Chl *a* (Fig. 3.5). Within the environmental variables, PAR and phosphate contributed the most to the variance partition (Fig. 3.8, B). Thus, reflecting the strong seasonality observed in the Chl *a* measurements.

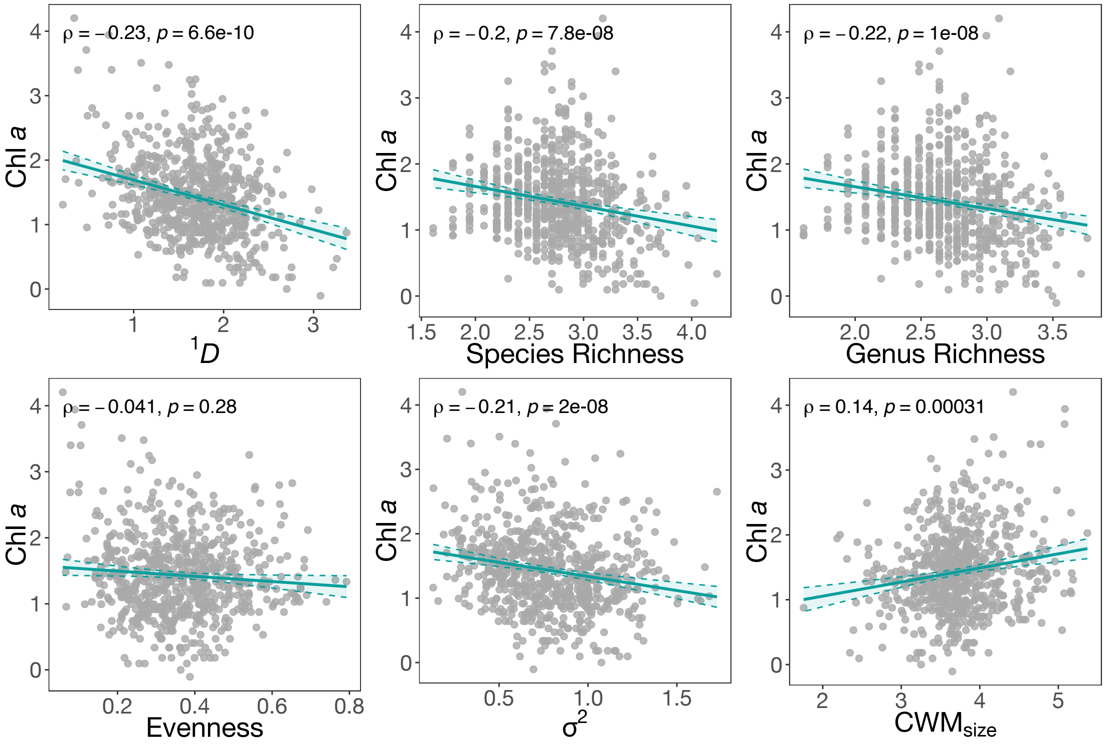

Figure 3.4: **Scatterplots of Chl *a* and diversity metrics.** Plots display the bidirectional relationship between diversity metrics and Chl *a* as a productivity proxy. Spearman's correlation (ρ) and p-values can be seen at the top left of each plot. All axis are natural log-transformed. ^1D: exponential Shannon; σ^2: size diversity.

3.4.1.3 Resource use efficiency (RUE)

Nutrients were negatively correlated with RUE (P: ρ = -0.31; Si: ρ = -0.43). Due to how RUE is calculated here (see Material and Methods), DIN was removed from all models and analyses in this part. Salinity was positively correlated (ρ = 0.18) with RUE as well as temperature (ρ = 0.10). Further, size was positively correlated with RUE (ρ = 0.57, CWM_{size}) (Fig. 3.6).

For diversity metrics, both size diversity (ρ = -0.61), evenness (ρ = -0.44) and ^1D (ρ = -0.33) had negative relationships with RUE. Both richness and genus richness displayed non-significant correlations with productivity (Fig. 3.6). As single predictors, diversity metrics did not explain >1% of the variance.

Looking at multiple regression, around 64% of the variance observed in the re-

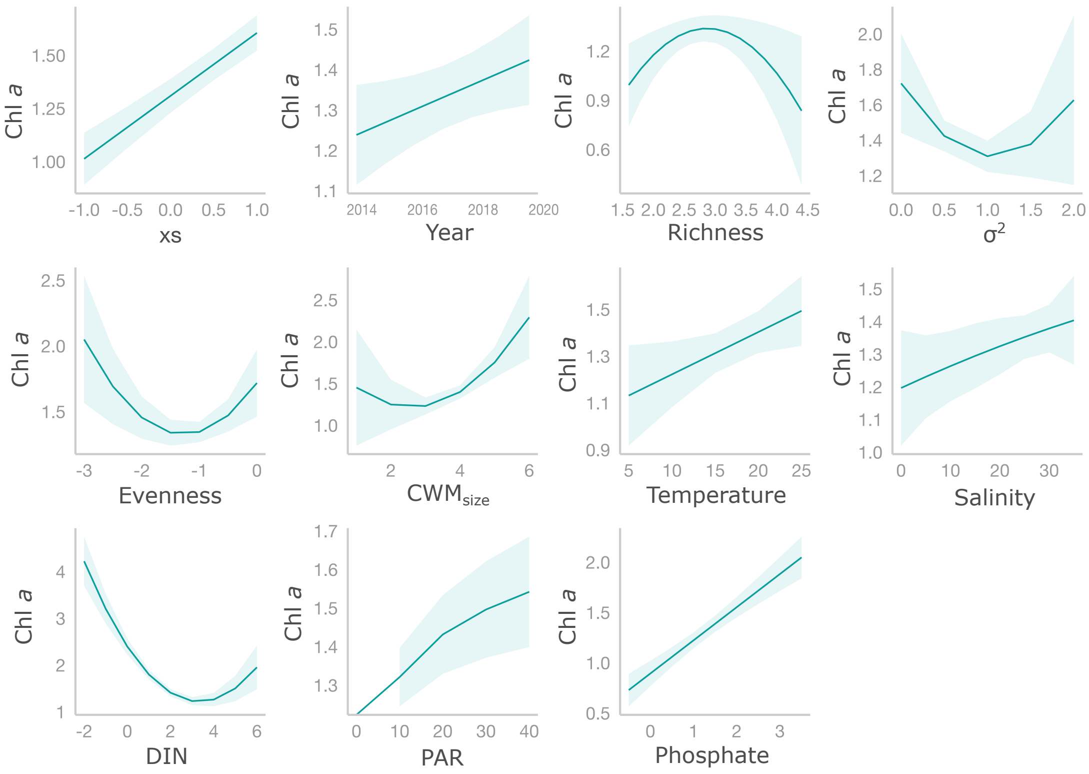

Figure 3.5: **Partial-effect plots from multiple regression model with Chl *a* as a response.** Shown here are the Chl *a* variability across seasons and years, richness, size diversity (σ^2), evenness, CWM$_{size}$, temperature, dissolved inorganic nutrient (DIN), PAR and phosphate.

sponse could be explained by the selected predictors. Similarly to Chl *a*, environmental and other variables were the most important predictors, highlighting the seasonal aspect that affects this productivity proxy, followed by diversity and trait (Fig. 3.8, C). Richness, CWM$_{size}$, PAR and phosphate scaled positively with RUE, unlike size diversity and temperature. Further, salinity displayed a non-linear trend with productivity (Fig. 3.7). Among diversity metrics, richness was more important (18%) than size diversity (14%). For the environment, PAR regime explains more of the variance observed (21%). When size diversity is not included, inter-annual variability appears to be the single most important factor in driving RUE.

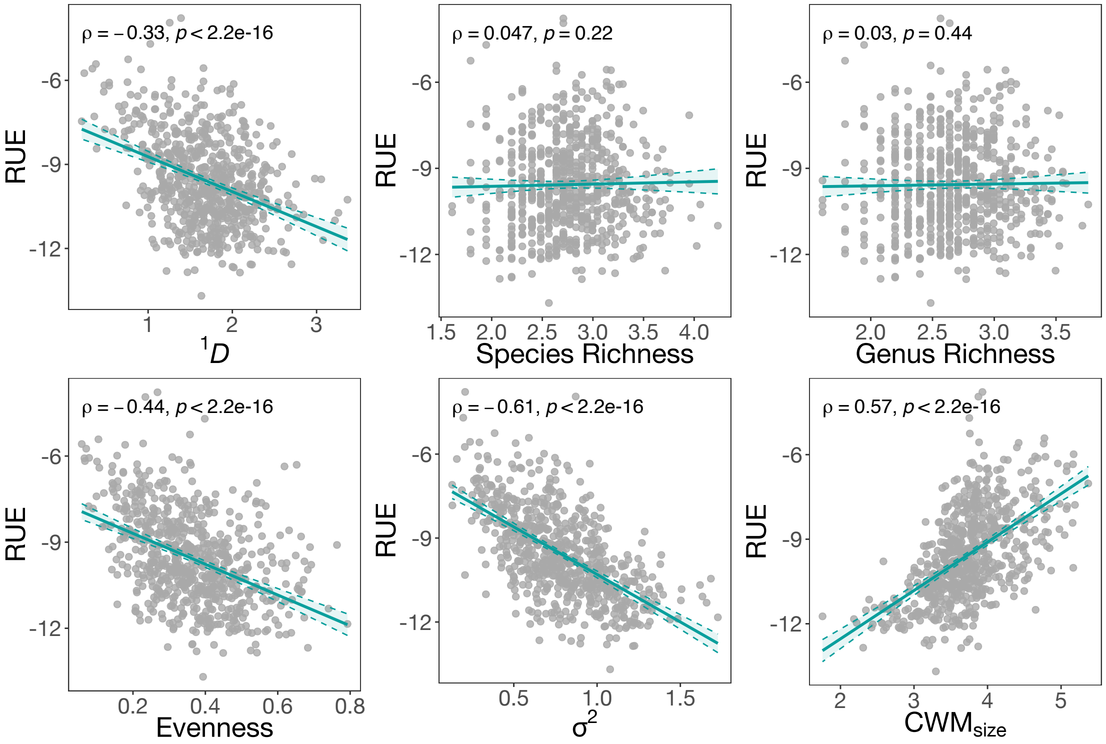

Figure 3.6: **Scatterplots of RUE and diversity metrics.** Plots display the bidirectional relationship between diversity metrics and resource use efficiency (RUE) as a productivity proxy. Spearman's correlation (ρ) and p-values can be seen at the top left of each plot. All axis are natural log-transformed. ^1D: exponential Shannon; σ^2: size diversity.

3.5 Discussion

Results reveal that community size structure, rather than species richness, drives productivity in the SFB region. Here, species richness had a weak or even non-existent effect on ecosystem function and it was not a strong predictor when accounting for environmental and temporal covariates. This fundamentally contradicts the expected pattern of positive effect of richness on productivity (Cardinale et al., 2002; Loreau, 2010; Tilman et al., 2014). Still, several studies have reported findings in marine natural and experimental communities that aligns with the results shown here (Bruno et al., 2006; Emery et al., 2021; Lehtinen et al., 2017; Maureaud et al., 2020).

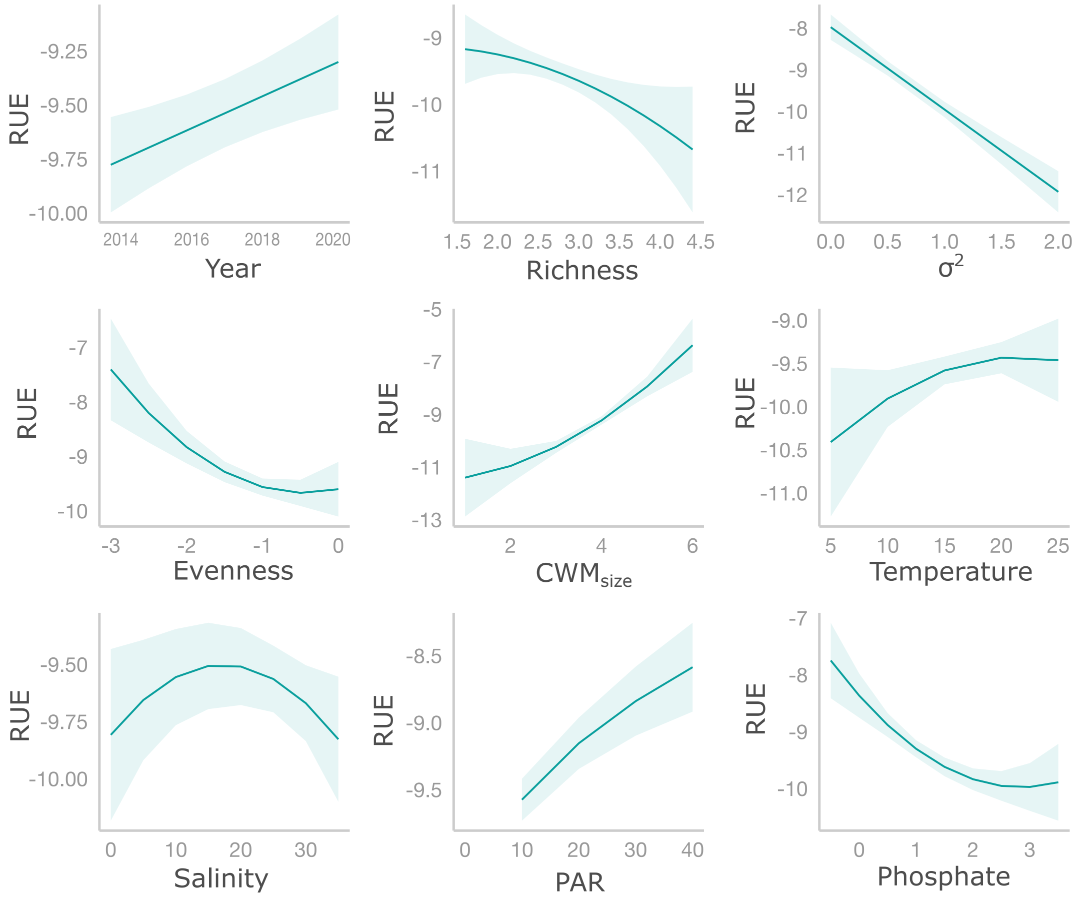

Figure 3.7: **Partial-effect plots of multiple regression model with RUE as response.** Most important predictors of RUE variability in the San Francisco Bay system, such as annual trends, richness, size diversity (σ^2), evenness, CWM$_{size}$, temperature, salinity, PAR and phosphate.

3.5.1 Environmental control on productivity

The SFB area is characterised by high nutrient concentrations (Conomos et al., 1985), leading to an increased mean cell size, lowered size diversity (σ^2) and evenness with increased biomass (Fig. 3.2) (Chen et al., 2012; Cloern, 2018). The phytoplankton community in SFB area is composed of large cells, mainly diatoms, that increase in dominance with increasing biomass (Cloern, 2018). This pattern is usually found in estuarine ecosystems, where elevated nutrient input coupled with mid- to high-latitude temperatures, actively selects larger cells by providing protection strategies

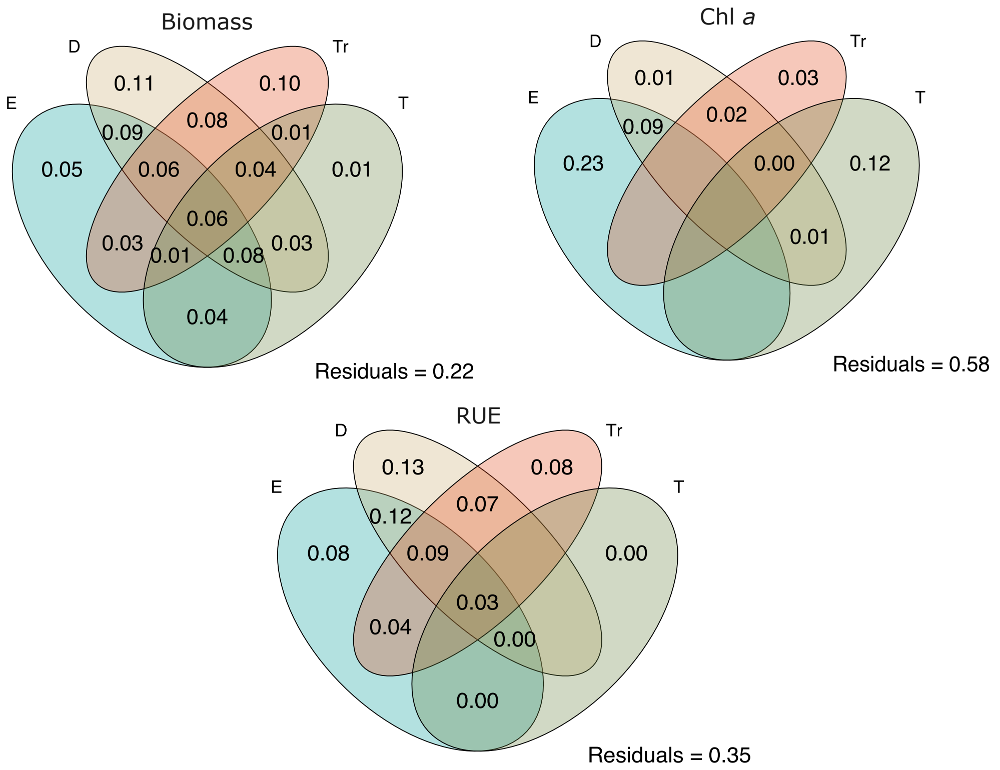

Figure 3.8: **Variance partitioning between environment, diversity, trait and temporal dynamics and productivity in the San Francisco Bay system.** Productivity proxies were biomass, chlorophyll *a* and resource use efficiency (RUE). E: environment, D: diversity, Tr: trait and T: temporal.

(i.e. larger cells are not easily predated) and by setting a high upper limit on growth (Chen and Liu, 2010; Cloern et al., 2017; Finkel et al., 2010). In coastal systems, environmental and nutrient variability can be subject to the effects of river discharge, urban and agricultural run-off (Cloern et al., 2017; Raimonet and Cloern, 2016). Thus, the availability of inorganic nutrients is a limiting factor on the distribution of phytoplankton biomass, with variability observed in systems with high nutrient loading.

Environmental variables (e.g. photosynthetic active radiation [PAR], nutrients) exhibited different relationships with each productivity proxy, usually displaying complex interactions. For instance, the non-linear effect of DIN on productivity (biomass and Chl *a*) suggests an optimal range for nutrient input levels. At intermediate nutrient levels, other limiting factors (such as light or perhaps competition) may be reducing productivity. Here, nutrients were never truly limiting and despite its strong effect on certain productivity proxies (e.g. Chl *a* and resource use efficiency [RUE]), nutrient supply alone did not explain the variability observed. Rather, the role of PAR in explaining variation suggests that light availability strongly influences productivity and may modulate nutrient and diversity effects (Cloern, 1999; Cloern et al., 1985).

Increase in biomass production and even blooms outside springtime have been observed in relatively low nutrient concentrations in the SFB area (Cloern et al., 2017). However, these observations were associated with a change in the trophic cascade within the SFB, with decreased predator presence and enhanced phytoplankton growth, leading to an increased biomass even at low nutrient concentrations, caused by changes in ocean-estuary inter-decadal dynamics (Cloern et al., 2017). Here, the interaction between light availability and high nutrient systems are strong drivers but will not necessarily lead to increased productivity, and may act by modulating community size structure and composition instead (Heinrichs et al., 2024).

Despite the dominance of larger cells in the region, biomass still decreased with increasing temperature. Temperature plays a role in constraining the dominance of large cells and therefore biomass accumulation by setting a threshold where grazing rates are faster than growth rates of large phytoplankton. So, at temperatures above a certain limit, the community size structure may be dominated by smaller cells and consequently, biomass is lowered (Cloern, 2018; Finkel et al., 2010; Heinrichs et al., 2024; Hillebrand et al., 2022b). Chl *a* and RUE, on the other hand, increased with increasing temperatures as a result of increased cell growth rates. This pattern has been reported (Berges et al., 2002; Otero et al., 2020; Stramski et al., 2002) and as a result, even if total biomass decreases with temperature, Chl *a* content might remain stable and even increase as the size structure of the community shifts towards smaller cells. The same is true for RUE, where smaller, faster-growing species might dominate under warmer conditions, increasing efficiency but reducing biomass overall (Cloern, 2018).

3.5.2 Diversity drives productivity in unexpected ways

Both mean size (CWM$_{size}$) and size diversity (σ^2) were the most important predictors of productivity. CWM$_{size}$ positively affected all productivity proxies, as large cells have larger ability to accumulate biomass and Chl *a*, and are able to capture resources more efficiently, leading to an increased RUE (Hillebrand et al., 2022a; Marañón et al., 2013). Cell size is a 'master' trait in ecology and it controls several physiological and ecological processes, such as metabolic rates (Brown et al., 2004), growth and grazing (Brose et al., 2006; Marañón et al., 2013), photosynthetic rates (Marañón et al., 2007) and even diversity (Cermeño and Figueiras, 2008), to name a few. Generally, CWM$_{size}$ is consistently decreasing each year in the SFB. As such, this could lead to even smaller productivity rates and further hinder the capability of coastal areas to act as a carbon sink (Finkel et al., 2010).

Increased σ^2 suggests the community was dominated by small- to intermediate-sized cells with relatively even contributions to total productivity. In this study, highest σ^2 was associated with the lowest biomass. This was due to the presence of cyanobacteria *Eucapsis microscopica* contributing to a relatively large portion of the biomass in the samples, leading to an increase in σ^2 but overall reduced biomass. Conversely, where σ^2 was lowest, a dominance of diatom was observed leading to maximum biomass levels and largest CWM$_{size}$. Chen et al. (2019) also reported negligible and even negative effects of size diversity on productivity, based on a 3D ocean circulation model of the North Pacific. In dynamic environments, high diversity is needed to achieve strong selection effects that enhance productivity (Chen et al., 2019). Species responses to the environment are more synchronized at high resource levels, which may reduce the importance of richness in determining productivity as the benefits of facilitation through complementarity are reduced (Chen et al., 2019). Instead, less productive species can dilute the overall productivity of the community, so the addition of new species may decrease productivity (thereby increasing σ^2), particularly if species' traits are not correlated to the function in question (i.e. size)

(Hagan et al., 2023; Hodapp et al., 2019).

Results also show that evenness was a strong negative predictor of ecosystem function, which could suggest that selection, instead of complementarity, is the mechanism driving productivity in marine communities (Cermeño et al., 2016). In spite of this, few studies have included evenness as predictor of function and results have been variable (Hordijk et al., 2023). Nevertheless, studies that do include evenness, report a strong negative effect on productivity in aquatic communities, supporting these findings (Filstrup et al., 2019; Hodapp et al., 2015; Lehtinen et al., 2017). Unlike terrestrial systems and experimental conditions, productivity in non-static systems appears to be sustained by selected traits (i.e. larger-sized cells), where resources are taken up by the best competitors. With that, evenness reflects the dominance of species that are thriving under the current environmental conditions, and unlike richness, might be more connected to ecosystem function (Lehtinen et al., 2017). When all species respond similarly to abundant resources (niches overlapping), the inclusion of less efficient species does not contribute additional benefits and can even reduce the average productivity, as these species occupy niche space and resources without significantly enhancing output (Chen et al., 2019; Vallina et al., 2017). Indeed, species' traits appear to have a larger impact on marine productivity than richness alone (Bruno et al., 2006).

As such, these results are not consistent with biodiversity-ecosystem function (BEF) experiments and many reported studies, even after accounting for environmental covariates (Cardinale et al., 2012; Otero et al., 2020; Ptacnik et al., 2008; Tilman et al., 2014; Vallina et al., 2017). Although in BEF experiments and modelling approaches, a positive relationship is usually reported, there is a compelling argument to be made that we should not expect positive relationships in field data (Hagan et al., 2021; Stachová and Lepš, 2010). BEF studies often manipulate the initial diversity, or the species that were sown in the habitat/patch during the community assembly process and this will consistently increase ecosystem function irrespective of the observed diversity ('realised diversity') at a future time point (Stachová and Lepš, 2010).

Initial diversity then boosts function via complementarity and selection effects, irrespective of how many species are currently present, or even declines in richness.

When complementarity dominates, many species co-occur partitioning resources and increasing function relative to monoculture expectations (i.e. species growing alone). This maintains diversity over time, with species coexisting and contributing to the overall community-level productivity (Loreau and Hector, 2001). However, when selection effects dominate, highly competitive and/or functioning species may dominate, leading to increased ecosystem function, but, as they outcompete others, this leads to reduced diversity over time (Chesson, 2000; Tilman, 2000). So, whether diversity will positively affect ecosystem function may not be dependent on the current observed diversity, but rather the initial diversity. As in both cases, high initial diversity is likely associated with high trait variation and as such, increased ecosystem function (Hagan et al., 2021; Loreau et al., 2001). The Stachová and Lepš (2010) model shows that the degree of competition and carrying capacity of a species interact to shape the relationship between diversity and productivity. With low competition coefficients leading to a positive selection effect in small species pool size, and therefore, increased productivity. Whereas at large species pool, such as in naturally assembled communities, species with high carrying capacity are selected. Leading to a negative relationship between diversity and productivity (Stachová and Lepš, 2010). In experiments, the difference between initial and realised diversity might not matter to overall functioning of the ecosystem, as positive effects observed in controlled conditions might not transfer to complex field environments. Yet, this difference is crucial in non-controlled settings, as the positive effects of initial diversity on functioning may not be observed if only realized diversity is available, which is often the case with field data, leading to variable relationships (Hagan et al., 2021; Kenkel et al., 2001; Stachová and Lepš, 2010).

3.5.3 We need to talk about proxies

The choice of productivity and diversity proxies has profound implications to the overall variability regarding the relationship between diversity and productivity, and it is inconsistent across studies (Mittelbach et al., 2001; Vallina et al., 2014).

In this study, biomass is simply a measure of standing biomass based on cell volume and despite being used as a proxy for productivity in several studies, it is important to highlight that is does not reflect production rates. Similarly, resource use efficiency (RUE) reflects biomass per unit of limiting nutrient (Hodapp et al., 2019). Each proxy provides distinct insights, with biomass capturing dominance of larger species, Chl *a* likely highlighting abundance patterns and photosynthetic potential, and RUE reflecting efficiency in nutrient uptake. However, caution should be exercised as no proxy truly captures current levels of productivity and they may reflect different aspects of the community. When taking RUE, for instance, there are several different approaches to calculate this proxy, it is mainly focused on a single nutrient ignoring co-limitation of multiple resources and often quantified using what was 'left-behind' in the water column instead of what is actually bioavailable (Hodapp et al., 2019). The same is true for biomass, as it function as a snapshot of the system and not the actual biomass turnover. This could lead to variable conclusions, as standing biomass as a productivity proxy might remain low due to high turnover (e.g. grazing or export) even if actually primary productivity rates are high. Chl *a* despite being a valuable measurement, might be decoupled from biomass and not reflect actual productivity rates, as Chl *a*:C ratios vary according to species-specific physiology, light and nutrient regimes (Litchman and Klausmeier, 2008). Not a single proxy is perfect, but keeping their biases in mind and using them in complementary ways might give us a more complete picture of how ecosystem function changes with changes in diversity.

The concept of diversity has multiple facets and choosing a proxy that accurately depicts which aspect of it matters for community functioning is crucial. For instance, richness is an easy measurement to obtain, which has contributed to its widespread use in literature. However, this metric has several ecological and statistical limitations as it is prone to sampling bias. First, richness is scale- and density-dependent, making comparison across different sites and/or time periods challenging. In addition, richness only reflects a limited aspect of the community being observed (i.e. changing number of species does not offer information on dominant species) (Chase and Knight, 2013; Jost, 2007). Furthermore, community composition is an important indicator of how a community can respond to disturbances, and changes in richness may not reflect species' turnover (i.e. immigration and extinction rates may remain stable) (Hillebrand et al., 2018). Finally, rate of function change may not be linked to decline in species number. Lack of species loss may not indicate loss of ecosystem function, and this has implications for the debate of whether protecting biodiversity has any impact on ecosystem function and services.

3.5.4 Implications and limitations

These findings highlight how variable this relationship can be in naturally assembled communities, and how crucial it is to determine causal drivers of productivity in our current climate emergency (Hillebrand and Matthiessen, 2009). The findings of this study add to the growing body of literature that argue that functional diversity and species' traits and dominance shifts are a better way to approach the effects of diversity on ecosystem function (Chen and Liu, 2010; Chen et al., 2019; Hagan et al., 2023; Hillebrand et al., 2022a; Hillebrand et al., 2018; Spaak and De Laender, 2021). Further, in this study, I only had access to realised diversity (i.e. current observed number of species). Initial diversity, or the number of species present at the time of community assembly, has been shown to boost productivity irrespective of realised diversity (Stachová and Lepš, 2010). This has been argued to be one of the reasons BEF relationships in field data varies from experimental expectations (Hagan et al., 2021).

The relationship between biodiversity and ecosystem function varies according to environmental settings, species interactions across temporal and spatial scales (Hagan et al., 2021), and, most importantly, species identities and their functional differences (Hillebrand and Matthiessen, 2009). In species-rich planktonic communities, the physical environment, resources, and species composition shift frequently. These constant changes create temporary conditions that favour certain species that can quickly exploit the available resources. The observed effects of community size structure and evenness illustrate this, with implications for how we discuss biodiversity loss impacts' on ecosystem function and services.

In natural ecosystems, where light, nutrient and ecological interactions all affect community structure and functioning, accounting for all confounding factors is a herculean task (Mayersohn et al., 2022). Much like proxy selection, choice of statistical framework for the analysis of hypotheses also impacts conclusions. Moving beyond bivariate analyses and examining whole-system dynamics can refine our understanding of what drives productivity under a rapidly changing climate and help us establish causal links (Chang et al., 2022; Grace et al., 2014; Grace et al., 2022). Naturally, this is easier said than done. Functional trait-based approaches coupled with multivariate analyses hold a lot of potential, as species' traits might be more directly linked to function and we can take into account environmental, temporal and spatial covariates.

3.6 Conclusions

The findings challenge the widely accepted positive biodiversity and ecosystem function (BEF) relationship. In the San Francisco Bay system, diversity and productivity often exhibited a negative relationship, with species richness having a weak or negligible effect on ecosystem function. Instead, trait diversity, particularly related to size, emerged as a stronger predictor of productivity. Large cells, such as diatoms, dominated under high biomass conditions, illustrating the importance of community size structure in driving productivity.

Environmental filtering affected productivity by modulating community composition and consequently, size structure. Specifically, light limitation coupled with increasing temperatures constrained biomass accumulation, even in a nutrient-rich system, by steadily shifting dominance towards smaller cells across the years. As such, nutrient supply alone does not explain productivity variability, but it does affect diversity in indirect ways, and with that, productivity. Further, this shift indicates potential long-term reduction in coastal productivity and carbon sequestration abilities.

Results also reveal that evenness negatively affects productivity, suggesting that few high functioning species dominate the community. These findings challenge previous observations in naturally assembled communities, by demonstrating that weak and even negative relationships between richness and productivity are possible due to environmental variability, species turnover and differences in trait dominance (Irigoien et al., 2004; Otero et al., 2020; Ptacnik et al., 2008). Positive relationships in field data may not be as common as experiments predict. As such, our expectations might be limiting our view on the effect of diversity, especially trait diversity, on productivity. And consequently, how ecosystems will change in face of rapid species loss. Additionally, the choice of productivity proxy can also influence conclusions, where proxies can be more directly or indirectly related to the ecosystem function in question, and this may influence the variability of the effect of diversity (Groner and Novoplansky, 2003).

Ultimately, these results highlight that functional traits, rather than species richness alone, are critical in driving productivity. Dominance of certain traits reflects transient dynamics of the community, where some species are better competitors and influence function more strongly. Yet, high diversity is still necessary to allow for complementarity and selection effects to take place, but it may not be directly linked with high productivity.

3.7 Future steps

The observed patterns give us some insight on how variable the biodiversity-ecosystem function can be. However, these observations do not provide answers as to what the causal drivers of these effects are. Rather, they are strong indicators only, as this chapter is only based on correlational analyses. Using these findings, I want to develop a mechanistic model to investigate the relationship between diversity and productivity. By controlling diversity changes in terms of the size structure and different nutrient input levels, I want to investigate whether nutrient regime or diversity drives productivity, and by which mechanism (selection or complementarity). For that, I parametrised a nutrient-phytoplankton and a nutrient-phytoplankton-zooplankton model, with species richness reflecting the addition of new cell sizes under 20 different nutrient input levels. The results of this model can be found in the following chapter.

Chapter 4

Beyond observations: modelling the role of diversity and trophic interactions on ecosystem functioning

4.1 Introduction

Understanding biodiversity and ecosystem function (BEF) relationships is key to determining how diversity loss influences ecosystem productivity and, consequently, how ecosystems might respond to rapid climate change (Hooper et al., 2012). In marine systems, communities are shaped by dynamic environmental conditions and trophic interactions, and the effects of diversity on productivity can vary significantly from theoretical expectations (Hagan et al., 2021; Smith et al., 2016; Stachová and Lepš, 2010). While mechanisms driving BEF relationships, complementarity and selection effects, are well-established (Cardinale et al., 2006; Loreau, 2010; Loreau and Hector, 2001), their quantification and relevance in naturally assembled communities remains an ongoing challenge.

Generally, diverse communities are found to be more productive, particularly in variable environments (Smith et al., 2016). Experimental evidence suggests that increasing the number of species allows for more efficient resource partitioning, leading to overall higher community-level performance via complementarity (Loreau et al., 2001). However, this expectation is variable in natural communities, where confounding factors, including environmental variability and trophic interactions, can obscure these relationships (Cermeño et al., 2016; J. A. Strong et al., 2015). Ptacnik et al. (2008) reports a positive effect of richness on ecosystem function in natural phytoplankton communities, but other studies have found negative and even no effects of diversity on community productivity under similar conditions (Emery et al., 2021; Lehtinen et al., 2017; Maureaud et al., 2020).

In addition to bottom-up drivers, top-down effects such as predation can also regulate productivity and diversity patterns (Thébault and Loreau, 2003). Predators can exert a strong influence on ecosystem processes and this influence can act largely indirectly by causing changes in dominance (Duffy, 2002; Paine, 2000). In marine systems in particular, this influence is expected to be stronger, partly due to reduced number of consumers as well as slower rates of production in terrestrial ecosystems (Paine, 2000; Terborgh et al., 2001). Duffy et al. (2007) argues that multi-trophic interactions can lead to more observed variation in BEF relationships (i.e. non-monotonic ones) that hinge on predators' dietary preferences, prey edibility, competitive ability among other reasons. Understanding the effect of trophic interactions in affecting community-level productivity in lieu of species decline is a current important challenge (Thébault and Loreau, 2003). Both bottom-up drivers, like nutrient availability, and top-down controls, such as predation, can strongly influence productivity and diversity patterns. Disentangling the effects of the environment from those of diversity is difficult, and integration of trophic interactions into BEF studies remains limited, despite the potential for predator-prey dynamics to alter diversity and productivity outcomes (Hillebrand and Matthiessen, 2009; Maureaud et al., 2020).

Observational and experimental studies have provided valuable insights into the BEF discussion, yet they are limited by confounding factors such as environmental variability and species interactions (Hillebrand and Matthiessen, 2009). For example, experiments have shown that adding consumers often weakens the positive effect of diversity on biomass at lower levels of prey richness (Mulder et al., 1999). Predators can also amplify or reduce diversity effects on productivity by selectively grazing (Shurin et al., 2002). In marine systems, the extent to which zooplankton diversity affects phytoplankton productivity remains under-explored. Here, where productivity is influenced by dynamic physical and biological processes, even controlled experiments can be difficult to scale, and long-term data often lacks the resolution needed to separate causation from correlation. To address these challenges, ecosystem models, such as nutrient-phytoplankton-zooplankton (NPZ) frameworks, provide powerful tools to isolate BEF effects, systematically varying biodiversity while controlling for environmental variability.

In Chapter 3, richness itself was a weak predictor of ecosystem function, challenging the current consensus (Loreau and Hector, 2001) and hinting at a more complex picture due to trophic interactions. In this chapter, I use nutrient-phytoplankton (NP) and nutrient-phytoplankton-zooplankton (NPZ) models to test whether these patterns hold under controlled conditions. I explore mechanistic explanations for how trait diversity (i.e. size), environmental conditions, and trophic interactions shape productivity. These models provide a simplified yet robust framework for disentangling the complex interactions between bottom-up and top-down controls of phytoplankton productivity. An NP model can help us explore and demonstrate how phytoplankton diversity influences productivity under different nutrient conditions (bottom-up effects), whereas a NPZ model allows for top-down control, helping to assess whether consumer diversity modifies phytoplankton productivity. By keeping environmental conditions constant (i.e. temperature), these models will help us isolate the effects of diversity, nutrient input and trophic interactions on productivity.

Given the central role of phytoplankton in carbon cycling and oxygen production, understanding how biodiversity influences productivity is key for predicting the impacts of its loss on global biogeochemical cycles in a rapidly changing climate. I want to determine: i) which mechanisms (complementarity or selection) are driving productivity in phytoplankton communities; ii) whether this relationship is driven by changes in diversity or nutrient input levels; and iii) how does the presence/absence of predators alter these observations. Specifically, I want to test the following hypothesis:

- *H0*: Changes in productivity are more strongly influenced by increases in species richness than by variations in nutrient levels.
- *H1*: The relationship between diversity and productivity depends on environmental conditions, such as nutrient input, with larger biodiversity effects under nutrient-limited conditions.
- *H2*: The absence of predators allows for increases in productivity due to increased richness, by reducing top-down pressures and enabling complementarity effects.
- *H3*: Selection effects, not complementarity, are dominant in phytoplankton communities, as trophic interactions lead to changes in species' dominance.

4.2 Methods

4.2.1 Model description and implementation

4.2.1.1 Nutrient-Phytoplankton model

To examine the question of the role of diversity in driving productivity in the oceans, I analysed models with two conditions: (i) absence and (ii) presence of zooplankton. For condition (i), I used a nutrient-phytoplankton (NP) model. This is a modified version of a nutrient-phytoplankton-zooplankton (NPZ) model following (Cloern, 2018; Taniguchi et al., 2014) with R ($2 \leq R \leq 20$) number of species (i.e., size classes) of phytoplankton (P), with the following equations for P [Eq. 4.1] and N [Eq. 4.2]:

Table 4.1: **NP model parameters.** Parameters and their symbols, unit and range of values for each parameter in the model. Nitrogen, phytoplankton and zooplankton parameter values are for initial conditions.

Parameter	Symbol	Unit	Value
Maximum specific phytoplankton growth rate	μ_{max}	d^{-1}	-
Size-dependent half-saturation constant	Ks	μM N	-
Activation energy for phytoplankton growth	E_p	-	0.32
Minimum phytoplankton concentration	pm	μM N	0.1
Phytoplankton mortality	m_p	d^{-1}	0.5
Degree of competition	ϕ	-	0.5
Nitrogen	N	μM	1 - 40
Phytoplankton	P	μM N	-

$$\frac{\mathrm{d}P_i}{\mathrm{d}t} = P_i \frac{\mu_i N}{N + K_{s,i}} - m_p \overline{P}^{1-\phi} P_i^{1+\phi} \tag{4.1}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -\sum_{i=1}^{R} P_i \frac{\mu_i N}{N + K_{s,i}} + m_p \overline{P}^{1-\phi} P_i^{1+\phi} \tag{4.2}$$

with i representing the i^{th} size class of phytoplankton, ranging from 2 to R. For the community with species richness R, the size classes were randomly drawn from a uniform distribution, based on the natural log-transformed minimal and maximal equivalent spherical diameter (ESD) observed in the San Francisco Bay (SFB), respectively (phytoplankton ESD_{min}: 3.7 μm, ESD_{max}: 178.4 μm). Competitive exclusion is an intrinsic model behaviour. To allow for coexistence of species in the model without zooplankton and with multiple phytoplankton compartments, and therefore diversity, a modified mortality term that is density-dependent with a new parameter, ϕ, after (Record et al., 2014) was introduced. Where m_p is a constant mortality and ϕ determines the degree of competition structuring the community by differences in abundance contribution, set at 0.5 (Table 4.1). A higher ϕ relates to a less even community, whereas a lower ϕ leads to a more even community. Further model specifications that are common to both (i) and (ii) models are described bellow.

4.2.1.2 Nutrient-Phytoplankton-Zooplankton model

To assess the effect of phytoplankton diversity in driving productivity in the presence of zooplankton, I used a simplified version of the same NPZ model described above (Cloern, 2018; Taniguchi et al., 2014) also with R ($2 \leq R \leq 20$) number of species (i.e., size classes) of both P and zooplankton (Z). I assume a constant (Z) to P size ratio (10:1 in length) (Ward et al., 2012), meaning each zooplankton size class is only able to feed on a single phytoplankton size class. The model thus includes the following $2R+1$ ordinary differential equations referring to P [Eq. 4.3], Z [Eq. 4.4] and nutrient N [Eq. 4.5]:

$$\frac{\mathrm{d}P_i}{\mathrm{d}t} = P_i \frac{\mu_i N}{N + K_{s,i}} - (P_i - pm)^c \frac{g_{m,i} Z_i}{(P_i)^c + (K_{z,i})^c} \tag{4.3}$$

$$\frac{\mathrm{d}Z_i}{\mathrm{d}t} = Z_i \frac{e g_{m,i} (P_i - pm)^c}{(P_i)^c + (K_{z,i})^c} - m_p \overline{Z}^{1-\phi} Z_i^{1+\phi} \tag{4.4}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -\sum_{i=1}^{R} P_i \frac{\mu_i N}{N + K_{s,i}} + \sum_{i=1}^{R} Z_i \frac{(1-e) g_{m,i} (P_i - pm)^c}{(P_i)^c + (\mathrm{K}_{z,i})^c} + m_p \overline{Z}^{1-\phi} Z_i^{1+\phi} \tag{4.5}$$

with i representing the i^{th} size class of either phytoplankton or zooplankton, ranging from 1 to R.

Both phytoplankton maximum specific growth rate (μ_i, [Eq. 4.6]) and half-saturation constant (K_s) depend on size [Eq. 4.7]. Maximum specific growth rate is then determined by μ_i, K_s and size. Zooplankton mortality was parametrized after Record et al. (2014), with a modified mortality term that is density-dependent with a new parameter, ϕ. As mentioned earlier, this parameter addresses the intrinsic model behaviour of competitive exclusion, where ϕ represents a varying degree of competition (here, set at 0.5). This parameter allows for coexistence and realistic biodiversity community patterns, beyond a simple quadratic function form for zooplankton mortality.

$$\mu_{max_i} = 1.36 \times ESD_i^{0.2} \tag{4.6}$$

$$K_s = 0.33 \times ESD_i^{0.48} \tag{4.7}$$

Rate of phytoplankton population change [Eq. 4.3] is dependent on both phytoplankton growth and zooplankton grazing. Grazing rate [Eq. 4.8] was described as a function of phytoplankton biomass, with constant K_z [Eq. 4.9]. c controls whether the zooplankton grazing functional response is Holling type II ($c = 1$) or type III ($c = 2$). For this model, I use Holling type III.

$$g_m = 33.96 \times ESD^{-0.66} \tag{4.8}$$

$$K_z = 17.92 \times ESD^{-0.64} \tag{4.9}$$

Zooplankton population changes over time [Eq. 4.4] are a balance between food consumption and mortality, m_z. Food intake is calculated as the $g_{m,i}$ scaled by growth efficiency e fixed at 0.32. m_z is set at 0.06. For [Eq. 4.5], the changes depend on P production and recycling via Z metabolism and mortality. The allometric equations used are derived from a set of experiments from Taniguchi et al. (2014). All parameter units and values used in the NPZ can be found in Table 4.2.

Both models ran for five years, and I used the R package *deSolve* (Soetaert et al., 2010) to solve model equations. Initial conditions for all sizes were P_i = 0.1 and Z_i = 0.01. Different N regimes (n = 20) were used (N_{min}= 1; N_{max} = 40) to determine changes in P biomass under increasing levels of nutrient input. Richness increased with each model run, from $P_2 Z_2$ to $P_{20} Z_{20}$. For each richness level (2 to 20), I randomly drew sizes from an uniform distribution with ten repetitions for each model. In total, I had 190 simulated communities and their final total values were averaged. Model replicates were included as random effects in the linear mixed-effects models used to determine main drivers of productivity.

In addition, to be able to quantify biodiversity effects, I calculated (see section below) the deviation of expected yield of biomass of a species in a given mixture treatment when compared to its idealized biomass yield in monoculture (i.e. species grown alone). In order to do that, I ran the NP and NPZ models based on single in-

Table 4.2: **Nutrient-Phytoplankton-Zooplankton (NPZ) model parameters.** Parameters and their symbols, unit and range of values for each parameter in the model. Nitrogen, phytoplankton and zooplankton parameter values are for initial conditions.

Parameter	Symbol	Unit	Value
Maximum specific phytoplankton growth rate	μ_{max}	d^{-1}	-
Maximum zooplankton grazing rate	g_{max}	d^{-1}	-
Gross growth efficiency of zooplankton	e	-	0.32
Size-dependent half-saturation constant	Ks	μM N	-
Activation energy for phytoplankton growth	E_p	-	0.32
Size-dependent half-saturation grazing constant	Kz	μM N	-
Activation energy for zooplankton growth	E_z	-	0.65
Minimum phytoplankton concentration	pm	μM N	0.1
Zooplankton mortality	mz	d^{-1}	0.06
Degree of competition	ϕ	-	0.5
Nitrogen	N	μM	1-40
Phytoplankton	P	μM N	0.1
Zooplankton	Z	μM N	0.01

dividual size classes of phytoplankton used here, to simulate monocultures (species grown alone). After, total primary productivity (PP) could then be calculated as the sum of the product of phytoplankton monoculture biomass and growth rate (μ_{max}) for each nutrient regime, richness level, model time step and replicate. Additionally, CWM$_{size}$, σ^2 and evenness were also estimated after simulation run.

4.2.2 Complementarity, selection and biodiversity effects

Complementarity (CE), selection (SE) and total biodiversity effects (TBE) for phytoplankton and zooplankton communities was computed following (Ghedini et al., 2022; Loreau et al., 2001). Deviation of the expected yield of biomass of a species i in a mixture (here, $P_{2:20}Z_{2:20}$) at any given time can be calculated as [Eq. 4.10]:

$$\Delta RY_i = \frac{Y_i}{M_i} - \frac{Y_{i_{ini}}}{totY_{ini}} \tag{4.10}$$

where Y_i and M_i is the observed biomass of species i in the mixture and monoculture, respectively, at any point in time, day$_x$. $Y_{i_{ini}}$ is the initial biomass (day$_0$) of species i in the mixture and finally, $totY_{ini}$ is the total biomass yield of the mixture. With that, I can quantify CE as $S \times \overline{\Delta RY} \times \bar{M}$, where S is the number of species present in the mixture (n = 20), $\overline{\Delta RY}$ is the average change in biomass yield for all species in the mixture, and $\bar{M}$, as the average monoculture biomass across all species present also in the mixture. Furthermore, SE can then be calculated as the covariance (Cov) between the biomass yield of a given species in monoculture and its relative yield in mixture times S; $S \times Cov(\Delta RY, M)$. The sum of CE and SE effects results in TBE.

4.2.3 Data Analyses

To examine the relationship between diversity, environment and productivity in the simulated communities, I used linear mixed-effects models (LMMs) [Eq. 4.11] with richness and nutrient regimes as predictors, as well as how they interact to drive productivity. I performed three-way analyses of variance (ANOVA) on LMMs outputs to determine the contribution of each predictor to the overall response, to account for the interaction term. Models were specified by the general form:

$$P = \beta_0 + \beta_1 \cdot \text{Nutrient}_i + \beta_2 \cdot \text{Richness}_i + \beta_3 \cdot (\text{Nutrient}_i * \text{Richness}_i) + \gamma_{\text{Rep}_i} + \epsilon \quad (4.11)$$

Where P is productivity, γ_{Rep_i} is the random effect of model replicates (Rep) and ϵ is the error term ($\gamma_{\text{Rep}_i} \sim \mathcal{N}(\mu, \sigma^2)$). Productivity proxies in the simulations were biomass and primary productivity (PP). For each model, I inspected the intraclass correlation coefficient (ICC) of random effects, in order to determine the amount of variance explained in the response due to this term [Eq. 4.12].

$$\text{ICC} = \frac{\sigma^2_{\gamma_{\text{Rep}}}}{\sigma^2_{\gamma_{\text{Rep}}} + \sigma^2_{\text{Residual}}} \quad (4.12)$$

All statistical analyses were conducted in R (v4.2.1), using the lme4 package for model fitting and the car package for ANOVA. Significance thresholds were set at

$p<0.05$.

4.3 Results

4.3.1 NP model

In the absence of zooplankton, total phytoplankton biomass and primary productivity (PP) increased with increasing richness. Both biomass and PP increased primarily with community weighted mean size (CWM$_{size}$), followed by richness, and decreased with increasing evenness and size diversity after simulation run (Figs. 4.1, 4.2, 4.3, 4.4). I use both biomass and PP as proxies for productivity because they relate to different aspects of community-level function, and therefore may have different drivers. Although richness differences had a small effect at very low nutrient levels, highest values of biomass and PP were observed at maximum richness values when nutrient availability was greater (Figs. 4.1, 4.3). Productivity levels in the absence of predators was mainly driven by changes in richness and to a lesser extent, by increased nutrient (Fig. 4.4), suggesting both richness and nutrient effects were not independent (Table 4.3).

Total biodiversity effects (TBE) on phytoplankton productivity were positive and largely driven by complementarity effects (CE) (Figs. 4.5, 4.10, left panels). CE was mainly driven by changes in richness levels, with species-rich communities increasing positive complementarity. Richness effects were not independent from nutrient input levels, with increasing nutrient leading to an increase in response estimates at certain richness levels (Figs. 4.5, 4.10, left panels). Selection effects (SE) were mainly driven by nutrient (Figs. 4.5, 4.10), with increasing nutrient associated with a decrease in SE. High nutrient - high richness levels displayed the smallest selection values. In this case, nutrient and richness effects were independent of each other (Table 4.3).

In all cases, variability introduced by simulation repetitions was negligible and

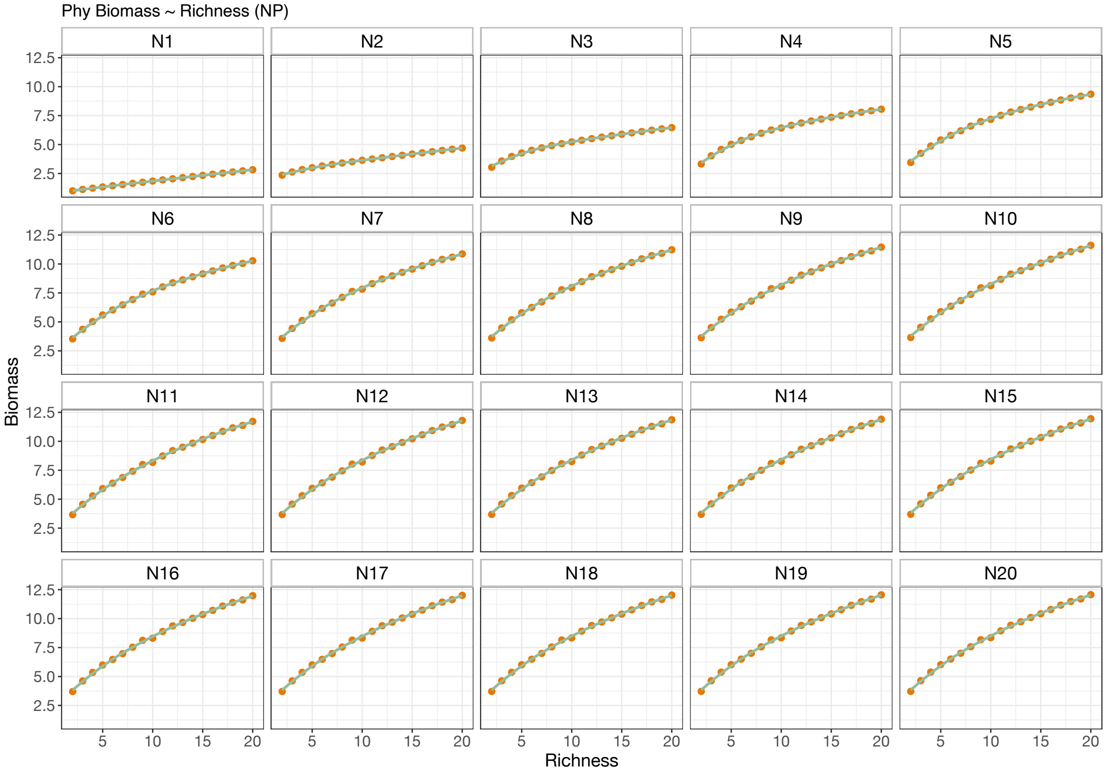

Figure 4.1: **Phytoplankton biomass across richness and nutrient levels in a NP model.** Average phytoplankton biomass and associated standard error across richness (R = 20) and nutrient (N1: N_{min} = 1, N20: N_{max} = 40) levels.

always smaller than model residual variance (Table 4.4).

4.3.2 NPZ model

In the presence of zooplankton, the main driver of total phytoplankton productivity (biomass and primary productivity; PP) was nutrients, with increasing nutrients leading to increased productivity (Fig. 4.4, right panels). The degree to which nutrient and richness changes jointly affect productivity was different depending on productivity proxy. Phytoplankton PP increased mainly with richness, followed by increasing CWM_{size} and evenness having a smaller effect. For biomass, richness was the most important predictor, followed by CWM_{size} and decreased with evenness (Fig. 4.7). However, the coupled nutrient and richness effect was much stronger, but only at high nutrient levels (Fig. 4.8). In particular, for biomass, in nutrient-rich en-

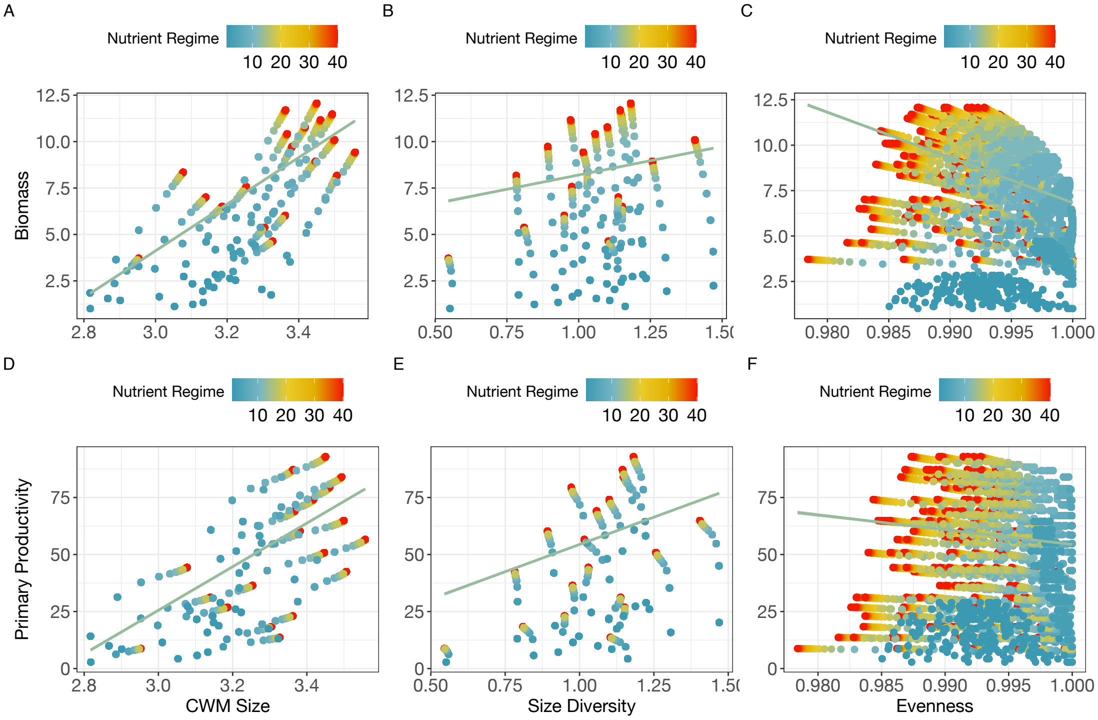

Figure 4.2: **Phytoplankton biomass and primary productivity changes over different diversity metrics in a NP model after simulation run.** Changes in productivity levels related to changes in CWM$_{size}$ (A, D), size diversity (B, E) and evenness (C, F) across several nutrient regimes.

Table 4.3: **Summary of three-way analyses of variance (ANOVA) of a linear mixed-effects model assessing the biodiversity effects on phytoplankton mixtures in a NP model.** Nutrient regime and richness as independent factors directly affecting total phytoplankton biomass and their interaction. Df: degrees of freedom; SS: sum of squares; MS: mean squares; F-value: F statistic; η_p^2: partial eta-squared as a measure of effect size. Numbers in bold represent statistical significance, p-value <0.05 for F-value and 95% confidence interval does not include zero for η_p^2.

		Total Biomass, μM N				Complementarity, $N \times \overline{\Delta RY} \times \bar{M}$				Selection, $N \times Cov(\Delta RY, M)$			
Effect	**Df**	**SS**	**MS**	**F-value**	η_p^2	**SS**	**MS**	**F-value**	η_p^2	**SS**	**MS**	**F-value**	η_p^2
Nutrient Regime	19	12212	642.8	**27460.28**	**0.99**	7639	402.04	**389.9**	**0.68**	0.79	0.04	**172.1**	**0.49**
Richness	18	15403	855.7	**36559.49**	**0.99**	14894	827.5	**802.7**	**0.81**	0.33	0.02	**76.6**	**0.29**
Nutrient:Richness	342	1439	4.2	**179.76**	**0.95**	1418	4.1	**4.0**	**0.29**	0.07	0.0002	0.87	0.08
		Total Primary Production, μM N d^{-1}				Complementarity, $N \times \overline{\Delta RY} \times \bar{M}$				Selection, $N \times Cov(\Delta RY, M)$			
Effect	**Df**	**SS**	**MS**	**F-value**	η_p^2	**SS**	**MS**	**F-value**	η_p^2	**SS**	**MS**	**F-value**	η_p^2
Nutrient Regime	19	241416	12706	**3269.6**	**0.95**	24278	1277.76	**171.1**	**0.49**	31.72	1.66	**106.2**	**0.37**
Richness	18	2123348	117964	**30354.9**	**0.99**	46411	2578.38	**1345.3**	**0.65**	19.6	1.08	**69.2**	**0.27**
Nutrient:Richness	342	62020	181	**46.6**	**0.82**	4613	13.49	**1.8**	**0.15**	3.1	0.009	0.5	0.05

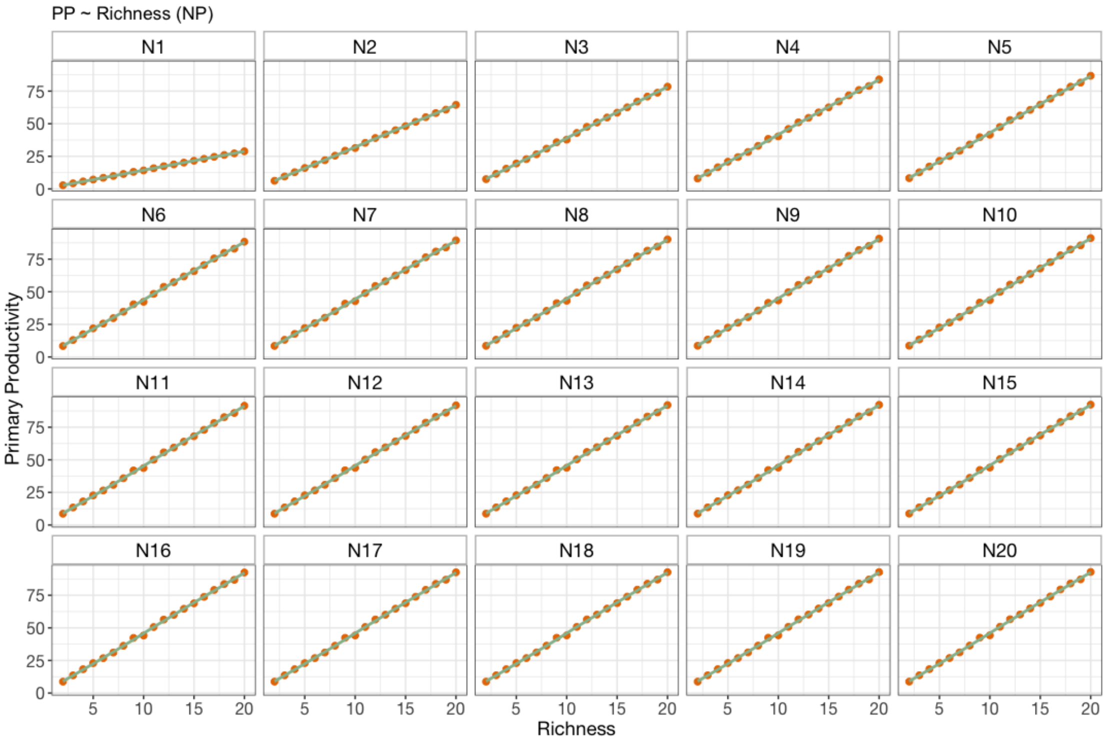

Figure 4.3: **Phytoplankton primary productivity across richness and nutrient levels in a NP model.** Average phytoplankton primary productivity and associated standard error across richness (R = 20) and nutrient (N1: N_{min} = 1, N20: N_{max} = 40) levels.

vironments, richness had little to no effect on the response (Fig. 4.6). Size diversity (σ^2) was highly correlated with CWM_{size}, and therefore, removed from analyses. Still, I ran separate linear models with both size diversity and CWM_{size} as predictors, but models with CWM_{size} as predictor explained more variance in the data.

Total biodiversity effects (TBE) on phytoplankton productivity in the presence of zooplankton were more variable and weaker, ranging from negative to positive values. For both productivity proxies, selection effects (SE) was the main driver of TBE. CE were mostly positive and solely driven by nutrient for both productivity proxies, with richness playing a negligible effect at high nutrient levels. Selection effects (SE) were negative and driven by nutrient. When biomass was the proxy, nutrient alone drove the diversity effects (Table 4.5). For PP, nutrient was the most important driver in these phytoplankton communities. Yet, nutrient interaction with richness at high

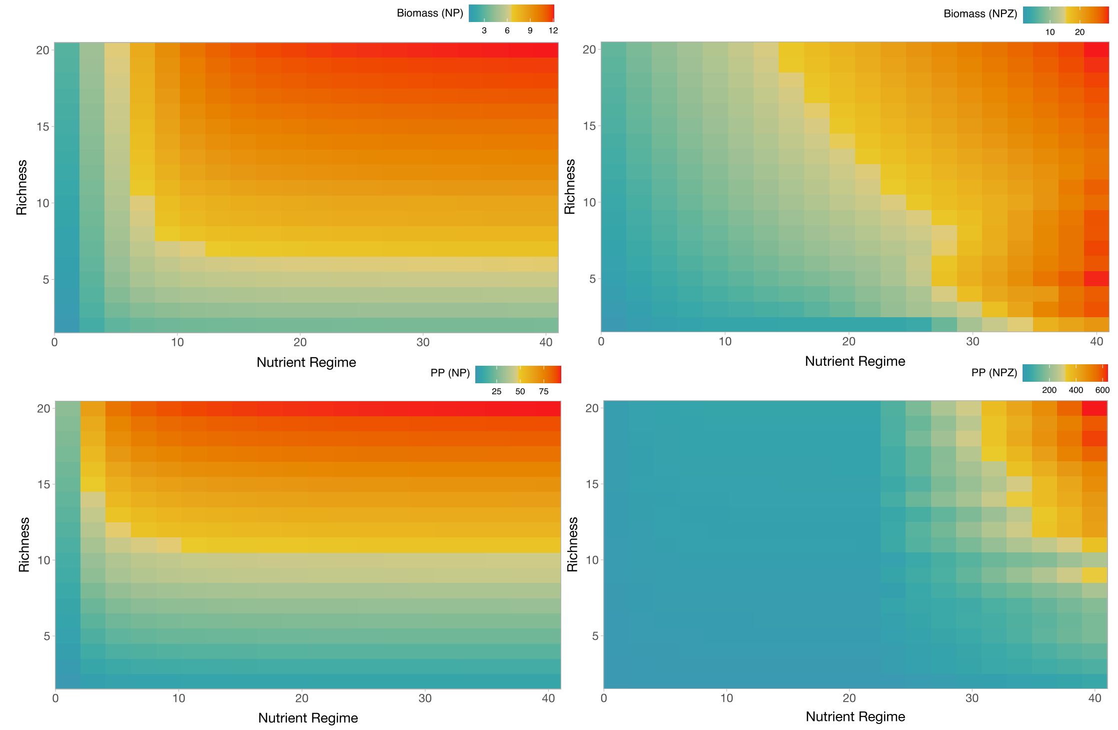

Figure 4.4: **Total biomass and primary production changes across a richness and a nutrient gradient.** Phytoplankton total biomass (top figures) and primary production (bottom figures) for NP and NPZ models, respectively.

nutrient levels was also important, leading to a decrease of the response at high richness levels (Table 4.5).

For zooplankton communities, biomass was mainly driven by nutrient, with richness contributing at high nutrient levels only (Fig. 4.11, upper left panel). At intermediate to low nutrient levels, richness had no effect by itself. Rather, with increasing nutrient, biomass saturated at higher richness levels (Fig. 4.9). When looking at community-level metrics, zooplankton biomass was driven primarily by CWM$_{size}$, followed by richness, which had a negative effect on overall productivity, size diversity and finally, evenness. TBE in zooplankton communities was driven by complementarity, which was in turn mainly driven by nutrient input. CE increased with increasing nutrient, particularly at high nutrient levels where richness came into play

Table 4.4: **Variance explained by random effects relative to total variance in mixed-effects models.** Intraclass correlation coefficient (ICC) values suggest minimal variance explained by model repetitions as random effects in the models. Bio: Biomass, PP: primary productivity, CE_{Bio}, SE_{Bio}: complementarity and selection effects based on biomass, resp. CE_{PP}, SE_{PP}: complementarity and selection effects based on primary productivity, resp.

Model	**Response**	**ICC**
NP	Bio	0.02
NPZ	Bio_{phy}	0.01
NPZ	Bio_{zoo}	0.01
NP	PP	0.02
NPZ	PP	0.01
NP	CE_{Bio}	0.02
NPZ	$\mathrm{CE}_{Bio_{phy}}$	0.01
NPZ	$\mathrm{CE}_{Bio_{zoo}}$	0.01
NP	SE_{Bio}	0.05
NPZ	$\mathrm{SE}_{Bio_{phy}}$	0.01
NPZ	$\mathrm{SE}_{Bio_{zoo}}$	0.01
NP	CE_{PP}	0.03
NPZ	CE_{PP}	0.01
NP	SE_{PP}	0.05
NPZ	SE_{PP}	0.01

to influence diversity effects together. SE decreased with increasing nutrient alone, with no effect mediated by richness (Table 4.6).

Model variance explained by replicates was also negligible for NPZ models, suggesting model results are consistent (Table 4.4).

4.4 Discussion

In this study, biodiversity effects on productivity were largely driven by complementarity in the absence of zooplankton. Selection exerted a larger influence when zooplankton was present, partially supporting *H2* and *H3*. Strongest effects were observed at higher nutrient levels, with zooplankton presence reducing the role of richness in driving productivity, particularly when using biomass as proxy. These findings highlight the importance of nutrient conditions in mediating biodiversity

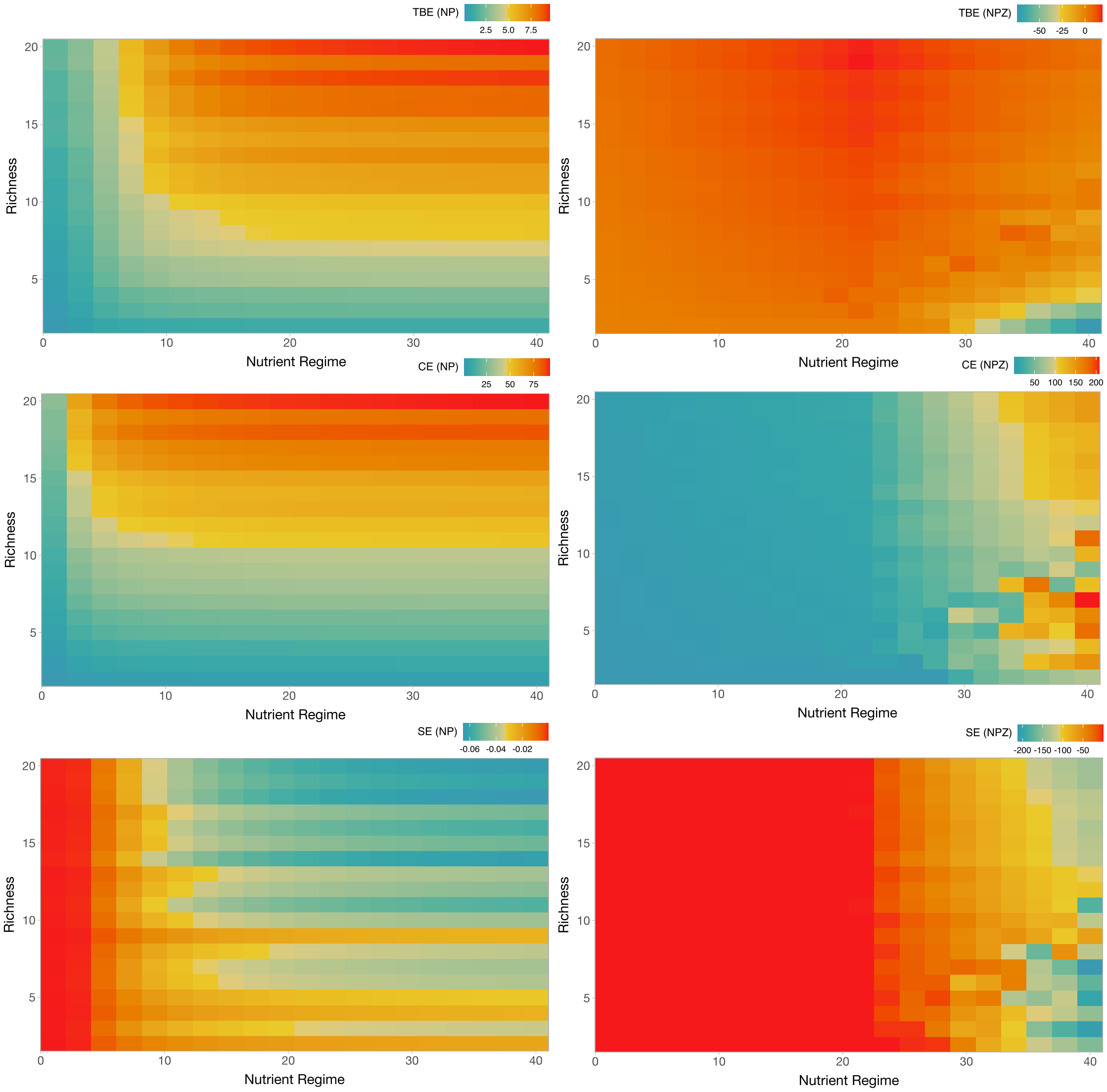

Figure 4.5: **Biodiversity effects on total phytoplankton biomass in a NP and NPZ model.** Total biodiversity effects (TBE), complementarity effects (CE) and selection effects (SE) in a NP (left panel) and NPZ (right panel) model, respectively.

effects on ecosystem function, with richness playing a secondary role that is more significant only under favourable nutrient conditions, supporting *H1* and rejecting *H0*.

This study highlights the dominant role of nutrient availability in driving productivity and biodiversity effects, with richness influencing productivity primarily at intermediate to high nutrient levels and in the absence of zooplankton. While

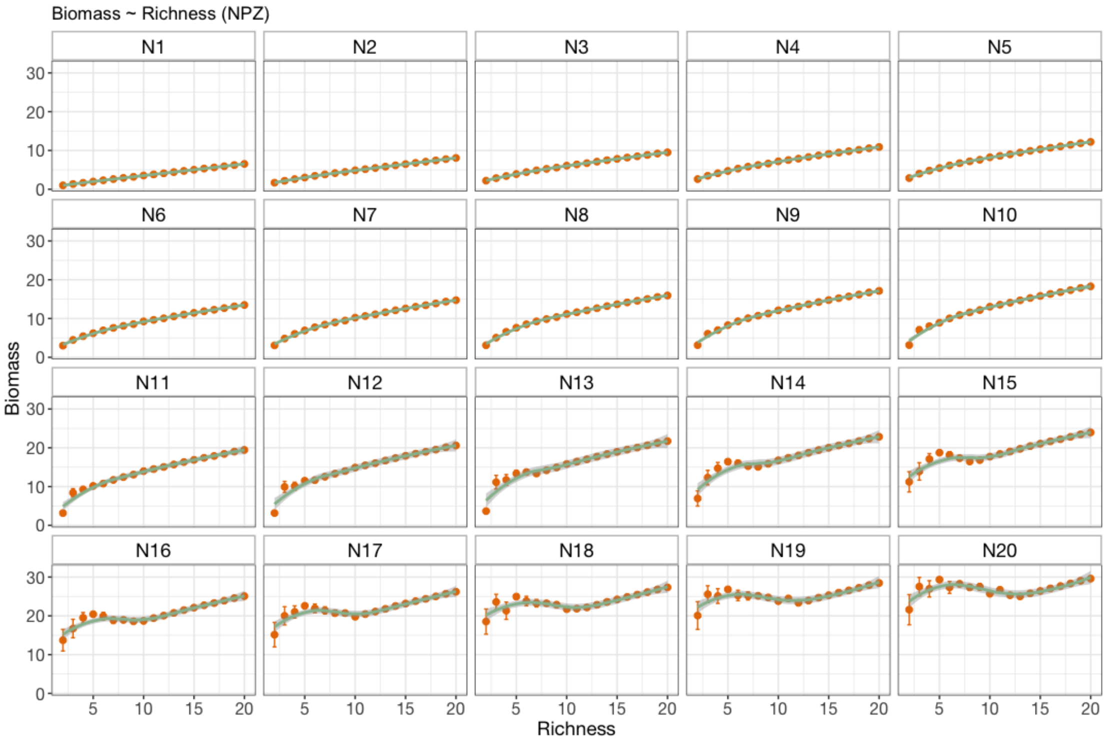

Figure 4.6: **Phytoplankton biomass across richness and nutrient levels in a NPZ model.** Average phytoplankton biomass and associated standard error across richness (R = 20) and nutrient (N1: $N_{min} = 1$, N20: $N_{max} = 40$) levels.

Table 4.5: **Summary of three-way analyses of variance (ANOVA) on a linear mixed-effects model assessing the biodiversity effects on phytoplankton mixtures in a NPZ-model.** Nutrient regime and richness as independent factors directly affecting total phytoplankton biomass and their interaction. Df: degrees of freedom; SS: sum of squares; MS: mean squares; F-value: F statistic; η_p^2: partial eta-squared as a measure of effect size. Numbers in bold represent statistical significance, p-value <0.05 for F-value and 95% confidence interval does not include zero for η_p^2.

		Total Biomass, μM N				Complementarity, $N \times \overline{\Delta RY} \times \bar{M}$				Selection, $N \times Cov(\Delta RY, M)$			
Effect	**Df**	**SS**	**MS**	**F-value**	η_p^2	**SS**	**MS**	**F-value**	η_p^2	**SS**	**MS**	**F-value**	η_p^2
Nutrient Regime	19	171847	9045	2194.8***	**0.92**	6268091	329900	111.3***	**0.38**	8066608	424558	131.8***	**0.42**
Richness	18	29729	1652	400.7***	**0.68**	203073	11282	3.8***	**0.02**	61789	3433	1.06	<0.01
Nutrient:Richness	342	5996	18	4.25***	**0.30**	658613	1926	0.64	0.06	649863	1900	0.58	0.06
		Total Primary Production, μM N d^{-1}				Complementarity, $N \times \overline{\Delta RY} \times \bar{M}$				Selection, $N \times Cov(\Delta RY, M)$			
Effect	**Df**	**SS**	**MS**	**F-value**	η_p^2	**SS**	**MS**	**F-value**	η_p^2	**SS**	**MS**	**F-value**	η_p^2
Nutrient Regime	19	43919369	2311546	**1434.7**	**0.89**	24982521	1314870	**100.7**	**0.36**	32932500	1733289	**114.7**	**0.39**
Richness	18	10948548	608253	**377.5**	**0.67**	615514	34195	**2.6**	0.01	340240	18902	1.2	0.01
Nutrient:Richness	342	13129540	38390	**23.8**	**0.70**	2769016	8097	0.6	0.06	3139092	9179	0.6	0.06

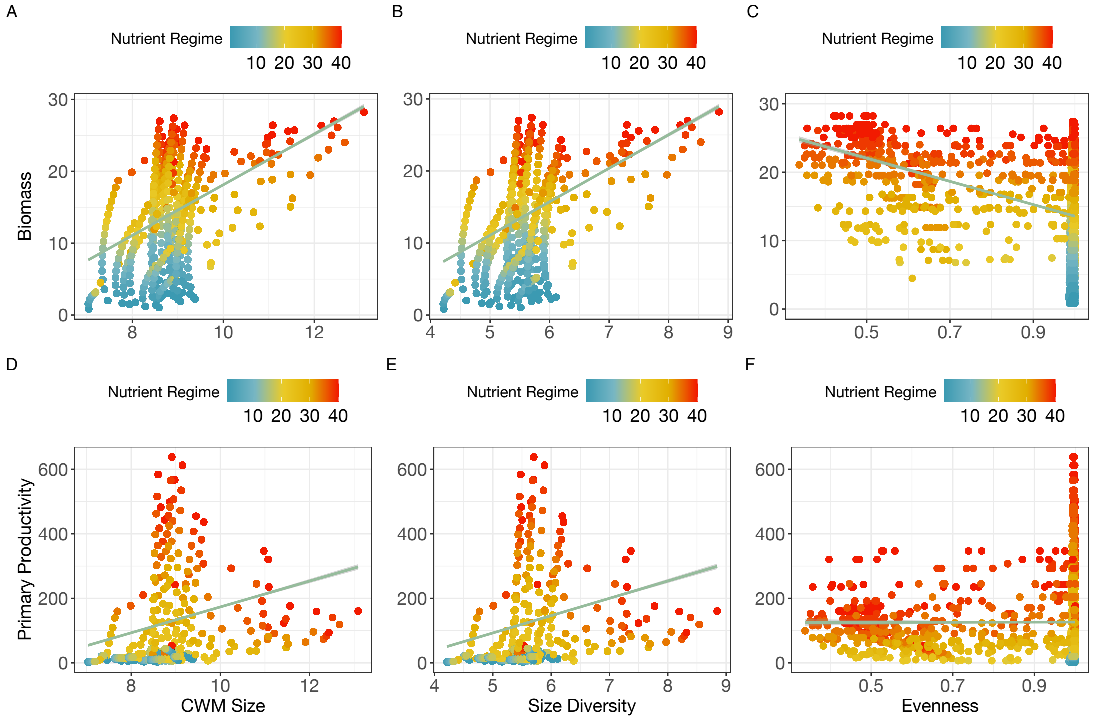

Figure 4.7: **Phytoplankton biomass and primary productivity changes over different diversity metrics in a NPZ model after simulation run.** Changes in productivity levels related to changes in CWM$_{size}$ (A, D), size diversity (B, E) and evenness (C, F) across several nutrient regimes.

Table 4.6: **Summary of three-way analyses of variance (ANOVA) on a linear mixed-effects model assessing the biodiversity effects on zooplankton mixtures in a NPZ-model.** Nutrient regime and richness as independent factors directly affecting total phytoplankton biomass and their interaction. Df: degrees of freedom; SS: sum of squares; MS: mean squares; F-value: F statistic; η^2_p: partial eta-squared as a measure of effect size. Numbers in bold represent statistical significance, p-value <0.05 for F-value and 95% confidence interval does not include zero for η^2_p.

		Total Biomass, μM N				Complementarity, $N \times \overline{\Delta RY} \times \bar{M}$				Selection, $N \times Cov(\Delta RY, M)$			
Effect	**Df**	**SS**	**MS**	**F-value**	η^2_p	**SS**	**MS**	**F-value**	η^2_p	**SS**	**MS**	**F-value**	η^2_p
Nutrient Regime	19	82125	4322.4	**14591.3**	**0.99**	95169	5008.9	**220.9**	**0.55**	22816.0	1200.8	**350.1**	**0.66**
Richness	18	2915	162.0	**546.7**	**0.74**	5089	282.7	**12.5**	**0.06**	147.3	8.2	**2.4**	0.01
Nutrient:Richness	342	5697	16.7	**56.2**	**0.85**	11073	32.4	**1.4**	**0.13**	638	1.9	0.5	0.05

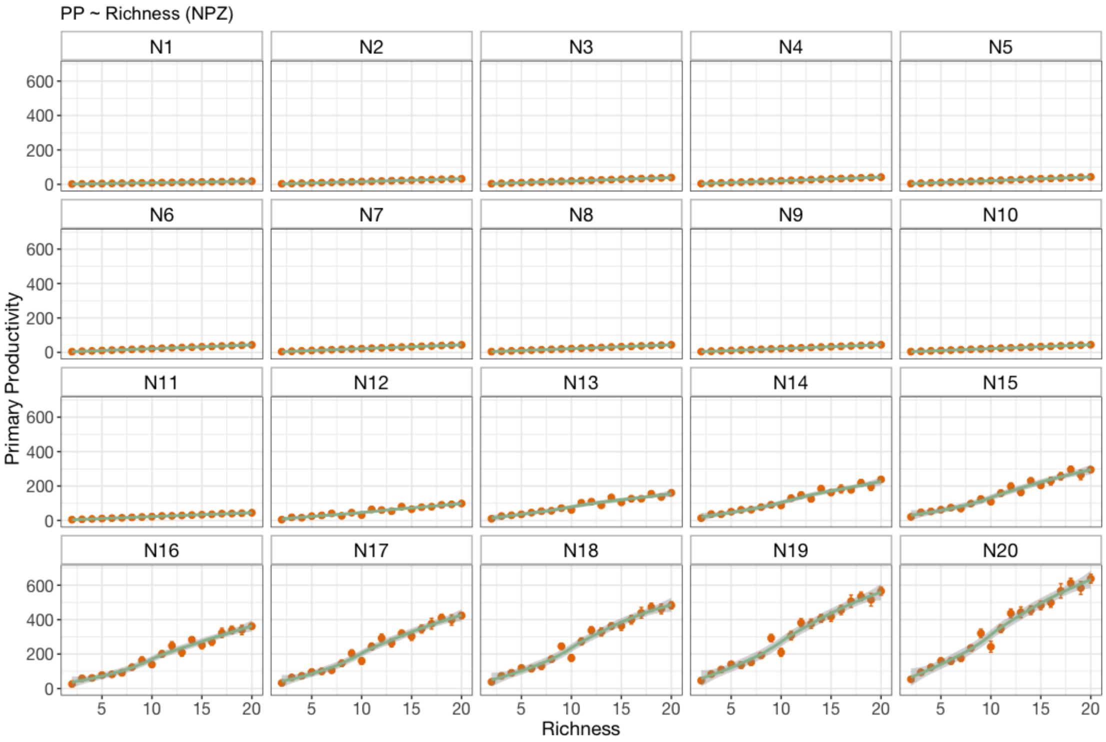

Figure 4.8: **Phytoplankton primary productivity across richness and nutrient levels in a NPZ model.** Average phytoplankton primary productivity and associated standard error across richness (R = 20) and nutrient (N1: $N_{min} = 1$, N20: $N_{max} = 40$) levels.

richness can enhance productivity through resource partitioning, its effects are often overshadowed by environmental factors and community structure, particularly in natural systems. Size-based metrics were stronger predictors of productivity than richness alone. The presence of zooplankton introduced top-down controls, altering dominance patterns and leading to higher overall productivity but a unimodal relationship between zooplankton richness and biomass. Total biodiversity effects were generally positive but varied, with negative selection effects observed in high-nutrient, low-richness communities likely due to weaker competitors dominating. The results suggest that trophic interactions mediate biodiversity-ecosystem function relationships by joint environmental and diversity effects, emphasising the need to consider predator-prey dynamics in understanding productivity patterns in marine ecosystems.

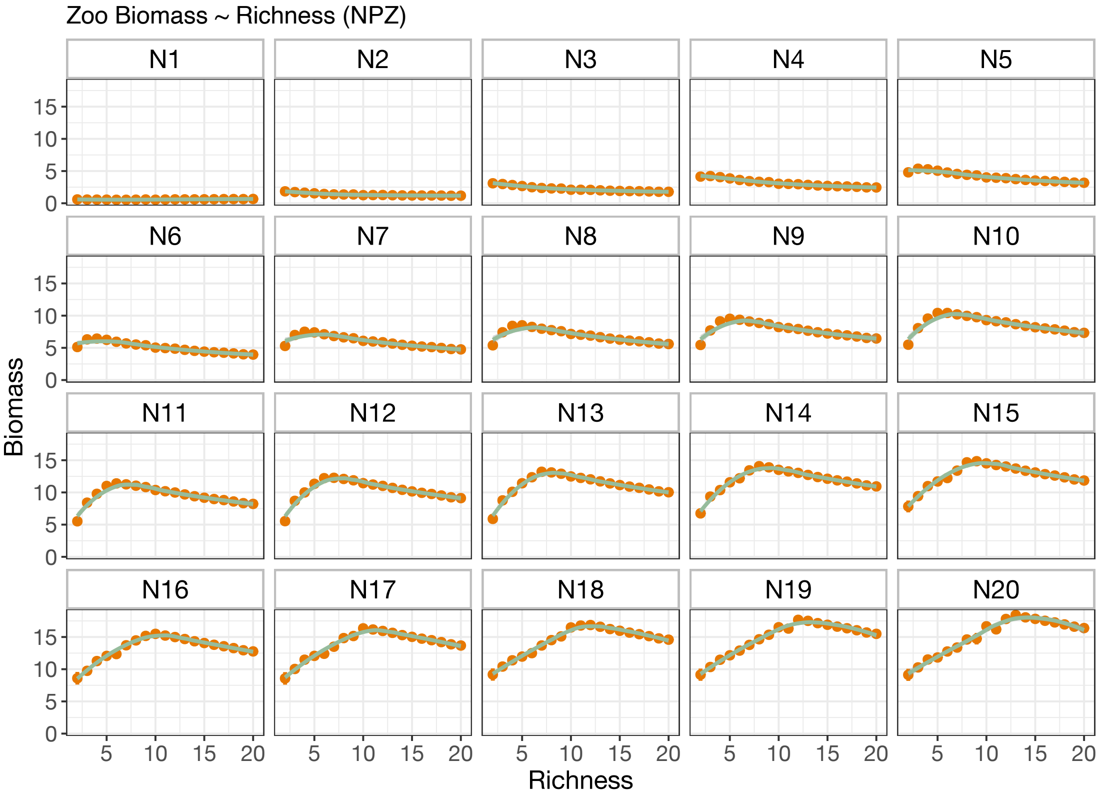

Figure 4.9: **Zooplankton biomass across richness and nutrient levels in a NPZ model.** Average zooplankton biomass and associated standard error across richness (R = 20) and nutrient (N1: $N_{min} = 1$, N20: $N_{max} = 40$) levels.

4.4.1 Environment drives productivity (most of the time)

Nutrient levels were consistently the most important driver of productivity, and consequently, biodiversity effects in the models. Richness is often regarded as the main driver of productivity as per biodiversity and ecosystem (BEF) theory (Loreau and Hector, 2001; Tilman et al., 2014). Yet, the role of resource availability in supporting productivity has been observed in both natural and experimental conditions (Lehtinen et al., 2017). It is notoriously difficult to account for the environment in non-experimental conditions (Fridley, 2002). Here, particularly at low nutrient levels, environmental limitations outweighed richness effects. Richness effects *per se* were the main driver of productivity only in the absence of zooplankton. This suggests that the reported variable effect of richness could be a consequence of a narrow focus on

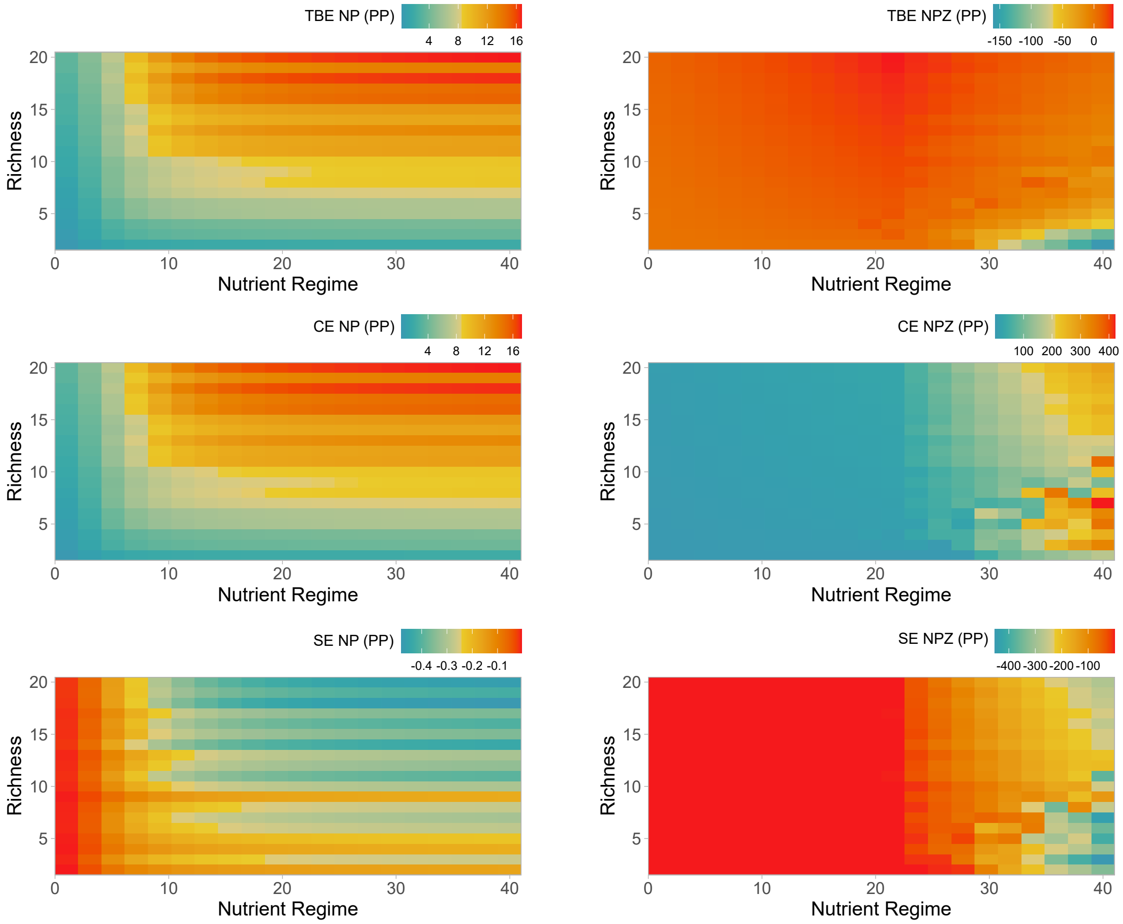

Figure 4.10: **Biodiversity effects on total phytoplankton primary production in a NP and NPZ model.** Total biodiversity effects (TBE), complementarity effects (CE) and selection effects (SE) in a NP (left panel) and NPZ (right panel) model, respectively.

richness itself, rather than taking the environment into account when analysing BEF relationships (Hillebrand and Matthiessen, 2009). Particularly resource availability (Fridley, 2002) and other diversity metrics (i.e. evenness, Hillebrand et al., 2008).

The interaction between diversity and environmental factors shaped productivity patterns in complex ways, with richness' role in driving productivity being strongest when nutrient levels were intermediate or high. In the absence of zooplankton, richness had greater effect on productivity. While increasing richness is expected to create opportunities for efficient resource use based on species-specific requirements, nutrient input seems to cap this potential (Cardinale et al., 2009; Hillebrand and

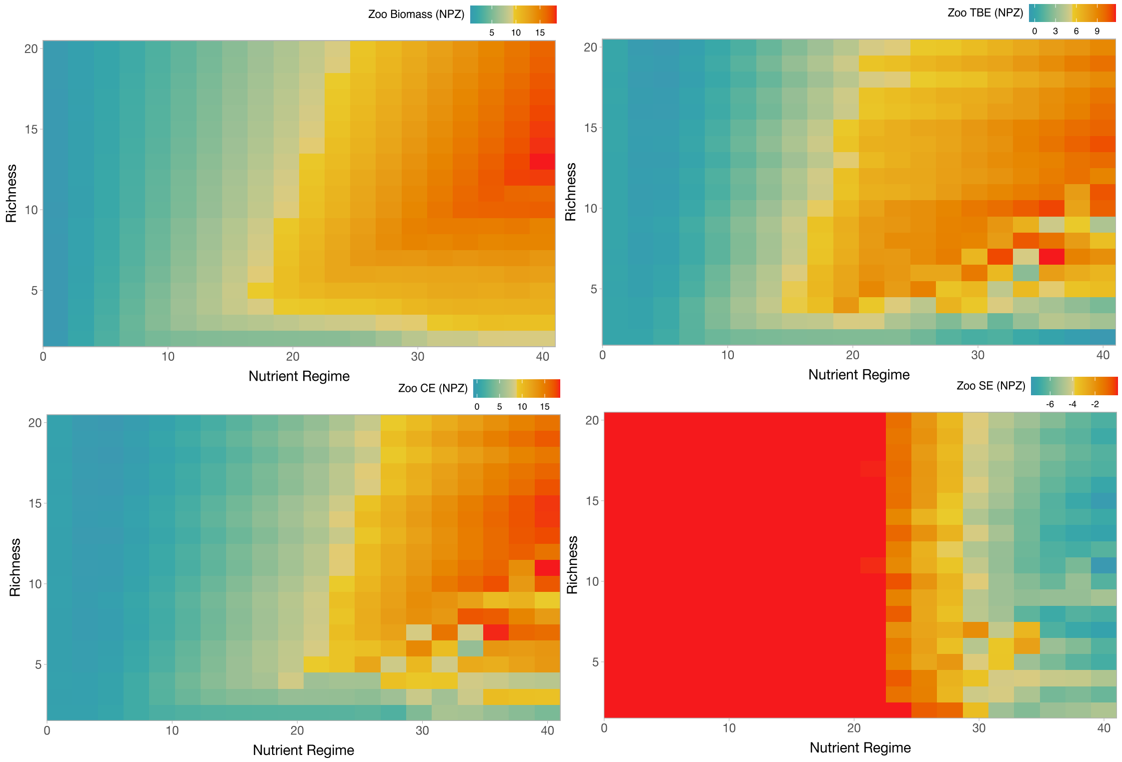

Figure 4.11: **Zooplankton biomass and diversity effects in a NPZ model.** Total zooplankton biomass, total biodiversity effects (TBE), complementarity effects (CE) and selection effects (SE) on zooplankton biomass.

Matthiessen, 2009). While richness differences had minimal impact at low nutrient levels, productivity levels reached their highest values at maximum richness when nutrient availability was greater. Fridley (2002) reported a similar effect, with resource availability consistently driving productivity in experimental plant mixtures, and richness' effects increasing with increased resource (i.e. soil fertility). When conditions are favourable, diverse communities are expected to be able to partition resources better leading to an increase of overall productivity via complementarity (Tilman, 2001). Resource partitioning then allows diverse communities to exploit a broader range of ecological niches, increasing community-level productivity. However, these diversity effects may be masked in natural habitats, due to confounding factors such as the environment, species identity and even predation, which in turn, would explain variability reported in BEF relationships (Loreau and Hector, 2001;

Worm et al., 2002).

When going beyond richness, metrics that related to community size structure were among the best predictors of overall function, similar to what was observed in Chapter 3. For phytoplankton, CWM$_{size}$ was the best predictor of biomass and PP in NP models, and richness was the best one in NPZ models, when nutrient input was not accounted for. This highlights the importance of a trait-based approach, particularly reflecting size structure, with dominance of large-sized cells leading to higher biomass accumulation and likely reducing richness effects (Acevedo-Trejos et al., 2018; Cadotte, 2017; Emery et al., 2021). Richness effects in NPZ models were stronger, possibly due to increased complexity in the presence of predators. The unimodal pattern of zooplankton biomass and richness could be a reflection of less available prey at high nutrient levels. This means that at high nutrient levels prey biomass may decouple from predators' biomass, leading to prey limitation and constraining zooplankton productivity. Contrarily for zooplankton, richness had a negative effect on productivity and evenness a positive effect, but CWM$_{size}$ remained the best predictor.

4.4.2 Predator's presence changes productivity patterns

Top-down control by zooplankton introduces an additional layer of complexity to phytoplankton community dynamics, altering dominance patterns and thereby modulating productivity. Generally in the models, community productivity was higher in the presence of zooplankton, increasing linearly with nutrient, but zooplankton biomass was an unimodal function of richness. This aligns well with findings reported by Thébault and Loreau (2003): a model where all species coexist and have a species-specific predator, prey biomass increases linearly with diversity. Whereas predator's biomass may exhibit an unimodal relationship with diversity. However, in the models, increasing predator diversity did not lead to a decrease of phytoplankton biomass, as previously suggested (Duffy, 2003). Here, predator mortality was modified in order to allow prey coexistence, which could have been responsible for stabilizing phytoplankton biomass variations, as seen by relatively high evenness values.

This study revealed that total biodiversity effects (TBE) were predominantly positive, aligning with theoretical predictions (Hooper et al., 2005; Loreau and Hector, 2001; Tilman, 2001). However, variability in TBE emerged, particularly in the presence of zooplankton, where low-richness, high-nutrient communities exhibited negative TBE due to strong negative selection effects (SE). Cermeño et al. (2016) argues that positive selection effects drives marine productivity due to the dynamic environmental structure in the oceans, constantly changing the resource landscape and consequently, community structure by favoring species best adapted to current conditions. In NPZ models, SE played a stronger role in shaping community net biodiversity effect, and consequently, productivity. However, negative SE suggest the community was dominated by weak competitors, i.e. diverse communities have lower biomass than in monocultures of their component species. I argue that selection here is driven by top-down controls, rather than direct selection of strong phytoplankton competitors, as evenness was consistently high at high nutrient levels and the models do not have extinction.

Extinctions are never random in nature, as the environment actively selects optimal traits for current conditions (Hillebrand et al., 2008). At low nutrient scenarios, the phytoplankton community is dominated by specialists and likely experiences enhanced predation, resulting in a small community-level productivity. With increasing richness, new species are added and phytoplankton is able to accumulate more biomass (i.e. larger species) and to decouple from predation pressure. But nutrient still caps overall productivity (Cardinale et al., 2011; Fox, 2004). This can lead to changes in dominance in the community that reflect this transient selection, as opposed to richness alone (Hillebrand et al., 2008). In models where all species coexisted, weak competitors were never removed from the community, leading to overall small contributions to community-level productivity, driven primarily by nutrient. This was particularly enhanced in the presence of zooplankton, as weak competitors were safe from predation at high nutrient-low richness levels. These results illustrate how trophic interactions complicate BEF relationships by intertwining environmental and diversity effects in driving productivity (Duffy et al., 2017; Thébault and Loreau, 2003). Further, top-down control in aquatic environments are stronger than in terrestrial ecosystems, due to edibility of phytoplankton (Leibold, 1989; Tessier and Woodruff, 2002) and rates of predation (Shurin et al., 2002; D. R. Strong, 1992) and biomass accumulation (Cebrian, 1999). These findings contribute to the understanding of variability observed in natural systems, where predator-prey dynamics are often unaccounted for in BEF studies, and may give us a better direction when investigating what drives productivity.

4.5 Conclusions

In the current study, nutrient input was consistently the main driver of productivity levels in phytoplankton and zooplankton communities in both models. Nutrient availability has been recognized to be a significant driver of community productivity, both directly by stimulating biomass accumulation and indirectly, by modifying competitive interactions, species dominance, and richness effects (Cardinale et al., 2011; Hodapp et al., 2015; Lehtinen et al., 2017; Tilman et al., 1997a; van der Plas, 2019).

Biodiversity effects were context-dependent, with species richness playing a secondary role. Richness effects were mostly important in the absence of predators and at intermediate to high nutrient levels, which suggests that indeed diverse communities lead to higher productivity through niche partitioning and resource use efficiency (Hooper et al., 2005; Loreau, 2010). These findings support the broader biodiversity-ecosystem function (BEF) framework, particularly in planktonic systems, where trait-based differences among species determine their ability to exploit available resources effectively (Cadotte, 2017; Litchman et al., 2010). Further, the interaction between richness and nutrient levels suggests that important community properties, i.e. size structure, are being filtered by the environment via indirect effects.

Community size structure emerged as the key driver of phytoplankton productivity, indicating that functional diversity rather than species richness *per se* is key to understanding productivity in marine systems. Cell size is a ‘master-trait’: size-based interactions play a fundamental role in shaping community dynamics, as larger species often dominate under high-nutrient conditions, while smaller species can thrive in resource-limited environments (Acevedo-Trejos et al., 2015; Acevedo-Trejos et al., 2018; Cloern, 2018). These findings highlight the need to move beyond species counts and consider trait-based approaches when assessing BEF relationships in planktonic ecosystems (Cadotte et al., 2009; Emery et al., 2021; Gamfeldt and Hillebrand, 2008; Le Bagousse-Pinguet et al., 2019).

The presence of zooplankton altered biodiversity and productivity relationships. Specifically, zooplankton reduced the role of richness and shifted the dominant mechanism from complementarity to selection. In the absence of zooplankton, productivity was primarily driven by complementarity effects, with richness increasing biomass and primary productivity, particularly at high nutrient levels (Isbell et al., 2018). Contrarily, when predators were present, selection effects were strong and negative, and richness played a minor role. This shift suggests that top-down control can override biodiversity effects on productivity, as zooplankton preferentially consume certain size classes, reducing competitive interactions among phytoplankton species and altering community composition (Shurin et al., 2002).

These results contribute to a growing body of evidence that the strength and direction of BEF relationships in aquatic ecosystems are modulated by environmental conditions and trophic interactions (Gamfeldt et al., 2015; Lehtinen et al., 2017), not by a single diversity metric.

4.6 Limitations and future steps

Although I examine the role of nutrient levels, other key environmental drivers (e.g., temperature changes, light limitation, or physical forcing) are not explicitly varied in the models. These factors have been reported to influence productivity levels, particularly in dynamic high nutrient systems (Chen, 2022; Cloern, 1999; Hillebrand and Matthiessen, 2009). Additionally, this study used a controlled modelling framework, which does not fully capture the full complexity of real-world plankton communities, such as seasonal succession (Sommer et al., 2012), species dispersal (Leibold et al., 2004), or disturbance regimes (Hillebrand et al., 2020).

While I analysed BEF relationships in more than one trophic level, parametrisation of predation was rather simple, with a strict predator-prey relationship based on allometric scaling. This was done to keep model complexity low, as I wanted to see the effects of two main axis alone: nutrient and richness. In natural systems, zooplankton have flexible feeding preferences, including omnivory and selective grazing, which in turn could alter productivity levels (Kiørboe, 2011; Steinberg and Landry, 2017). Mortality was introduced in a way where no extinction was allowed, to keep competitive exclusion from taking place (Record et al., 2014), creating highly idealised conditions.

The interaction between nutrient and richness levels highlights the role of environmental control on community diversity and ultimately, in the variability observed in BEF relationships (Hillebrand and Matthiessen, 2009). Biodiversity effects are often linked to mechanisms such as complementarity and selection, still, the strength and direction of these effects are highly context-dependent, varying with nutrient availability and the presence of higher trophic levels.

In the final chapter of this thesis, I employ a structural equation model (SEM) framework to evaluate the direct and indirect effects of the environment and community diversity in jointly driving productivity levels. SEM provides a robust framework for quantifying direct and indirect pathways linking environmental drivers (e.g., nutrient levels, temperature, light limitation) to community diversity and ultimately phytoplankton productivity. Unlike simpler statistical approaches, SEM allows for simultaneous estimation of multiple causal relationships, incorporating both observational data and theoretical expectations to refine our understanding of ecosystem functioning.

Chapter 5

Phytoplankton diversity and ecosystem function: a structural equation modelling approach

5.1 A brief history of Structural Equation Models

The effects of the environment and diversity on ecosystem productivity are difficult to disentangle. Multivariate approaches, such as structural equation models (SEM), can help us understand direct and indirect effects of community properties on ecosystem function as they offer a good scientific framework to investigate causality in biological systems.

SEMs are a multivariate quantitative modelling approach and their usage has gained increased support in ecological investigations of causal relationships (Grace et al., 2010; Hodapp et al., 2015). One of SEMs strengths lies on their ability to model and estimate direct and indirect effects between variables, going beyond correlations (Bollen, 1989; Eisenhauer et al., 2015). Determining true causality is challenging, particularly in complex biological systems. SEMs provide a strong tool for inferring causality in observational ecological data, unlike other multivariate methods (e.g.

MANOVA, CCA, multiple regression) that are focused on net effects (Grace, 2006). Modern SEMs combine two statistical methods that can be traced back to the analyses of path relations in evolutionary genetics (Wright, 1920) and factor analyses (Galton, 1889), and are attributed to the works of Karl Jöreskog in the 70s, work that incorporated maximum likelihood methods and covariance structure of the data for model estimation (Jöreskog, 1969, 1970).

SEMs are represented via path diagrams, where nodes represent variables and arrows represent the relationship between them. For instance, a single arrow represents a causal relationship between the independent and dependent variables, also known in SEM language as exogenous and endogenous variables, respectively. A key aspect of SEMs is the ability to estimate unmeasured influences and/or causes, also known as latent variables. Latent variables can be defined as those that indicate a cause/effect, share common indicators, but are not available in your data. The concept of happiness is an example of a latent construct, i.e. there is no direct way to measure happiness, but we can indirectly estimate its value from a number of correlated measures. First report of latent variable estimation using factor analyses are attributed to Pearson and Lee (1903). Another key aspect is the use of SEMs to estimate indirect effects between two variables via a mediator. This allows us to partition effects between variables (i.e. environmental effects), helping disentangle complex interactions and mechanisms that influence the outcome of interest (Gunzler et al., 2013).

The causal backbone of modern SEM comes from the works of Pearl (2003). Pearl (2003) provided the causal framework that ensures the hypotheses tested in the model have causal mechanisms and not just correlations. A causal relationship of a structural equation can be supported if it can be assumed that a sufficient manipulation of x would result in a subsequent change in the values of y, independent of influences of any other factors. Through the use of latent variables, graphical models and counterfactual thinking, modern SEMs couple both approaches of robust model estimation and causal interpretation. Despite its many advantages, SEMs are mostly used in social, medical and psychological sciences. Still, the use of SEMs for understanding natural systems is growing steadily, with reports of nearly 260 ecological studies using this approach (Eisenhauer et al., 2015; Fan et al., 2016; Grace et al., 2010).

5.2 Structural Equation Models in aquatic ecology

In aquatic ecology, the SEM framework has been applied in a myriad of research topics. A few examples range from understanding phytoplankton diversity patterns and community structure (Pan et al., 2022; Stomp et al., 2011), to trait variation (Breton et al., 2017; Heinrichs et al., 2024), food-web dynamics (Rogers et al., 2024) and even conservation efforts (Santibáñez-Andrade et al., 2015). Particularly, employing SEMs to understand the role of biodiversity on ecosystem function is quite useful as researchers are able to determine the effect of the environment both as driver of function, as well as mediator (Nhu Y et al., 2019). For instance, Lewandowska et al. (2016) built on the framework of Cardinale et al. (2009) and used a coupled meta-analyses and SEM approach, observing that productivity was largely driven by resource availability, and that the effect of richness varied with habitat type. Studies have also focused on different dimensions of diversity, e.g. evenness and phylogenetic diversity, showing that richness itself is not a sufficient metric to understand how diversity drives productivity (Flynn et al., 2011; Lehtinen et al., 2017; Lewandowska et al., 2016; Virta et al., 2019).

Determining causality, finding generalizations and understanding the complex network of ecological systems is key to forecasting ecosystem health in a changing world. As Grace et al. (2014) explored in his rebuttal to Pierce (2014), multivariate approaches are the only framework capable of yielding results based on quantitative analyses of causal relationships, not merely associative ones based on two variables alone. Going beyond the simplistic nature of bivariate analyses, we can look into the underlying mechanisms leading to relationships observed, take the whole system into consideration and shine light on new avenues of hypotheses, leading to scientific progress (Grace et al., 2014). This forward look into plankton ecology fits well with the biodiversity and ecosystem function field that built on the classic productivity-diversity relationship view (PDR), ultimately leading to a mechanistic understanding of what drives ecosystem function in aquatic ecosystems.

This chapter employs a SEM framework to investigate how diversity and the environment influence biomass production in phytoplankton and zooplankton communities. By incorporating size structure—derived from mean size, evenness, and size diversity, the model used here aims to clarify the contributions of species richness, size-based traits, dominance and nutrient dynamics to ecosystem productivity. This approach provides new insights into the functional roles of biodiversity and how shifts in community composition may impact ecosystem productivity. I will test the following hypotheses:

- *H1*: Evenness directly affects productivity reflecting phytoplankton dominance patterns.
- *H2*: Community size structure affects productivity not richness.
- *H3*: Environmental filtering drives productivity, rather than diversity.

5.3 Methods

5.3.1 Phytoplankton, environmental and ecosystem function data

I used two sets of data in this study: i) the San Francisco Bay (SFB) dataset and ii) Nutrient-Phytoplankton-Zooplankton (NPZ) simulation results from Chapter 4. The SFB dataset, spanning from 2014 to 2020, offers high-resolution, long-term observations of naturally assembled phytoplankton communities. It includes species composition, biovolume, and cell size measurements, alongside key abiotic parameters such as temperature, salinity, and nutrients. Diversity parameters that relate to community size structure, trait and dominance patterns (e.g. size diversity, mean size, evenness) were calculated based on available information on the dataset. For details on data collection and source, transformation and diversity metrics calculations, refer to Chapter 2. For (ii), only two axis of variation were included in the model: nutrient input and richness levels. Using simulation results as input for a structural equation model, I was able to test causal hypotheses about phytoplankton dynamics under controlled conditions, complementing the observational SFB dataset by isolating specific drivers of productivity. The NPZ model simulated diverse communities by varying size classes of phytoplankton and zooplankton, representing key functional traits influencing ecosystem dynamics. For more details on NPZ model specification, refer to Chapter 4. Since the relationships embedded in the simulation framework are known, I can then test whether SEM correctly recovers the hypothesised causal links. This allows us to evaluate the model ability to infer the underlying processes from observational data.

5.3.2 Structural Equation Model: setup and analyses

Models with different productivity proxies (e.g. biomass, primary productivity (PP), resource use efficiency (RUE)) were evaluated separately. Assumptions lie on the multivariate nature of productivity being jointly driven by diversity and environmental factors. I was particularly interested in what aspects of diversity (e.g. species richness, evenness, size diversity), environmental factors (e.g. nutrient, abiotic factors, seasonality) and trait (i.e. mean size) drive ecosystem function. I used the package lavaan v0.6-17 (RStudio v4.2.1) to assess the causal relationships driving phytoplankton biomass accumulation, RUE and PP. Prior to model fitting, I used the relationships between diversity and ecosystem function observed in Chapters 3 and 4 to inform causal assumptions.

A SEM is composed of two parts, a measurement model that relates to the latent constructs; and the structural model, that via path analyses evaluates all hypothetical relationships among variables. Observed variables are represented by rectangles, with arrows between them relating to the direction of effect between them (Fig. 5.1).

In SEM, we evaluate a set of structural equations to model multivariate relationships (Grace, 2006). In Fig. 5.1, we have the following set of equations:

$$y_1 = \alpha_1 + \gamma_{11} x_1 + \zeta_1 \tag{5.1}$$

$$y_2 = \alpha_2 + \beta_{21} y_1 + \gamma_{21} x_1 + \zeta_2 \tag{5.2}$$

$$y_2 = \alpha_3 + \beta_{32} y_2 + \gamma_{31} x_1 + \zeta_3 \tag{5.3}$$

Where y_{1-3} are endogenous (dependent) and x_1 are exogenous (independent) variables, β represents the effect of endogenous variables on other endogenous variables, γ represents the effect of exogenous variables on endogenous ones. α and ζ are the slope and error terms (Eqs. 5.1, 5.2, 5.3). Error terms are assumed to be independent and normally distributed. However, where necessary, I specified residual error covariances to account for shared unmeasured influences between variables.

5.3.3 Model specification, evaluation and selection

The SEM construction process is heavily dependent on *a priori* knowledge of the relationships under investigation, as such, both results from previous chapters and theoretical expectations between variables were used to inform the hypotheses and evaluate the models (Grace et al., 2014). Each model consisted of a productivity proxy as the main response variable, with several direct and indirect causal predictors, where each predictor also had its own series of direct and indirect predictors. This is known as the structural model. Indirect effects were estimated as the product of two direct pathways (Fig. 5.1).

For each productivity proxy used (e.g. biomass, Chl *a* and RUE), I ran and analysed models that hypothesized causal pathways between exogenous (predictors) and endogenous (response) variables (Table 5.1). Models of good-fit where those in which the predicted covariance structure of the selected model did not significantly differ from the observed covariance structure of the data. I used a base model for each

Table 5.1: **Rationale behind hypothesised causal relationships in models.** Here, I summarise the theoretical reasoning behind the assumed paths between productivity (Biomass, RUE, Chl *a*), size structure (CWM$_{size}$, σ^2), diversity (richness, evenness) and the environment (temporal scale, DIN, phosphate, silicate, PAR, salinity, temperature).

Causal Pathway	**Rationale**	**References**
Diversity → Productivity	As per Biodiversity-Ecosystem Function (BEF), richness is expected to lead to a positive effect on productivity. Evenness has been reported to have a negative effect on productivity, reflecting dominance patterns in community structure.	Hodapp et al. (2015), Lewandowska et al. (2016), Loreau (2010), Maureaud et al. (2020), and Tilman et al. (2014)
Size Structure → Productivity	CWM$_{size}$ and σ^2 represent the effect of trait diversity in driving productivity. Size diversity has been reported to have a negative effect on productivity, but the relationship is non-linear and might reflect environmental control.	Acevedo-Trejos et al. (2018), Chen et al. (2019), and Hillebrand and Matthiessen (2009)
Environment → Productivity	Nutrient, light, temperature, temporal changes and salinity have been reported to control growth, distribution, trait selection, yet their effect has not been partitioned.	Maureaud et al. (2020) and van der Plas (2019)
Environment → Size Structure and Diversity	Environmental control is filtering the community by favouring cells based on size and leading to changes in dominance and composition.	Finkel et al. (2010) and Litchman et al. (2007)

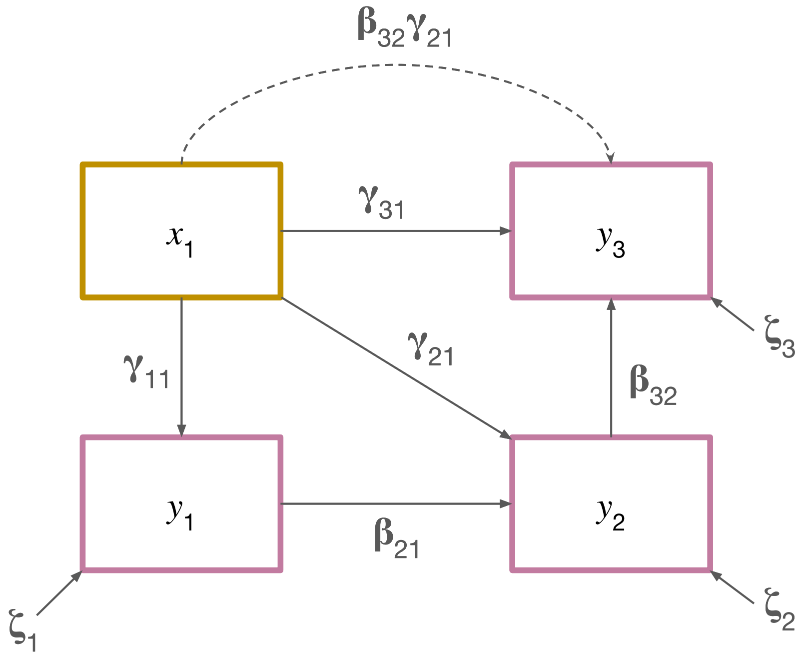

Figure 5.1: **Graphical representation of a structural equation model.** This model contains one exogenous (yellow box, x_1) and three endogenous (pink boxes, y_{1-3}) variables. Boxes are observed variables. Straight-line arrows between variables indicate causal relationships. Dashed arrow indicates indirect effect of x_1 on y_3 via the mediator, y_2. γ represents effects of x on y variables and β represents effects of endogenous variables on other endogenous variables (y's on y's). ζ are error terms for endogenous variables. Modified after Grace (2006).

proxy with the same hypothesized pathways between variables and updated assumptions according to model fit (Fig. 5.2).

As suggested by Grace (2020), I followed a 'weight of evidence' approach when evaluating and selecting the models. This framework suggests a series of steps to be considered when selecting the final model in a reliable manner. Global model fit was assessed based on χ^2, with significance thresholds set at p-value >0.05. Non-significant pathways were removed one by one, and then links between variables were added to improve fit by means of χ^2 and decreased root mean square error of approximation (RMSEA; <0.05). Akaike Information Criteria (AIC) and RMSEA were also used in model comparison, as suggested by Grace (2020). All correlations between variables were tested beforehand and highly correlated variables were re-

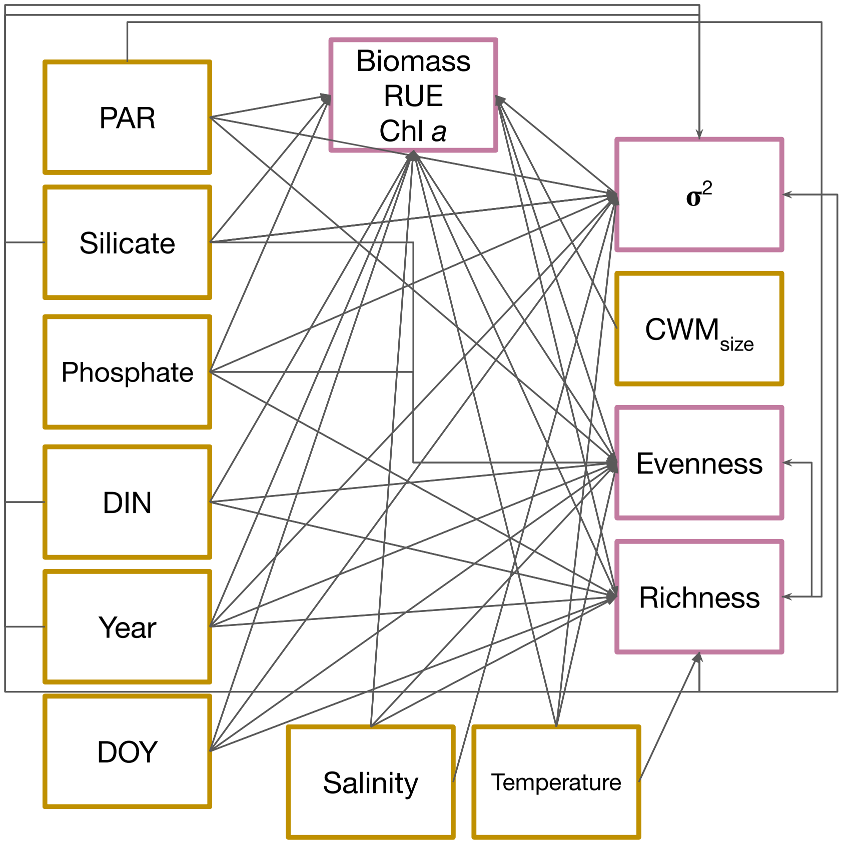

Figure 5.2: **Initial structural equation model.** In this model, hypothesised relationships between endogenous (pink boxes) and exogenous (yellow boxes) variables are represented by one-way arrows. RUE: resource use efficiency; Chl *a*: chlorophyll *a*; DIN: dissolved inorganic nitrogen; DOY: day of year; CWM$_{size}$: community weighted mean size; σ^2: size diversity.

moved from analyses.

5.4 Results

5.4.1 *In situ*: path analyses

For biomass as a proxy, best-fitting model (χ^2 = 4.7, p-value = 0.86; Table 5.2; Figs. 5.3, 5.7) consisted of four endogenous (response) variables: biomass, richness, size diversity (σ^2) and evenness; and ten exogenous (predictors) variables. I found that biomass (R^2 = 0.75) decreased with increasing σ^2 (β = -0.31) and years (γ = -0.22).

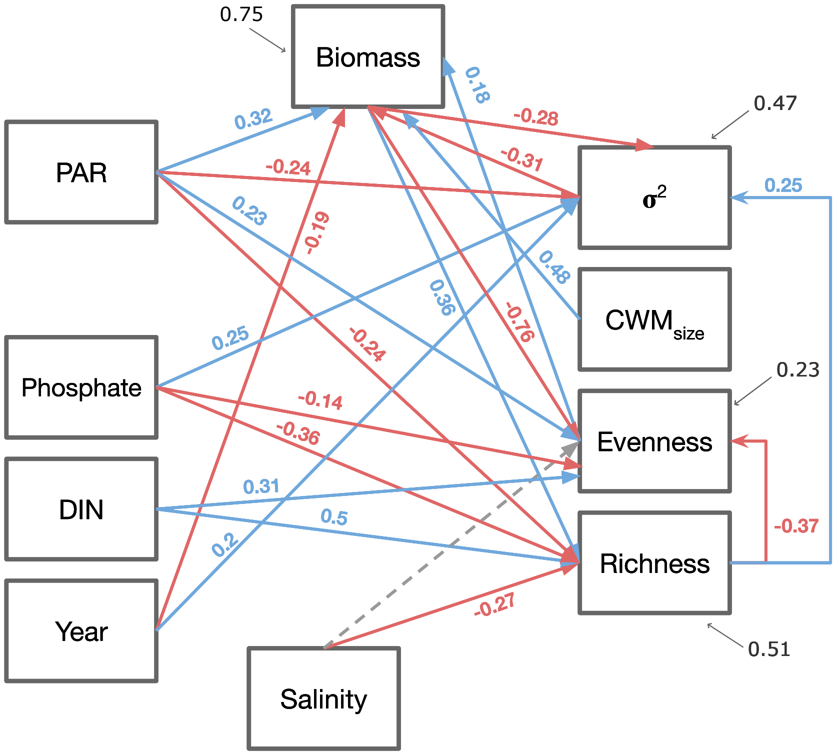

Figure 5.3: **Final revised structural equation model for biomass as productivity proxy.** Blue and red arrows represent positive and negative effects, respectively. Dashed grey arrows represent non-significant pathways. Effect sizes as standardised parameter estimates are shown for each arrow path. R^2 for each endogenous variable (biomass, evenness, richness, σ^2) are given. Only direct pathways are shown. PAR: photosynthetic active radiation; DIN: dissolved inorganic nitrogen; CWM$_{size}$: community weighted mean size; σ^2: size diversity.

Contrarily, biomass increases were directly associated with increasing community weighted mean size (CWM$_{size}$; γ = 0.49), evenness (β = 0.19) and photosynthetic active radiation (PAR; γ = 0.31). Biomass and richness display a complex relationship, with a significant negative covariance observed. Richness had a weak indirect negative effect on biomass via its impact on σ^2 (β = -0.07) and evenness (β = -0.07). Nutrients also had an indirect effect on biomass via evenness, richness and σ^2 (Table 5.3). Other environmental variables, such as year, salinity and PAR, also had indirect effects on biomass accumulation via community size structure (Table 5.3).

Biomass (β = 0.36) alongside dissolved inorganic nitrogen (DIN) (γ = 0.48) had a positive direct effect on richness (R^2 = 0.51), whereas PAR (γ = -0.24), salinity (γ

Table 5.2: **Summary of selected structural equation models.** χ^2, associated p-value and main fit measures of each model. n: number of observations; df: degrees of freedom; RMSEA: root mean square error of approximation; CFI: comparative fit index.

Model	n	χ^2	df	**p-value**	**RMSEA**	**CFI**
Biomass (*in situ* data)	713	4.7	9	0.86	<0.05	>0.9
RUE	713	5.13	6	0.53	<0.05	>0.9
Chl *a*	713	7.75	8	0.46	0.01	>0.9
Biomass (simulated data)	380	2.2	3	0.53	<0.05	>0.9

= -0.27) and phosphate (γ = -0.36) changes led to a decrease in richness (Figs. 5.3, 5.7). Indirectly, richness was affected by the environment as well as community size structure via biomass, with an overall positive net effect. σ^2 (R^2 = 0.47) increases were observed across years (γ = 0.21), with increasing richness (β = 0.25) and phosphate (γ = 0.25), but decreased with PAR (γ = -0.21) and biomass (β = -0.30) levels (Table 5.3, Fig. 5.3). Phosphate (γ = -0.09) and DIN (γ = 0.12) mediated σ^2 via richness (Table 5.3). Size diversity was also indirectly affected by CWM$_{size}$, evenness, nutrients and PAR across the years via biomass and richness changes (Table 5.3). Finally, evenness (R^2 = 0.23) was observed to decrease with increasing biomass (β = -0.74), richness (β = -0.39) and phosphate (γ = -0.15) levels, but evenness increased with PAR (γ = 0.21) and DIN (γ = 0.33) (Fig. 5.3). Evenness was indirectly mediated by several variables, including size diversity, CWM$_{size}$, biomass, nutrients, salinity, PAR and year (Table 5.3).

Resource use efficiency (RUE, R^2 = 0.85) based on carbon biomass increased with increasing DIN (γ = 0.87), CWM$_{size}$ (γ = 0.28) and PAR (γ = 0.16), whereas, RUE decreased with increasing σ^2 (β = -0.20), richness (β = -0.20) and phosphate (γ = -0.13) (Figs. 5.4, 5.7). The final model also consisted of four endogenous variables – RUE, richness, σ^2 and evenness, and ten exogenous variables (χ^2 = 5.13, p-value = 0.53; Table 5.2). CWM$_{size}$ (γ = 0.02), phosphate (γ = 0.07), salinity (γ = 0.06), PAR (γ = 0.05, 0.07) and year (γ = 0.02, -0.05) indirectly affected RUE via richness and σ^2, respectively (Table 5.4). Environmental variables were the most important in directly

Table 5.3: **Indirect effects from structural equation model with biomass as a productivity proxy.** Indirect paths indicate mediation from $x \rightarrow$ mediator $\rightarrow y$. Effect size is the standardised path coefficient between endogenous variables, estimated as the product of standardised direct path coefficients (γ or β). σ^2: size diversity; CWM$_{size}$: community weighted mean size; PAR: photosynthetic active radiation; DIN: dissolved inorganic nitrogen. All indirect effects reported are significant.

Productivity Proxy	**Indirect path**	**Effect size**
Biomass	Richness → σ^2 → Biomass	-0.08
	Phosphate → σ^2 → Biomass	-0.08
	PAR → σ^2 → Biomass	0.07
	Year → σ^2 → Biomass	-0.06
	DIN → Evenness → Biomass	0.05
	PAR → Evenness → Biomass	0.04
	Phosphate → Evenness → Biomass	-0.02
Total Indirect Effect (∑)		-0.08
	CWM$_{size}$ → Biomass → σ^2	-0.15
	DIN → Richness → σ^2	0.12
	PAR → Biomass → σ^2	-0.09
	Evenness → Biomass → σ^2	0.07
	Year → Biomass → σ^2	0.07
	Phosphate → Richness → σ^2	0.07
Total Indirect Effect (∑)		0.09
	CWM$_{size}$ → Biomass → Evenness	-0.37
	DIN → Richness → Evenness	-0.18
	Phosphate → Richness → Evenness	-0.14
	Biomass → Richness → Evenness	-0.14
	Salinity → Richness → Evenness	0.10
	PAR → Richness → Evenness	0.09
	σ^2 → Biomass → Evenness	-0.06
	Year → Biomass → Evenness	-0.04
Total Indirect Effect (∑)		-0.74
	CWM$_{size}$ → Biomass → Richness	0.18
	PAR → Biomass → Richness	0.10
	Evenness → Biomass → Richness	0.06
Total Indirect Effect (∑)		0.34

affecting richness levels (R^2 = 0.52), with richness decreasing with phosphate (γ = -0.33), salinity (γ = -0.28), PAR (γ = -0.24) and across the years (γ = -0.11) (Fig. 5.4). Size diversity (R^2 = 0.34) increased with time (γ = 0.27), richness (β = 0.28) and phosphate (γ = 0.27), but decrease with increasing CWM$_{size}$ (γ = -0.13) and PAR (γ = -0.35) levels (Fig. 5.4). Indirectly, size diversity was negatively affected by year (γ = -0.03), PAR (γ = -0.06), phosphate (γ = -0.09) and salinity (γ = -0.07), all via richness (Table 5.4). On the other hand, evenness (R^2 = 0.26) decreased with increasing richness (β = -0.4) and phosphate (γ = -0.26). However, increasing DIN (γ = 1.28), PAR (γ = 0.21) and salinity (γ = 0.11) all led to increases in evenness levels across years (γ = 0.12) (Fig. 5.4). RUE and evenness positively co-varied. Evenness was indirectly affected by CWM$_{size}$ (γ = -0.35), σ^2 (β = 0.25), DIN (γ = -1.1), phosphate (γ = 0.43) and PAR (γ = -0.20, 0.09) through richness and RUE (Table 5.4).

For Chl *a* (R^2 = 0.37) as a productivity proxy, best-fit model (χ^2 = 7.74, p-value = 0.46; Table 5.2) consisted of four endogenous and eight exogenous variables. Salinity and silicate were highly correlated, but removing either from the model resulted in model instability. As such, after inspection of both sets of regression residuals, I kept the one that led to better model fit, i.e. salinity. Increases in Chl *a* were related to increased phosphate (γ = 0.65), CWM$_{size}$ (γ = 0.24) and PAR (γ = 0.26) levels, whereas productivity decreased seasonally (γ = -0.15), with DIN (γ = -0.32) and the residual salinity concentration after accounting for silicate (γ = -0.58) (Figs. 5.5, 5.7). Richness (R^2 = 0.28) decreased with evenness (β = -0.13), salinity (γ = -0.64) and Chl *a* (β = -0.6), but increased with DIN (γ = 0.39) and CWM$_{size}$ (γ = 0.18) (Fig. 5.5). Richness was indirectly affected via 11 pathways through Chl *a* and evenness, with a weak negative indirect net effect (β = -0.06, Table 5.5). In addition, σ^2 (R^2 = 0.38) also increased with phosphate (γ = 0.30) across the years (γ = 0.23), but decreased with Chl *a* (γ = -0.11) and PAR (γ = -0.32) levels (Fig. 5.5). Size diversity was mediated through Chl *a* and richness by several variables, such as nutrients, day of year, CWM$_{size}$, salinity and evenness, with a total indirect net effect of -0.03 (Table 5.5). Lastly, evenness (R^2 = 0.25) levels increased with increasing salinity (γ = 0.23) and DIN (γ = 0.10) across the

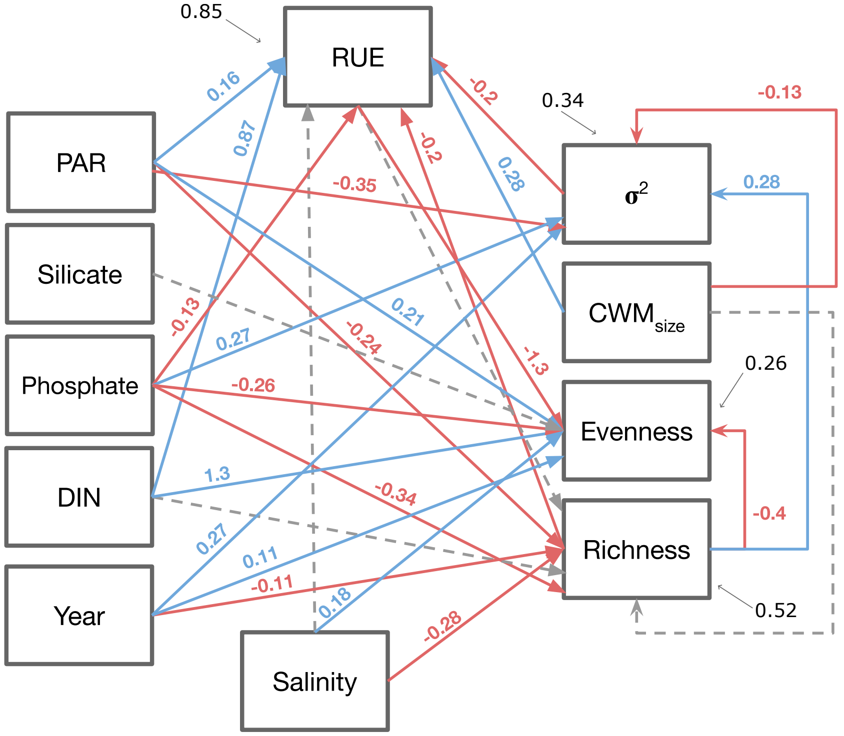

Figure 5.4: **Final revised structural equation model for resource use efficiency (RUE) as productivity proxy.** Blue and red arrows represent positive and negative effects, respectively. Dashed grey arrows represent non-significant pathways. Effect sizes as standardised parameter estimates are shown for each arrow path. R^2 for each endogenous variable (RUE, evenness, richness, σ^2) are given. Only direct pathways are shown. CWM$_{size}$: community weighted mean size; σ^2: size diversity; PAR: photosynthetic active radiation; DIN: dissolved inorganic nitrogen.

years ($\gamma = 0.18$), but decreased with CWM$_{size}$ ($\gamma = -0.39$) (Fig. 5.5). The model did not reveal any indirect effect on evenness.

5.4.2 Simulated data: path analyses

Using the results from the simulations in Chapter 4, the best-fitting model ($\chi^2 = 2.2$, p = 0.53) included four endogenous variables. Phytoplankton biomass increased with higher species richness ($\beta = 0.36$), nutrient availability ($\gamma = 0.06$), zooplankton biomass ($\beta = 0.13$), and size diversity ($\beta = 0.03$) but decreased with greater phytoplankton evenness ($\beta = -0.2$) (Fig. 5.6). Phytoplankton biomass was indirectly affected by richness ($\beta = -0.03$), zooplankton CWM$_{size}$ ($\beta = 0.01$) and σ^2 ($\beta = 0.02$), nu-

Table 5.4: **Indirect effects from structural equation model with RUE as a productivity proxy.** Indirect paths indicate mediation from $x \rightarrow$ mediator $\rightarrow y$. Effect size is the standardised path coefficient between endogenous variables, estimated as the product of standardised direct path coefficients (γ or β). σ^2: size diversity; CWM$_{size}$: community weighted mean size; PAR: photosynthetic active radiation; DIN: dissolved inorganic nitrogen. All indirect effects reported are significant.

Productivity Proxy	**Indirect path**	**Effect size**
RUE	Phosphate → Richness → RUE	0.07
	PAR → σ^2 → RUE	0.07
	Salinity → Richness → RUE	0.06
	PAR → Richness → RUE	0.05
	Year → σ^2 → RUE	-0.05
	CWM$_{size}$ → σ^2 → RUE	0.02
	Year → Richness → RUE	0.02
Total Indirect Effect (∑)		0.24
	DIN → RUE → Evenness	-1.10
	Phosphate → Richness → Evenness	0.13
	CWM$_{size}$ → RUE → Evenness	-0.36
	σ^2 → RUE → Evenness	0.25
	PAR → RUE → Evenness	-0.20
	Phosphate → RUE → Evenness	0.16
	PAR → Richness → Evenness	0.09
Total Indirect Effect (∑)		-1.03
	Phosphate → Richness → σ^2	-0.09
	Salinity → Richness → σ^2	-0.08
	PAR → Richness → σ^2	-0.07
	Year → Richness → σ^2	-0.07
Total Indirect Effect (∑)		-0.31

trient availability (β = 0.01) and phytoplankton evenness (β = 0.04) via zooplankton biomass (Table). In contrast, zooplankton biomass increased with phytoplankton evenness (β = 0.30), nutrient availability (γ = 0.09), zooplankton size diversity (β = 0.14), and CWM$_{size}$ (β = 0.07) but declined with increasing phytoplankton richness (β = -0.26) (Fig. 5.6). The model explained 97% of the variance in phytoplankton biomass and 96% in zooplankton biomass.

Phytoplankton σ^2 increased with zooplankton σ^2 (β = 0.33) and CWM$_{size}$ (β = 0.66) but decreased with higher phytoplankton evenness (β = -0.4) and richness (β

Table 5.5: **Indirect effects from structural equation model with Chl *a* as a productivity proxy.** Indirect paths indicate mediation from $x \rightarrow$ mediator $\rightarrow y$. Effect size is the standardised path coefficient between endogenous variables, estimated as the product of standardised direct path coefficients (γ or β). Chl *a*: chlorophyll *a*; σ^2: size diversity; CWM$_{size}$: community weighted mean size; PAR: photosynthetic active radiation; DIN: dissolved inorganic nitrogen; DOY: day of year. All indirect effects reported are significant.

Productivity Proxy	**Indirect path**	**Effect size**
Chl *a*	Salinity → Richness → σ^2	-0.12
	CWM$_{size}$ → Evenness → σ^2	-0.08
	DIN → Richness → σ^2	0.07
	Phosphate → Chl *a* → σ^2	-0.07
	Salinity → Chl *a* → σ^2	0.06
	Salinity → Evenness → σ^2	0.04
	PAR → Chl *a* → σ^2	-0.03
	CWM$_{size}$ → Chl *a* → σ^2	-0.03
	DIN → Chl *a* → σ^2	0.03
	CWM$_{size}$ → Richness → σ^2	0.03
	Year → Evenness → σ^2	0.03
	DIN → Evenness → σ^2	0.02
	Evenness → Richness → σ^2	-0.02
	DOY → Chl *a* → σ^2	0.02
Total Indirect Effect ($\sum$)		-0.03
	Phosphate → Chl *a* → Richness	-0.38
	Salinity → Chl *a* → Richness	0.34
	DIN → Chl *a* → Richness	0.19
	PAR → Chl *a* → Richness	-0.15
	CWM$_{size}$ → Chl *a* → Richness	-0.15
	DOY → Chl *a* → Richness	0.09
	CWM$_{size}$ → Evenness → Richness	0.05
	Year → Evenness → Richness	-0.02
	Salinity → Evenness → Richness	0.02
	DIN → Evenness → Richness	-0.01
	PAR → Evenness → Richness	0.01
Total Indirect Effect ($\sum$)		-0.06

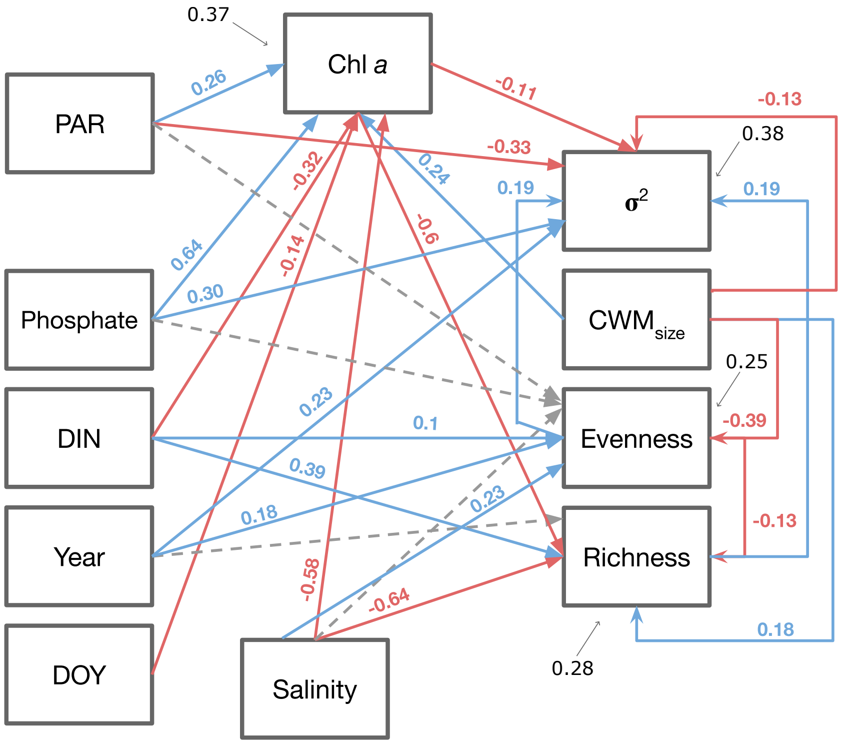

Figure 5.5: **Final revised structural equation model for Chl *a* as productivity proxy.** Blue and red arrows represent positive and negative effects, respectively. Dashed grey arrows represent non-significant pathways. Effect sizes as standardised parameter estimates are shown for each arrow path. R^2 for each endogenous variable (Chl *a*, richness, evenness, σ^2 are given. Only direct pathways are shown. PAR: photosynthetic active radiation; DIN: dissolved inorganic nitrogen; DOY: day of year; CWM$_{size}$: community weighted mean size; σ^2: size diversity.

= -0.05) (Fig. 5.6). Lastly, phytoplankton CWM$_{size}$ increased with phytoplankton and zooplankton size diversity (β = 0.35 and 0.15, resp.), phytoplankton biomass (β = 0.04), and zooplankton CWM$_{size}$ (β = 0.45) but decreased with richness (β = -0.03), phytoplankton evenness (β = -0.23), and zooplankton biomass (β = -0.03). Indirectly, phytoplankton CWM$_{size}$ was affect via 13 pathways mediated by phytoplankton and zooplankton biomass, as well as phytoplankton σ^2 (Table 5.6).

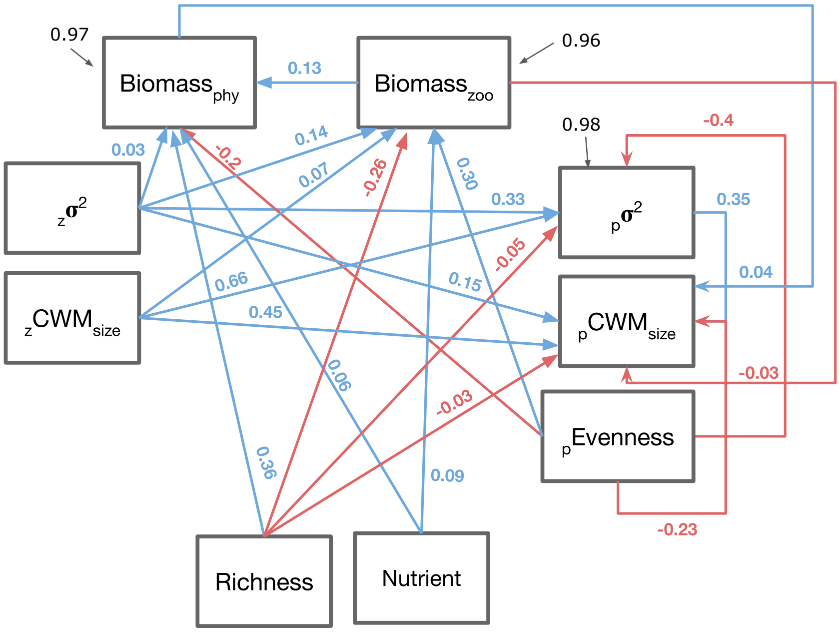

Figure 5.6: **Final revised structural equation model for biomass as productivity proxy using simulated data.** Blue and red arrows represent positive and negative effects, respectively. Effect sizes as standardised parameter estimates are shown for each arrow path. R^2 for each endogenous variable (Biomass$_{phy}$, $_p$Evenness, richness, $_p\sigma^2$) are given. Only direct pathways are shown. $_{z,p}$CWM$_{size}$: zooplankton and phytoplankton community weighted mean size; $_{z,p}\sigma^2$: zooplankton and phytoplankton size diversity; $_{z,p}$Evenness: zooplankton and phytoplankton evenness; Biomass$_{zoo,phy}$: zooplankton and phytoplankton biomass.

5.5 Discussion

The findings suggest that phytoplankton productivity in the San Francisco Bay system is primarily driven by environmental control on community size structure, particularly light availability and nutrient concentrations, with biodiversity playing a secondary role. Species richness had minimal influence on productivity, while size structure and evenness emerged as stronger predictors. These results again emphasise the need to integrate environmental drivers into Biodiversity-Ecosystem Function (BEF) frameworks, as relationships in natural ecosystems are often mediated by abiotic conditions rather than diversity alone.

Table 5.6: **Indirect effects from structural equation model using simulated data with biomass as a productivity proxy.** Indirect paths indicate mediation from x → mediator → y. Effect size is the standardised path coefficient between endogenous variables, estimated as the product of standardised direct path coefficients (γ or β). ${}_{p,z}\sigma^2$: phyto- and zooplankton size diversity; ${}_{p,z}\text{CWM}_{size}$: phyto- and zooplankton community weighted mean size; PAR: photosynthetic active radiation; DIN: dissolved inorganic nitrogen; $\text{Bio}_{phy,zoo}$: phyto- and zooplankton biomass. All indirect effects reported are significant.

Productivity Proxy	**Indirect path**	**Effect size**
Bio_{phy}	${}_{p}\text{Evenness} \rightarrow \text{Bio}_{zoo} \rightarrow \text{Bio}_{phy}$	0.04
	$\text{Richness} \rightarrow \text{Bio}_{zoo} \rightarrow \text{Bio}_{phy}$	-0.03
	${}_{z}\sigma^2 \rightarrow \text{Bio}_{zoo} \rightarrow \text{Bio}_{phy}$	0.02
	$\text{Nutrient} \rightarrow \text{Bio}_{zoo} \rightarrow \text{Bio}_{phy}$	0.02
	${}_{z}\text{CWM}_{size} \rightarrow \text{Bio}_{zoo} \rightarrow \text{Bio}_{phy}$	0.01
Total Indirect Effect (∑)		0.06
${}_{p}\text{CWM}_{size}$	${}_{z}\text{CWM}_{size} \rightarrow {}_{p}\sigma^2 \rightarrow {}_{p}\text{CWM}_{size}$	0.23
	${}_{p}\text{Evenness} \rightarrow {}_{p}\sigma^2 \rightarrow {}_{p}\text{CWM}_{size}$	-0.14
	${}_{z}\sigma^2 \rightarrow {}_{p}\sigma^2 \rightarrow {}_{p}\text{CWM}_{size}$	0.12
	$\text{Richness} \rightarrow {}_{p}\sigma^2 \rightarrow {}_{p}\text{CWM}_{size}$	-0.02
	$\text{Richness} \rightarrow \text{Bio}_{phy} \rightarrow {}_{p}\text{CWM}_{size}$	0.02
	${}_{p}\text{Evenness} \rightarrow \text{Bio}_{zoo} \rightarrow {}_{p}\text{CWM}_{size}$	-0.01
	${}_{p}\text{Evenness} \rightarrow \text{Bio}_{phy} \rightarrow {}_{p}\text{CWM}_{size}$	-0.01
	$\text{Richness} \rightarrow \text{Bio}_{zoo} \rightarrow {}_{p}\text{CWM}_{size}$	0.01
	${}_{z}\sigma^2 \rightarrow \text{Bio}_{zoo} \rightarrow {}_{p}\text{CWM}_{size}$	-0.004
	$\text{Nutrient} \rightarrow \text{Bio}_{zoo} \rightarrow {}_{p}\text{CWM}_{size}$	-0.003
	${}_{z}\text{CWM}_{size} \rightarrow \text{Bio}_{zoo} \rightarrow {}_{p}\text{CWM}_{size}$	-0.002
	$\text{Nutrient} \rightarrow \text{Bio}_{phy} \rightarrow {}_{p}\text{CWM}_{size}$	0.002
	${}_{z}\sigma^2 \rightarrow \text{Bio}_{phy} \rightarrow {}_{p}\text{CWM}_{size}$	0.001
Total Indirect Effect (∑)		0.19

5.5.1 The importance of environmental control

Environmental factors not only directly drive total productivity, but also act as filters that shape species composition via indirect effects on functional traits. Nutrients, PAR, and salinity played a key role in explaining variance in RUE, biomass and Chl *a*. Particularly, PAR was an important driver of productivity, reflecting the light limitation regime in the San Francisco Bay (SFB) system (Cloern, 2018).

In BEF studies, the role of the environment is usually minimised and/or not ac-

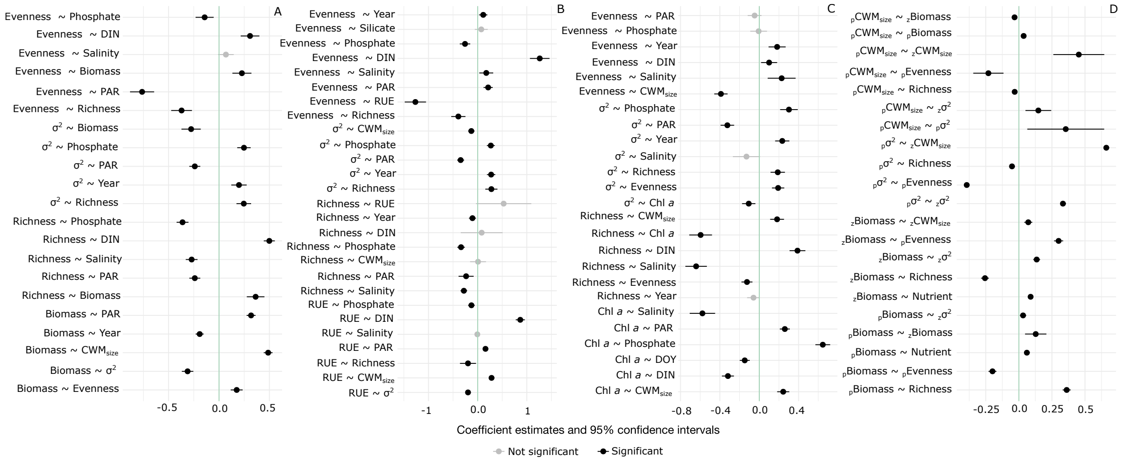

Figure 5.7: **Standardised parameter estimates for all selected models.** Coefficient estimates for (A) *in situ* biomass, (B) resource use efficiency (RUE), (C) Chl *a* and (D) simulated biomass. Significant (black circles) and non-significant (grey circles) estimates are shown. DIN: dissolved inorganic nitrogen; PAR: photosynthetic active radiation; CWM$_{size}$: community weighted mean size; RUE: resource use efficiency; σ^2: size diversity; DOY: day of year. P and Z subscripts represent phytoplankton and zooplankton variables.

counted for, as BEF focuses on biodiversity's role (Brose and Hillebrand, 2016; Loreau and Hector, 2001). Still, in dynamic environments, i.e. the pelagic ocean, the environment is constantly exerting some level of disturbance that leads to variation in expected BEF relationships, most commonly via changes in community structure and composition (Brose and Hillebrand, 2016). In the model, for example, nutrients had no direct effect on biomass accumulation, but rather an indirect effect via community size diversity (σ^2) and evenness. For Chl *a*, phosphate and DIN had a positive and negative effect respectively. In hypereutrophic conditions (>100 μg L^{-1}) such as in the SFB, highest Chl *a* levels were observed at highest phosphate concentration, whereas Chl *a* declined with increasing nitrogen levels, with the response of Chl *a* to nitrogen changing according to phosphate levels (Filstrup and Downing, 2017). This environmental forcing likely varies throughout the year, as suggested by the seasonality effect on Chl *a* levels. Further, since nutrient levels in this region do not necessarily reflect supply rates, the observed spatial differences in nutrient distributions can also indicate environmental filtering of community composition across the bay.

These seasonal dynamics suggest that nutrient availability interacts with other environmental factors, such as light, to shape phytoplankton community structure across spatial and temporal scales, and ultimately also shapes productivity. Diatoms are uniquely apt to thrive in nutrient-rich conditions, with metabolic pathways allowing for rapid assimilation of various nitrogen forms and large storage capacity due to cell size, and indeed they are the major biomass contributors to the SFB system (Armbrust, 2009; Cloern, 2018). On the other hand, excess phosphate could favour cyanobacteria dominance, due to their ability to store and quickly respond to N:P imbalances (Aubriot and Bonilla, 2018). However, light availability limits productivity levels in the SFB system, and despite cyanobacteria being the most abundant group in the bay, their contribution to RUE is essentially lost due to how RUE is calculated in the current study (see Chapter 2). Different species can exhibit distinct nutrient acquisition strategies and trade-offs, allowing certain taxa to dominate under specific nutrient conditions or during particular seasons (Litchman and Klausmeier, 2008; Meunier et al., 2018). The dataset contained dinoflagellates that are known to have an affinity for phosphorous (Meunier et al., 2018), and though their overall contribution to productivity and diversity proxies was removed, their nutrient uptake rates was not. This could explain the negative effect phosphate had on productivity, relating to the drawdown caused by these organisms that was not reflected in the community productivity proxy (Meunier et al., 2018), once again hinting at the importance of community composition.

Likewise, the environment controls diversity patterns, directly and indirectly, by filtering the community composition. Results show that increasing phosphate concentrations led to reduced community evenness, likely due to the competitive advantage of specific taxa, such as cyanobacteria, which can efficiently store and utilise phosphorus. Whereas, increasing DIN levels increased evenness and richness in all models, suggesting increasing DIN supports a broader range of species, including diatoms. All these diversity proxies represent different aspects of the community. Evenness relates to taxonomic diversity and how equal the biomass contribution of each species is, whereas σ^2 relates to size heterogeneity of the phytoplankton community weighted by their relative biomass contribution.

Increasing nutrient allows more species to coexist, disproportionally favouring large cell sizes that can dominate biomass and reduce σ^2 and evenness in the process (Acevedo-Trejos et al., 2018; Finkel et al., 2010). Lower evenness hint at dominance of species with certain traits, suggesting that selection effects are more important in driving ecosystem function (Hillebrand et al., 2008; Loreau and Hector, 2001). Contrarily, higher evenness could indicate that there is an increased complementarity resource use among species, which could lead to higher productivity (Cardinale et al., 2006; Tilman et al., 1997a). This mechanism is suggested to be responsible for community 'overyielding', where a polyculture outperforms the most productive monoculture due to niche partitioning and facilitation (Marquard et al., 2009). Additionally, PAR reduced richness and σ^2. Light limitation selects for smaller cells that have strategies for better light absorption (i.e. 'package effect', Finkel et al., 2010; Finkel, 2001), leading to a reduced range in organisms' sizes, and when light is abundant, it may help larger species to grow and accumulate biomass, increasing the mean cell size and potentially decreasing σ^2. In high PAR conditions, large-sized cells grow rapidly and reduce the contribution of smaller- and intermediate-sized cells to the overall productivity, thus, reducing size diversity. Nutrient supply can further amplify this effect by promoting the growth of large species, particularly in eutrophic coastal systems where mild temperatures create optimal conditions for their dominance (Acevedo-Trejos et al., 2015; Acevedo-Trejos et al., 2018; Cloern, 2018). This pattern is also reflected in the negative indirect effects of CWM$_{size}$ and PAR, where increasing mean cell size leads to a reduced σ^2.

In this study, salinity decreased richness and increased evenness. Richness levels have been observed to be at their lowest at intermediate salinity levels. This phenomenon is a reflection of species' ability to cope with varying salinity gradients, with lower richness being explained by the presence of few true brackish water species (Olli et al., 2019; Olli et al., 2023). Salinity increases southwards in the SFB, whereas richness decreases in the same direction, reflecting this relationship and the community present. Salinity changes helped increase evenness in RUE and Chl *a* models, likely by altering richness patterns, competitive dynamics and grazing pressure, leading to more even communities (Larson and Belovsky, 2013).

As such, the environment (e.g. PAR, nutrients, salinity) acts by either directly enhancing or decreasing productivity, but also indirectly, via changes in diversity structure of the community, leading to changes in productivity levels. Overall, the role of the environment cannot be overlooked as its effects are intertwined in the community dynamics, with no single parameter acting in an isolated manner.

5.5.2 Size structure is a strong driver of productivity, not richness

The relationship between diversity and productivity was highly dependent on environmental conditions. Contrary to classical BEF theory, species richness was not a strong predictor of productivity when environmental and temporal covariates were accounted for. Instead, productivity was primarily driven by community size structure. The same was observed for Chl *a*, with CWM_{size} being the most important variable. Richness had a negative effect on RUE, with σ^2 and CWM_{size} also affecting the response, suggesting that increased diversity did not necessarily enhance resource partitioning. This result contrasts with many BEF experiments that report positive effects of richness on productivity (Otero et al., 2020; Ptacnik et al., 2008), highlighting the complexity of diversity effects in natural systems. While the simulations here suggested a stronger positive effect of richness on productivity, observational data indicated that environmental factors played a dominant role, potentially masking any positive richness effects (Hodapp et al., 2015; Olli et al., 2023). Evidence suggests that richness and productivity are not mechanistically linked, and the patterns reported relate to a complex set of interactions between the environment, diversity and productivity, especially within a single trophic level (Adler et al., 2011; Grace et al., 2007). Richness is an insufficient metric to describe the mechanisms underlying ecosystem function levels, but it is also widely used and easy to acquire. This has led to a narrow focus on the effect of richness on productivity, which has dictated the direction of the BEF research field for decades. It is now being challenged (Hillebrand et al., 2018).

Evenness emerged as a key driver of productivity, though its effects differed between observational and simulated datasets. In the SFB, higher evenness was associated with greater biomass, likely due to more stable community composition and reduced dominance by a single taxa. However, in simulations, evenness had a negative effect on productivity, suggesting that selection effects (where a few highly productive species dominate) may drive productivity under controlled conditions, particularly in high nutrient-low richness scenarios. Trait-based shifts were evident in the community-weighted mean (CWM) of cell size, which varied spatially and with time and greater σ^2 having a consistent negative effect on productivity. Higher σ^2 was linked to lower biomass. This suggests that functional differences in size did not necessarily enhance resource partitioning in this system. In contrast, periods of low productivity showed greater σ^2, with smaller taxa likely contributing to increase σ^2. This aligns with previous studies (Chen et al., 2019; Smith et al., 2016) showing that greater trait variability can reduce competitive efficiency if it leads to increased niche overlap or weaker dominance by highly productive species. The interplay between selection and complementarity effects may then depend on environmental stability, resource availability, and the degree of functional redundancy in the community (Loreau and Hector, 2001).

A key finding of this study is that size structure, rather than species richness, was the strongest predictor of productivity, highlighting the role of trait-based mechanisms in shaping ecosystem function. During periods of high productivity, i.e. spring, the community was dominated by large diatoms, leading to increased CWM_{size} but lower σ^2 (see Chapter 2). Diatoms dominated the community, leading to a community with large-sized cells, low size diversity, but relatively high evenness, due to similar biomass contribution of species present. Size diversity, accordingly, was low (because cells had similar sizes, as reflected by the dominance of diatoms species), but evenness was relatively high, leading to increased productivity. This contradicts the expected relationship between evenness and productivity for natural aquatic environments (Hodapp et al., 2015; Lehtinen et al., 2017; Lewandowska et al., 2016; Maureaud et al., 2020), but aligns with the observation that high evenness supports stable biomass accumulation via increased complementary resource use (Hillebrand et al., 2008; Hordijk et al., 2023; Kirwan et al., 2007).

Furthermore, grazing pressure is stronger in aquatic communities which could lead to changes in dominance, and thus, productivity via a positive evenness effect. Aquatic and terrestrial environments differ in fundamental ways (e.g. grazing and biomass production rates, prey edibility), resulting in stronger top-down control in phytoplankton communities (Cebrian, 1999; Shurin et al., 2002). Disturbance levels, trait variance, and resource availability can influence whether evenness helps or hinders biomass accumulation (Norberg et al., 2001). The positive effect observed could also relate to the levels of disturbance on community processes over a long time scale, with higher evenness leading to higher productivity via better adaptive capacity of organisms in non-static environments (Norberg et al., 2001; Smith et al., 2016). In addition, changes in evenness levels can change community dynamics by altering intra- and interspecific competition, causing positive species interactions and reducing the dominance of single species, which can alter ecosystem function both negatively and positively (Hillebrand et al., 2008; Norberg et al., 2001; Polley et al., 2003; Schwartz et al., 2000).

5.6 Conclusions

Phytoplankton productivity in the San Francisco Bay system was not driven by species richness. Rather, productivity was a result of the interactions between the environment and community size structure, with richness playing a secondary role, mainly via its indirect effects on size diversity and evenness. Diversity of traits, particularly related to size, are a better predictor of ecosystem function. While larger cell sizes promoted productivity, higher size diversity and richness reduced ecosystem function, likely due to the inclusion of inefficient species and/or small cells with low biomass contributions (Chen et al., 2019; Norberg et al., 2001; Smith et al., 2016). Environmental filtering strongly shaped community structure, which in turn affected productivity. Neither nutrient supply nor richness alone accounted for all the variation in productivity, with nearly all indirect effects being mediated by either productivity proxies or diversity. This suggests that indeed biomass and richness are not linked mechanistically, but rather the relationships between these two variables are a consequence of the complex set of interactions linking them.

The role of evenness in mediating productivity is variable and context-dependent, with contrasting findings highlighting the limited understanding of this relationship (Hillebrand et al., 2008). These findings suggest that higher evenness enhances biomass when resource complementarity among species dominates, contrasting with previous expectations of a negative relationship driven by selection effects. When resources are efficiently partitioned, high evenness can boost productivity. In other contexts, evenness may simply reflect the dominance of species best adapted to prevailing environmental conditions (Lehtinen et al., 2017). Unlike richness, evenness appears more directly linked to ecosystem function, making it a key trait in understanding BEF relationships.

Finally, structural equation models (SEM) proved to be a valuable framework for disentangling causal relationships in these complex, non-linear ecological systems, while also increasing the amount of variance explained in the data. While multiple linear regression can be a better alternative than simple bivariate analyses, it does not test causal links between parameters (Grace et al., 2010). By explicitly modelling direct and indirect effects, SEM have been shown to be well-suited to evaluate hypothesis in complex systems, leading to a more mechanistic understanding of the links between biodiversity, community structure, and ecosystem function (Grace et al., 2010).

5.7 Limitations and outlook

A key limitation in this study was the strong correlation between resource use efficiency (RUE) and dissolved inorganic nutrient (DIN) (>0.7) due to how RUE was calculated (RUE = Biomass/DIN). Ideally, highly correlated variables should be removed from analyses, but removal of DIN from the analyses led to model instability. As such, this strong correlation means that interpreting the observed effects of DIN on RUE requires caution. Additionally, DIN had a strong positive effect on RUE, while phosphate had a negative effect. Given that RUE is directly derived from DIN, this result was expected. But it reinforces the need for caution in interpreting direct causal links. Future studies should explore alternative metrics of resource use efficiency that minimize intrinsic correlations with key environmental drivers (Hodapp et al., 2019).

Furthermore, evenness in this study was not controlled at the beginning of model simulations nor field data, and because of that, this metric can be interpreted as an emergent property of the community. One that is not independent of productivity nor richness. Very few studies have attempted to manipulate evenness (Wilsey and Potvin, 2000), specially in aquatic environments. The results regarding evenness as a driver of productivity, albeit not strictly causal, provide us with a more in-depth understanding of its role in affecting ocean productivity, at least indirectly.

Proxy selection remains an issue to be addressed. Each proxy represents a different aspect of ecosystem function, and their interpretation depends on the ecological contexts in which they are used. Biomass primarily captures dominance effects, as it tends to be driven by a few highly productive species that contribute disproportionately to overall community biomass. However, biomass alone does not account for the efficiency of resource use or the functional diversity within the community (i.e. RUE) (Hodapp et al., 2019). Chl *a* reflects phytoplankton abundance and community composition, but it is an imperfect measure of productivity because pigment concentration varies across taxa and is influenced by environmental factors (Litchman and Klausmeier, 2008). Individually, each of these proxies may be misleading if their limitations are not appreciated. For example, a system dominated by large, slow-growing species might have high biomass but low RUE, while another, with a mix of fast-growing taxa, could have high RUE but lower standing biomass. Similarly, Chl *a* might indicate high phytoplankton abundance, but without considering biomass or RUE, it is difficult to assess whether this represents high productivity or a shift in community composition favouring smaller, less productive taxa. I recommend a complementary approach to productivity estimation that integrates multiple proxies whenever possible. The selection of proxies should be guided by factors such as data availability, correlation with ecosystem function, and ecological relevance to the system under study.

Moving forward, understanding how environmental change influences trait-based community shifts will be crucial for predicting ecosystem responses to anthropogenic pressures.

Chapter 6

Final remarks and outlook

This thesis focused on building a causal understanding of biodiversity and ecosystem function (BEF) relationships, with the specific focus on the role of size structure and environmental control in driving productivity. Using a combination of long-term observational data from San Francisco Bay (SFB) and size-based numerical simulations, we assessed how different levels of diversity influence ecosystem functioning under varying environmental conditions. Across both datasets, we found that productivity was primarily driven by community size structure, with environmental control strongly mediating this effect. These findings provide important insights into the complexity of BEF relationships in marine ecosystems, challenging traditional assumptions and emphasizing the importance of trait-based approaches.

One of the major strengths of this study is the use of long-term, high-resolution monitoring data, which allowed us to investigate BEF relationships in a natural aquatic system. Additionally, the integration of numerical simulations enabled us to test mechanistic hypotheses that would be difficult to isolate from observational data alone. The use of Structural Equation Modelling (SEM) was instrumental in disentangling complex ecological relationships, allowing us to go beyond bivariate analyses and better understand indirect pathways influencing productivity. We are aware that observational data inherently includes confounding environmental factors, making it difficult to establish definitive causal relationships, or even separate the effects of diversity and environment. While SEM helps address this issue, it does not completely eliminate the limitations of bivariate analyses. In going beyond the simple nature of bivariate analyses, we were able to develop a stronger understanding of direct and indirect causal drivers of productivity by integrating theoretical with empirical knowledge. Furthermore, the approach used here primarily focused on size-based metrics, which, while invaluable, may not be directly linked to certain productivity proxies. Future research should consider integrating additional trait measures that relate to ecological functions, such as reproduction, nutrient uptake efficiencies, and predator avoidance, in order to gain a more comprehensive understanding of diversity effects on productivity and multifunctionality.

The results challenge the widely accepted positive BEF relationship. We showed that higher species richness does not necessarily lead to increased productivity (e.g., biomass, resource use efficiency, Chl *a*), even when accounting for environmental covariates. Instead, richness had a weak effect that was often mediated by environmental control, while size diversity (σ^2) emerged as a stronger predictor of ecosystem function. In both field and simulated data, size-based metrics such as community-weighted mean size (CWM_{size}) and (σ^2) were key drivers of phytoplankton productivity. Large-sized species, particularly diatoms, dominated and contributed significantly to biomass accumulation under high nutrient conditions, while increased (σ^2) often led to reduced productivity due to the presence of weak competitors.

Environmental factors exerted both direct and indirect controls on community productivity, with their strength and direction highly context-dependent. High nutrient availability did not always translate into higher biomass, due to light limitation and trophic interactions shaping community structure. This highlights that, despite the important role of nutrient control, nutrient supply alone does not drive productivity. Rather, it mediates diversity by filtering the community via their size structure. Additionally, the presence of zooplankton influenced BEF relationships, shifting the balance between selection and complementarity effects, thereby demonstrating the context dependency of biodiversity effects.

The findings of this thesis reinforce the need to refine biodiversity metrics used in BEF studies. Moving forward, studies should prioritize functional traits over species richness alone, particularly in aquatic ecosystems where size structure plays a dominant role. Future research could explore the combined effects of functional and phylogenetic diversity, which have been shown to outperform richness as predictors of biomass in some systems (Thompson et al., 2015). Thompson et al. (2015) reported that functional and phylogenetic diversity outperformed richness as a predictor of phytoplankton and zooplankton biomass in a natural pond. While this avenue of research has been mostly explored in terrestrial ecosystems (Cadotte et al., 2009; Flynn et al., 2011; Srivastava et al., 2012), its application in marine and freshwater environments remains limited. Expanding these analyses to different marine ecosystems, such as open-ocean phytoplankton communities or even nutrient-limited ones, could help determine the generality of these patterns across environmental gradients. Further, integrating BEF relationships into climate change models could improve our ability to predict shifts in ecosystem productivity and resilience under future scenarios. Palaeoecological records can provide a valuable long-term perspective on biodiversity and ecosystem function. By coupling classic ecological time-series with palaeoecological datasets, we can attempt to determine changes in biodiversity levels across a long timespan (from decades to millennia). This approach allows us to relate changes driven by the environment and its consequences on ecosystem function (Jonkers et al., 2019), and also determine whether the mechanisms driving BEF relationships today were consistent over historical timescales. Or if they varied in response to past ecological disturbances.

We observed relationships between size structure and productivity. They suggest that shifts in species composition and relative contributions, driven by climate change or anthropogenic impacts, could lead to fundamental changes in ecosystem function. Current biodiversity conservation frameworks often emphasise species richness as a key metric. However, recognizing that diversity is a multifaceted concept and not the sole driver of ecosystem function is crucial for understanding changes in ecosystem functioning in response to global changes. Finally, relying on appropriate statistical frameworks and understanding the limitations of productivity proxies is important. A mechanistic understanding of the factors driving productivity, combining empirical data with theoretical models, will be key to forecasting ecosystem health and ensuring the sustainable management of marine resources in the face of accelerating environmental change.

Appendix A

Supplementary files

A.1 Data files

Environmental, phytoplankton and associated data used in this thesis can be found here. *Disclaimer for the printed version of this thesis*: the available data and scripts used here can also be requested directly to the author via email: dflivia@gmail.com; livia.oliveira@hifmb.de.

A.2 Chapter 2

All .R scripts used to retrieve samples, data summary and figures in this chapter are available for download:

- Data Processing and working dataset generation .R script
- Map plot .R script
- Data description plots .R script

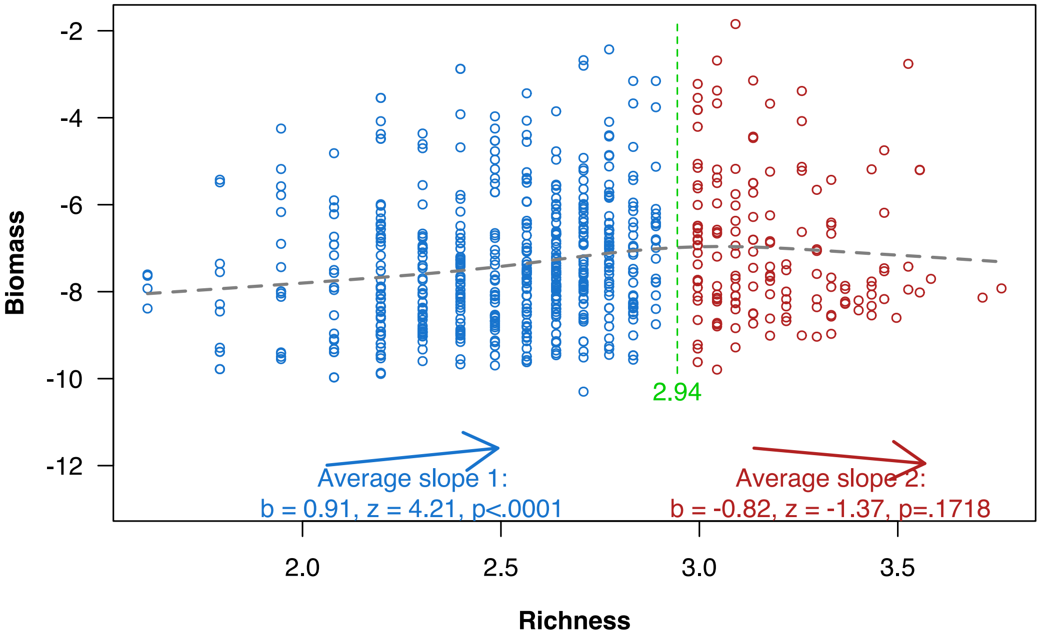

Figure A.1: **Two line test example plot.** The graph shows the bivariate relationship between biomass and richness in the San Francisco Bay system. The test estimates an interrupted regression for the predictor hypothesised to have an unimodal relationship with the response. The test suggests the observed relationship is not unimodal.

A.3 Chapter 3

All .R scripts used for 3 analyses and figures.

- Data analyses and figures
- Two line test function script after Simonsohn, 2018
- Correlation plots

A.4 Chapter 4

All .R scripts used for 4 analyses and figures.

- NP, NPZ models, analyses and figures

A.5 Chapter 5

All .R scripts used for 5 analyses and figures.

- SEM models, analyses and figures

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