USING FUNCTIONAL DIVERSITY COMPONENTS TO DESCRIBE PHYTOPLANKTON COMMUNITY ASSEMBLY PROCESSES IN TURKISH SHALLOW LAKES

A THESIS SUBMITTED TO
THE GRADUATE SCHOOL OF NATURAL AND APPLIED SCIENCES
OF
MIDDLE EAST TECHNICAL UNIVERSITY

BY

VİLDAN ACAR

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR
THE DEGREE OF MASTER OF SCIENCE
IN
BIOLOGY

APRIL 2022

Approval of the thesis:

UNDERSTANDING PHYTOPLANKTON COMMUNITY ASSEMBLAGE PROCESSES OF TURKISH SHALLOW LAKES USING DIFFERENT FUNCTIONAL DIVERSITY COMPONENTS

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ABSTRACT

USING FUNCTIONAL DIVERSITY COMPONENTS TO DESCRIBE PHYTOPLANKTON COMMUNITY ASSEMBLY PROCESSES IN TURKISH SHALLOW LAKES

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April 2022, 81 pages

The recent increase in biodiversity loss due to various anthropogenic effects makes it crucial to understand the relationship between biodiversity and ecosystem functioning for the conservation and preservation of ecosystems. Classically, biodiversity and ecosystem functioning studies use species diversity as a measure of biodiversity, but functional diversity has been shown in some cases to better explain and predict ecosystem-level processes. In this study, we investigated the role of dispersal, environmental filtering and limiting similarity in the assembly of phytoplankton communities from 44 Turkish lakes. Dispersal drives both local and regional diversity patterns, while environmental filtering and limiting similarity affect local community structure. At the local level, species traits are expected to converge as a result of environmental filtering or diverge due to limiting similarity. The study firstly found that dispersal limitation was not of importance for the phytoplankton community assembly in study lakes. Some functional traits were affected only by environmental filtering (i.e. unicellularity, silica demand) or limiting similarity (i.e. toxin production, mixotrophy) or both processes acted simultaneously on other traits (i.e. sexual reproduction). Also, the effects of different assembly processes varied along different environmental gradients such as total nitrogen or salinity.

Keywords: assembly, function, functional traits, phytoplankton

ÖZ

FARKLI FONKSİYONEL ÇEŞİTLİLİK ÖLÇÜMLERİ KULLANILARAK TÜRKİYENİN SIĞ GÖLLERİ İÇİN FİTOPLANKTON KOMÜNİTELERİNİN OLUŞMASINDA ETKİLİ OLAN FAKTÖRLERİN ARAŞTIRILMASI

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Nisan 2022, 81 sayfa

Biyoçeşitlik kaybının son zamanlarda insan etkisiyle artmasıyla birlikte, biyoçeşitlilik ve ekosistem fonksiyonları arasındaki ilişkinin anlaşılması ekosistemlerin korunması açısından önem arz eder hale gelmiştir. Klasik olarak, biyoçeşitlilik ve ekosistem fonksiyonları çalışmaları biyoçeşitliliğin ölçümü olarak tür çeşitliliğini kullanmıştır fakat fonksiyonel çeşitliliğin ekosistem düzeyindeki süreçleri anlamada daha kullanışlı olduğu farklı çalışmalarla ortaya konulmuştur. Bu çalışmada, Türkiyedeki 44 gölün fitoplankton komünitelerinin oluşumunda dağılım, çevresel filtreleme ve sınırlayıcı benzerlik etkisi araştırılmıştır. Dağılım lokal ve bölgesel çeşitlilik örüntülerini entegre ederken çevresel filtreleme ve sınırlayıcı benzerlik lokal komünite yapısını etkilemektedir. Tür karakterlerinin lokal komüniteler seviyesinde çevresel filtreleme ektisiyle birbirine yaklaşması beklenirken sınırlayıcı benzerlik etkisiyle birbirinden uzaklaşması beklenmektedir. Bu çalışmada ilk olarak dağılımın fitoplankton komünitelerinin oluşmasında sınırlayıcı bir etkisi olmadığı bulunmuştur. Ayrıca tek hücrelilik ve silika gereksinimi gibi bazı fonksiyonel karakterlerin yalnızca çevresel filtrelemeden etkilenirken toksin üretimi ve miksotrofi gibi karakterlerin sınırlayıcı benzerlikten etkilendiği bulunmuştur. Eşeyli üreme gibi karakterlerin ise her iki süreçten de eş zamanlı olarak etkilenebileceği belirlenmiş ve farklı komünite oluşum süreçlerinin etkisinin toplam nitrojen ve tuzluluk gibi çevresel gradyanlar üzerinde farklı etkileri olabileceği saptanmıştır.

Anahtar Kelimeler: asamble, fonksiyon, fonksiyonel karakter, fitoplankton

To the one who is always there

ACKNOWLEDGMENTS

First of all, I want to thank my supervisor *Meryem Beklioğlu* for her wisdom and supervision but also for her constant support even when I thought I won't make it this far.

I also want to thank *Şeyda Erdoğan* and *Kaan Özgencil* for their help and support since the beginning of this study. I thank *Erik Jeppesen* and *Juan Pablo Pacheco* for all the times they offered help.

Also, I want to thank all the members of METU Limnology Laboratory for sharing their experiences with me or experiencing the same hardships together with me so I can see that everything will be fine in the end.

I am very grateful to my friends, who listened to all my complaints and excitements in the last two years and never seemed to get bored with my unsolicited scientific talks and facts. They are the ones who gave me the strength to keep trying after a bad day.

I want to thank my family, especially my sisters *Gülcan* and *Şükran* because they always believed in what I wanted to do with my life.

And lastly, I want to thank my partner, *Ton*, for always keeping me afloat. I am so lucky to know that I will never be alone.

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INTRODUCTION

1.1 The Concept of Functional Diversity

The increase in biodiversity loss and effects of climate change made it crucial to understand the relationship between biodiversity and ecosystem functioning (BEF) for the conservation and preservation of the ecosystems (Jax, 2005; Laureto et al., 2015; Cadotte et al., 2011; Violle et al., 2007). Classically, BEF studies used species diversity as a measure of biodiversity (Cadotte et al. 2011; 2015). However, species diversity assumes all species in a community are similar concerning functions they provide to ecosystems. Even though some species can be quite similar in terms of the functions they provide, usage of functional diversity as a metric of biodiversity in BEF studies gained importance because contrary to species richness, functional diversity metrics measured by the functional trait values considers each species in a community as unique in their roles in ecosystem functioning (Bengtsson, 1998; Walker, 1992).

Even if the concept of functional diversity gained importance in ecological research, there is still no consensus made on either definition or measurement of functional diversity (Petchey & Gaston 2006). Even if many different definitions exist, the most widely accepted definition made by Tilman (2001) as *"the value and the range of those species and organismal traits that influence ecosystem functioning"* and he stated that functional diversity is an important component of biodiversity since it is considered to be a key for ecosystem processes (Laureto et al., 2015; Jax, 2005). For example, ecosystems with higher diversity of functional traits, consequently with higher functional diversity, perform more efficiently

(Tilman et al., 1997). Or according to the insurance hypothesis, if a community consists of many species bearing the same or similar trait values (functional redundancy), the loss of a species can be reimbursed by other species and the ecosystem function still can be maintained (Yachi & Loreau, 1999) and therefore functional diversity can be crucial for resilience of ecosystems (Walker, 1992). With all this information in mind, in a community, one of the most ecologically relevant biodiversity metric will often be functional diversity (Diaz & Cabido, 2001).

1.1.1 History

Even though functional diversity studies gained more attention in the last two decades, the origins of the idea can be traced way back to 300 B.C, in *Enquiry into Plants* of Theophrastus and in his work, he classified plants into different groups according to their height and stem density traits (Weiher, 1999). Way long after that, in the 19th century, Darwin's observations in *On the Origin of Species* (Darwin, 1859) about areas with higher plant diversity having higher primary production brought up new questions about the effect of biodiversity on ecosystem functioning. Almost one century after Darwin's *On the Origin of Species*, Charles Elton (1927) divided animal communities into different groups according to different resource use habits. Root (1967) further developed this idea and coined the term "guild" and defined a guild as:

"…a group of species that exploit the same class of environmental resources in a similar way."

7 years later after the definition of the term guild, Cummins (1974) stated the need for identification of "functional groups" to answer process-oriented ecological questions on a broader scale than guilds. In 1987, in the first issue of the journal *Functional Ecology,* Calow proposed the idea of functional ecology to be a

subdiscipline of ecology to bring ideas together. Since then, functional approaches continued to be an important aspect of ecological studies.

1.1.2 Trait Selection

Even if a variety of definitions exist today, Tilman's (2001) functional diversity definition is the most widely accepted. This definition directly relates functional traits to ecosystem functioning and further brings the need for a definition of functional traits. Like functional diversity, the term functional trait also has different definitions, such as *a trait that strongly influences organismal performance* (McGill et al., 2006), *any trait which impacts fitness indirectly via its effects on growth, reproduction, and survival* (Violle et al., 2007) or *aspects of phenotypes at the individual scale that exists along a continuum of response and effect* (Weiss & Ray, 2019). Different definitions exist because of the multifaceted nature of functional diversity, hence functional traits. The abundance of different definitions creates a disagreement on which traits to use to measure functional diversity. It is agreed that the selection of appropriate functional traits depends on which ecological question is being investigated (Laureto et al., 2015). If the main question is to understand ecosystems level processes, the question of how those processes operate and which organisms or traits are more affected by or affect those processes becomes an important issue in the selection of functional traits (Petchey & Gaston, 2006). If the main goal is to understand species interactions and performance, traits related to species-environment and species-species relationships become important (Díaz & Cabido, 1997; Petchey & Gaston, 2006). For example, diversity in P_{saff} (indicator for the competitive ability for phosphate) for phytoplankton might not be the best option to use in a dataset consisting of eutrophic lakes, where P limitation is not a problem and thus competition for phosphate is minimal (Edwards et al., 2013).

Besides the fundamental issue that which traits to use, several decisions need to be made about species traits (i.e. number of traits to use and whether it is better to use single traits or trait combinations). Making those decisions again depends on which ecological question to be answered (Lepš et al., 2006). Under certain circumstances, diversity in a single well-selected trait might predict community better than diversity measured with a combination of traits (Lepš et al., 2006). However, the first filter in the determination of which traits to use, in practice, is the availability of the trait values. Some traits for some groups of species might be readily available because they are relatively easy to measure but one has to be aware that those easily available traits are generally correlated to each other (Garnier et al., 2004). However, some traits can be functionally distinct even if they are correlated (Lepš et al., 2006).

Thus, after deciding on the usage of a single or combination of multiple traits, selected traits (1)should be relevant to the ecological question investigated, (2)consider species-environment relationships, and (3) needs to be available to use or relatively easier to measure.

1.1.3 Measurement of Functional Diversity

As the attention on the concept of functional diversity (FD) increased, a debate on how to measure FD started especially because now FD is considered as a fundamental driver of the functioning of ecosystems and their responses (Legras et al., 2018).

Petchey & Gaston (2006) prepared an extended review on the different measurements of FD and proposed a list of requirements for a suitable measure of FD to have. According to their proposal, an appropriate FD measurement requires: (1) a selection of relevant functional traits, (2) weighing of traits according to their functional importance, (3) having desirable mathematical characteristics, (4) being able to explain and predict the variation in ecosystem-level processes.

Some of the suggested functional diversity metrics and their measurements can be seen in Table 1.1. There are several reviews discussing which metric is the most suitable for measuring functional diversity but so far no consensus has been made (Schleuter et al., 2016; Mouchet et al., 2010; Petchey et al., 2009; Mason & Mouillot, 2013).

Table 1. 1 Functional diversity measures. d_{ij}: dissimilarity between species (or functional unit) *i* and *j*. S: the total species richness. p_i: relative abundance of species *i*. dG: mean distance center of gravity. Δd: sum of abundance-weighted deviances. Δ|d|: absolute abundance-weighted deviances from the center of gravity. PEW: partially weighted evenness. i': branch presence ⁄absence row vector. h^2: branch length vector

Index		Description	Formula	Source
Functional Attribute Diversity	FAD	Sum of pairwise distances between species	$FAD = \sum_{ij}^{S} d_{ij}$	Walker, Kinzig & Langridge 1999
Functional Diversity	FD	Sum of branch length of a functional classification	$FAD = i' \times h^2$	Petchey & Gaston 2002
Rao's quadratic entropy	Q	Sum of pairwise distances between species weighted by relative abundance	$Q = \sum_{ij}^{S} d_{ij} \times p_i \times p_j$	Rao, 1982
Community weighted mean	CWM	Sum of trait values weighted by relative abundance	$CWM = \sum_{i=1}^{S} p_i \times x_i$	Garnier et al, 2004
Functional Richness	FRic	Convex Hull Volume	Quickhull algorithm	Cornwell, Schwilk & Ackerly 2006; Villeger, Mason & Mouillot 2008
Functional Evenness	FEve	Sum of trait values weighted by relative abundance	$FEve = \frac{\sum_{i=1}^{S-1} \min\left(PEW_i, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$	Villeger, Mason & Mouillot 2008
Functional Divergence	FDiv	Species deviance from the mean distance to the centre of gravity weighted by relative abundance	$FDiv = \frac{\Delta d + \overline{dG}}{\Delta\lvert d\rvert + dG}$	Villeger, Mason & Mouillot 2008

1.2 Functional Approaches in Community Assemblage

Mechanisms behind the species' coexistence is one of the main interests of community ecology since the early days of ecological research. Some researchers like Clements (1916) viewed communities as distinct units that only exist in certain combinations, while Gleason (1939) opposed that view and argued that the assemblage of communities is only a result of "coincidence". While these two views precisely oppose each other, recent thinking considers both stochastic and deterministic (non-random) processes in the determination of community assemblages. Species coexistence is assumed to be the result of two opposing forces: environmental filtering that increases the similarity between species through abiotic filtering (Weiher & Keddy, 1995) and competitive interactions that prevent species to become too similar (MacArthur & Levins, 1967). Weiher & Keddy (1995) assumes that functional diversity based on functional traits is low in high environmental stress (environmental filtering) and higher where competitive forces are the dominant force in community assembly (limiting similarity).

Environmental filtering and competitive forces (limiting similarity) may act simultaneously and thus, the main concern is not which processes are valid but which one is the dominant acting force on communities (Mouchet et al., 2010) and functional diversity may reveal those underlying processes in assembly rules driven by functional traits (Mason et al., 2007; Mouillot et al, 2007).

1.2.1 Defining Assembly Rules

The term "assembly rule" was first used by Diamond in 1975 and the rules he set out mainly focused on competition as the reason for non-random community compositions. While the original *assembly rules* referred only to biotic relations as the regulator of community assemblages, Keddy (1992) redefined the term with a hierarchical point of view as any biotic or abiotic processes that *filter* species from species pool to select species in the final community composition.

Even though Keddy's definition claimed that filters act on species traits and eliminate species bearing unsuitable traits rather than species themselves, community assembly was studied with the presence/absence or abundance of species for much of the intellectual history of community ecology (Cadotte et al., 2015). Like other topics in community ecology, trait-based methods gained interest in the last two decades also in assembly studies (McGill et al., 2006; Götzenberg et al., 2011; Borics et al., 2020).

Considering only stochastic processes, Hubbell's (2001) neutral model of community assembly assumes all species are ecologically equivalent and, speciation and ecological drift are the main rules that drive community assembly (Vellend, 2010). For other processes, the term assembly rule can refer to any of the following processes: (1) dispersal, (2) environmental filtering, (3) limiting similarity (Fig. 1)

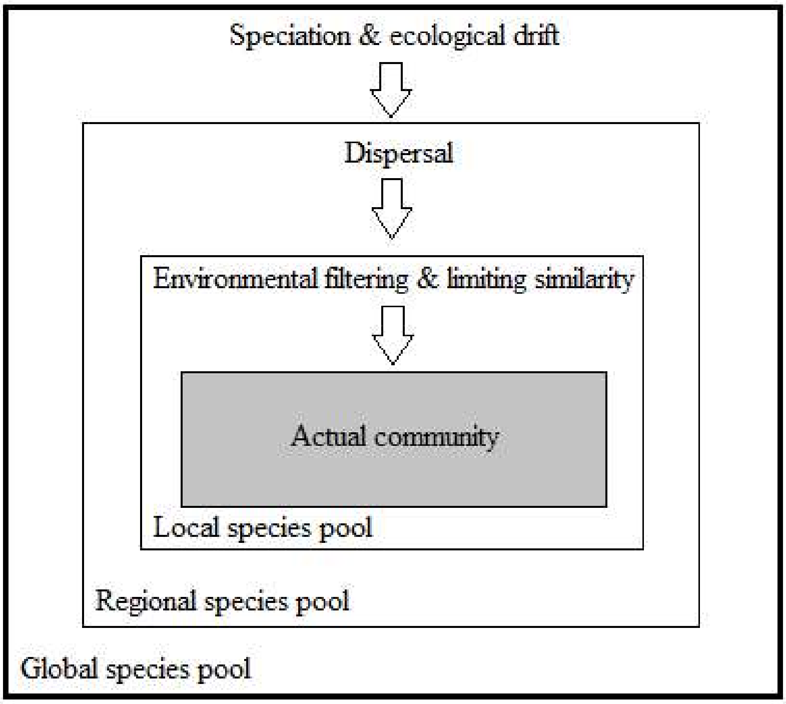


Figure 1. 1 Different mechanism that produces assembly rules at relative scales (adapted from Zobel, 1997). Any point in time, from the global species pool to the regional species pool, is determined by speciation and ecological drift. From the regional species pool, species that are capable to disperse a local site determine the local species pool. Environmental filtering and limiting similarity then act on the local species pool to determine actual assemblage in the community.

1.2.1.1 Dispersal

In his conceptual synthesis of community ecology, Vellend (2010) put dispersal as one of the four main processes that make up ecological communities and defined dispersal as “the movement of organisms across space”. Dispersal in community ecology especially became important with the metacommunity concept (Holyoak et al., 2005), which is specifically interested in the role and function of dispersal affecting community patterns at multiple scales. Community models address the role of dispersal as to whether organisms across space are distributed continuously or in discrete patches.

In community ecology, there exist two kinds of dispersal models: (1) mainland-island models which assume dispersal as a one-way movement from an infinite sized community to smaller discrete local communities, and (2) island models which assume dispersal as a two-way movement between a network of communities, that are called “metacommunities” (Holyoak et al., 2005), without a distinct mainland community (Vellend, 2010).

Dispersal as a community assembly rule was introduced by Hubbel (2001) while explaining the biodiversity patterns of trees in the forests and argued that biodiversity in forests can be explained by dispersal alone. In the metacommunity concept, dispersal is the process that integrates both local and regional diversity patterns (Spasojevic et al., 2014) and therefore is an important assembly process that bridges the gap between local and regional species pools. Moreover, the “effective community size” hypothesis recognizes dispersal as a process that increases effective community size – the size associated with competitive interactions and ecological drift – by mixing individuals from different local communities (Ron et al., 2018). In this hypothesis, dispersal is expected to reduce the relative importance of demographic stochasticity, thereby lowering drift while inflating the relative importance of selective processes (i.e., abiotic and/or biotic filters) as dominant forces in community assembly (Ron et al., 2018). Thus, where dispersal is not a limiting factor, environmental filtering and limiting similarity are the main forces determining community assembly.

1.2.1.2 Environmental Filtering and Limiting Similarity

According to the environmental filtering principle, in an area where dispersal is not a limiting factor for species occurrence, environmental conditions determine which species can establish, survive and reproduce there (Lhotsky et al., 2016). That is, according to Keddy’s (1992) assembly rules, the environment filters for the species bearing traits suitable for that environment. As a result, species coexisting in a particular area have similar traits that qualify them to inhabit that area. This principle of environmental filtering causes functional convergence with an assemblage of functionally more similar species than expected by chance.

The term “limiting similarity” originates from the competitive exclusion principle of Gause that is adapted by MacArthur & Levins (1967) to describe the limit of maximum similarity two species can have in their resource-use patterns to coexist with a reduced competition pressure. Thus, species inhabiting an area without dispersal limitation should have traits dissimilar enough to exploit different resources (Götzenberger et al., 2012). As a result, this dissimilarity causes a functional divergence in the species that inhabit that environment.

Here, it is necessary to state that, in a given community, limiting similarity and environmental filtering can both operate simultaneously on different traits or the same traits and can compensate each other (Mason et al., 2013; Borics et al., 2020).

1.2.2 Null Model Approach

Since the early days, one of the main methods to investigate assembly rules underlying community compositions, whether it is the biotic or abiotic processes, is the null model approach (Götzenberger et al., 2012). The null model approach allows generating random communities using an assumed species pool that is taught to represent a “null model”. Comparing observed values of functional diversity with expected values calculated from the null model approach can remove trivial effects of species richness (Mason et al., 2013). Here, the null model refers that any patterns present in those randomly generated communities can only be a product of chance alone. A more detailed definition for ecological null models was made by Gotelli & Graves (1996):

“A null model is a pattern-generating model that is based on randomization of ecological data or random sampling from a known or imagined distribution. The null model is designed concerning some ecological or evolutionary process of interest. Certain elements of the data are held constant, and others are allowed to vary stochastically to create new assemblage patterns. The randomization is designed to produce a pattern that would be expected in the absence of a particular ecological mechanism.”

In the early uses, null models were mainly based on presence-absence data, however, recent research predominantly focuses on the abundance-based community data combined with the use of functional traits (Götzenberger et al., 2012). These studies are mainly based on two non-random assembly processes: 1) limiting similarity (MacArthur & Levins ,1967) and 2) environmental filtering (Götzenberger et al., 2016). Which randomization pattern to use when detecting community assemblage processes is discussed since the early usage of null models (Götzenberger et al., 2016). Since the number of possible null models increases with an increasing number of modified parameters of communities, a null model should only randomize the features that are being tested (Gotelli, 2000).

1.3 Functional Approaches in Phytoplankton Studies

Phytoplankton is a diverse polyphyletic group of photosynthetic protists and cyanobacteria. The first phytoplankton, cyanobacteria, was assumed to be appeared around 3 billion years ago (Hedges et al., 2001) and they oxygenated Earth’s atmosphere, making it possible for other life forms to evolve. They are responsible for almost half of the primary production today and community composition affects the cycling of many elements such as carbon, nitrogen, and phosphorus (Falkowski et al., 2004). Because phytoplankton as a group has a great impact on ecosystem functioning and global climate, and climate change will likely change phytoplankton community structure (Litchman et al., 2006), it is crucial to understand underlying phytoplankton community assemblage processes.

Phytoplankton can also be considered to be a model organism for functional research to answer ecologically important questions because of their small size, short generation times, and large population numbers (Litchman & Klausmeier, 2008).

Like any other organism, assemblage studies of phytoplankton were mainly based on taxonomic structure and trait-based functional studies only recently gained more attention. Trait-based functional diversity studies in phytoplankton communities are pioneered by Margelef (1978), who focused on the occurrence of phytoplankton life forms as a response to nutrient and turbulence gradients. Reynolds (1984, 2002) further contributed to the functional approaches to phytoplankton studies by developing a systematic functional group classification. Following their studies, interest in functional group classifications (Kruk & Segura, 2012) and trait-based functional diversity (Weithoff, 2003; Litchman & Klausmeier 2008; Litchman et. al., 2010) of phytoplankton communities became a popular topic.

Weiss and Ray (2019) advocate the selection of traits that are functional for given ecological questions when conducting functional trait analyses. Consequently, the question of how species assemble can also be answered with the correct set of functional traits. Species living in the same community share the same biotic and abiotic space, and naturally have commonalities in their functional trait compositions. However, species occurrence is not solely a result of environmental constraints but also a function of community dynamics. Therefore, to find community assembly rules in phytoplankton communities, the selection of a broad set of functional traits is needed.

The functioning of individual phytoplankton species is mainly determined by their ability in resource acquisition, predator avoidance, or reproduction (Litchman & Klausmeier, 2008). However, those “hard traits” are not easily measured. Instead, “soft traits” that are easily measurable are used as surrogates for hard traits (Lepš et al., 2006). In phytoplankton species, for example, cell size is a good surrogate for the species' ability of resource acquisition (Litchman & Klausmeier, 2008) since it is relatively easier compared to measuring nutrient uptake and metabolism. Therefore, interpretations of available functional diversity metrics depend on the availability of trait values.

1.4 Research Questions in This Study

This thesis aims to answer following questions:

RQ1: Is dispersal a limiting factor for phytoplankton assemblages in Turkish shallow lakes?

RQ2: Are phytoplankton functional traits under the effect of environmental filtering or limiting similarity?

RQ3: What is the relationship between functional traits and environmental gradients?

CHAPTER 2

MATERIALS AND METHODS

2.1 Data

2.1.1 Sampling Sites

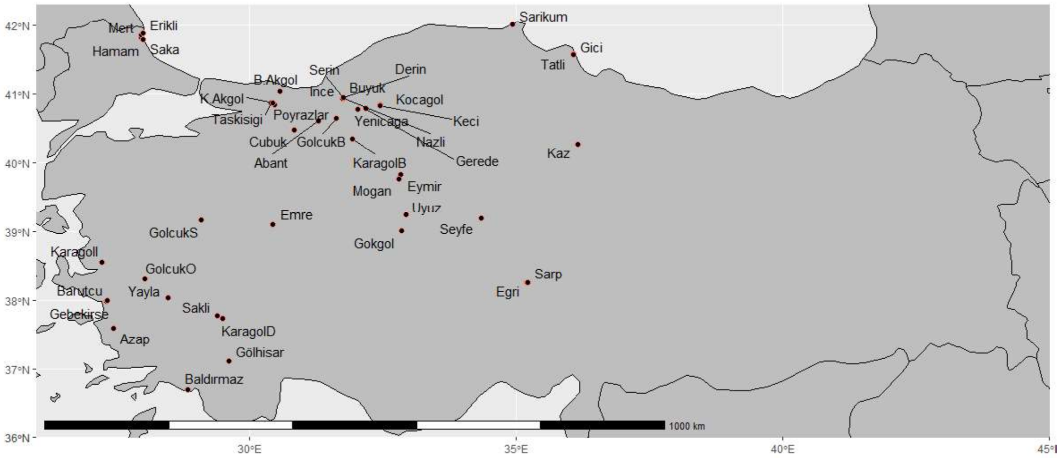


Figure 2. 1 Study lakes on the map of Turkey.

A total of 44 lakes were sampled during the growing season between July – August 2007 – 2013 following a snapshot sampling protocol described by Moss et. al. (2003). (See Figure 2.1) For detailed sampling protocol and analyses see (Beklioğlu et al., 2020; Levi et al., 2014, Çakıroğlu et al., 2014; Erdoğan et al., 2021)

2.1.1.1 Biological and Environmental Variables

The size of lakes in this study ranged between 0.1 – 635.0 ha and maximum depth ranged between 71.7 – 1740.0 cm, mostly dominated by shallow lakes with a total mean depth of 93.7 cm (Table 2.1). Study lakes are mostly freshwater but have 9 lakes ranging from slightly saline(eg. Lake Eğri 1.5‰) to highly saline (eg. Lake Mert 14.5‰) (Beklioğlu et al. 2020). The productivity of the lakes also has a large scale with resources total phosphorus (TP) (15.0-632.6 μg L^{-1}) and total nitrogen (TN) (238.8-2340 μg L^{-1}). Other biotic and abiotic variables of the study lakes can be seen in Table 2.1. ((Beklioğlu et al., 2020; Levi et al., 2014, Çakıroğlu et al., 2014; Erdoğan et al., 2021)

Table 2. 1 Main biotic and abiotic variables of study lake (n=44) ((Beklioğlu et al., 2020; Levi et al., 2014, Çakıroğlu et al., 2014; Erdoğan et al., 2021)

Variables	**Range**	**Mean**	**Median**
Area (ha)	0.1 - 635.0	74.5	20.0
Temperature (°C)	8.3 - 32.2	22.5	23.3
pH	6.3 - 9.5	8.2	8.0
Salinity (‰)	0.0 - 14.5	1.2	0.3
Secchi Depth (cm)	20 – 900	133.6	97.5
Mean Depth (cm)	71.7 - 1740.0	393.7	330.0
Chl-a (μg L^{-1})	1.8 - 181.1	29.1	14.4
PVI (%)	0 - 79.9	21.2	9.1
Fish Biomass (number of fish net^{-1} $night^{-1}$)	0 – 1425	170.1	54.0
TP (μg L^{-1})	15.0 - 632.6	120.8	85.6
TN (μg L^{-1})	238.8 - 2340.0	1075.2	972.9
Zooplankton Biomass (μg L^{-1})	0 - 978.3	46.4	9.8

2.2 Estimation of Dispersal

To test if dispersal is a limiting factor in species assemblages, species abundances and longitude-latitudes information of lakes were transformed into pairwise distance matrices. Latitude-longitude information turned into geographic distances using the Haversine formula that accounts for the spherical shape of Earth. Geographic distances are calculated using the distm function in the *geosphere* package in R. For community distances, abundance data are transformed into a pairwise dissimilarity matrix. Bray-Curtis dissimilarity is used as a dissimilarity metric to obtain community distances vegdist function in the vegan package. A Mantel test with 9999 permutations was used to explore the relationship between distance matrices.

The Mantel test is a correlation test that measures the correlation between two matrices which are commonly geographic distances and community dissimilarity matrices in ecology. To calculate the correlation, non-redundant portions of matrices are transformed into one long column vector and use permutations are used to determine the significance of the test. A significant Mantel test indicates distances in one matrix are related to distances in another matrix which indicates dispersal limitation if matrices are correlated. Mantel test conducted with mantel function from *vegan* package in R.

To further support the Mantel test results, multiple regression on distance matrices (MRM) was performed between geographic distance and community dissimilarity matrices. MRM was conducted using the MRM function from the *ecodist* package in R.

2.3 Trait Selection and Construction of Species-Trait Matrix

The selection of phytoplankton functional traits to construct a species-trait matrix for this study followed the suggestions in the literature (see below). Environmental filtering and limiting similarity via trait convergence and/or divergence were investigated with a total of 13 functional traits (Table 2.3) that included biological form as (1) unicellular, (2) filament, (3) colonial, (4) silica demand, (5) presence of mucilaginous sheath, (6) capacity for nitrogen fixation, (7) capacity to reproduce sexually, (8) capacity to produce toxins, motility ability as (9) presence of flagella or (10) gas vesicles, (11) capacity for mixotrophy, and size-related traits as (12) length and (13) width.

All chosen functional traits can be grouped under 3 major ecological functions of phytoplankton that are reproduction, resource acquisition, and/or predator avoidance as seen in Table 2.2. (Litchman & Klausmeier, 2008).

Table 2. 2 Phytoplankton functional traits used in the study with their units and related ecological functions

Traits		**Scale**	**Related ecological functions**		
			Reproduction	**Resource acquisition**	**Predator avoidance**
Life form	Unicellular	Binary		×	×
	Filament	Binary		×	×
	Colony	Binary		×	×
Silica demand		Binary		×	
Nitrogen fixation		Binary		×	
Mucilage		Binary		×	×
Sexual reproduction		Binary	×		
Toxin production		Binary			×
Size	Length	Continuous	×	×	×
	Width	Continuous	×	×	×
Motility	Flagella	Binary		×	×
	Gas vesicles	Binary		×	×
Mixotrophy		Binary		×	

All traits were measured as a binary trait variable except size-related traits, which were on a continuous scale. Continuous size traits (length, width) are standardized between 0 -and 1 before statistical analyses to make each trait comparable with the other. Information to build a species-trait matrix for binary traits was gathered from the literature (see below).

Since the smallest identification level for phytoplankton was the genus in the dataset, traits showing differences in their trait values within the genus are scored for the majority of the genus of interest.

A representation of the species trait matrix can be seen in Table 2.3. A list of resources and a complete list of trait values of the final species-trait matrix are presented in Appendix 1.

Table 2. 3 Species trait matrix representation

	Trait 1	Trait 2	Trait 3	Trait 4	Trait 5	Trait x
Species 1	1	0	0	0	0	….
Species 2	0	0	0	1	0	….
Species 3	0	0	1	1	0	….
Species 4	1	1	1	1	1	….
Species 5	1	1	1	0	1	….
Species x	….	….	….	….	….	….

2.3.1 Life Form

The life form was evaluated in three different categories as unicellular, colony, and filament forms. Coenobia formations are considered under the colony trait and pseudofilaments formations are considered under the filament trait. Any genus that can be found as different life forms simultaneously is scored for both life forms. If a genus is mainly dominated by a single life form and only a few species can exist in different forms, the only dominant life form is scored.

2.3.2 Silica Demand

Silica demand trait allows the separation of diatoms and Chrysophytes from other groups of phytoplankton (Reynolds 2006). Also, the presence of silica increases the specific weight and causes them to sink faster, causing higher sedimentation rates (Weithoff, 2003).

2.3.3 Nitrogen Fixation

Phytoplankton with the ability to fix atmospheric nitrogen possesses a competitive advantage under nitrogen limiting conditions (Weithoff, 2003). Cyanobacteria is the only group that possesses this ability (Herrero & Flores, 2008), however, not all cyanobacteria are nitrogen fixers. Nitrogen fixers can be present in unicellular and filamentous forms and filamentous forms of nitrogen fixation occur in specialized cells that are called heterocysts (Berman-Frank et al., 2007). Under limited nitrogen conditions, the presence of nitrogen fixers may increase the nitrogen availability in the water column for other phytoplankton groups too (Litchman & Klausmeier, 2008).

2.3.4 Presence of Mucilage

Mucilage is a polymer of carbohydrates and is a substance resembling acrylic (Reynolds, 2007). The presence of mucilage can reduce sinking rates, help some phytoplankton (e.g. raphe-bearing diatoms) in movement, assist spore dispersal, prevent bacterial infection, and provide adhesion (Boney, 1981). Mucilage also provides chemical and mechanical defense against grazing or predators (Margalef, 1978), helps digestion, and provides resistance to metal poisoning (Reynolds, 2007). Generally, the presence or absence of mucilage is taxon-dependent but when grown in culture, some phytoplankton (especially Cyanobacteria) stop the production of mucilage proving that the presence of mucilage is also responsive to the environment (Reynolds, 2007).

2.3.5 Sexual Reproduction

Some phytoplankton groups (e.g, diatoms, dinoflagellates, and green algae) can reproduce both sexually and asexually depending on the environmental conditions (Hiltz et al 2000), while other groups (e.g., cyanobacteria, cryptophytes) can only reproduce asexually (Sandgren 1988). Sexual reproduction increases genetic variation and becomes advantageous for changing environments with selection pressure (Lynch et al 1991). In this study, the ability to reproduce sexually was scored for genus level.

2.3.6 Toxin Production

Toxin production is considered as a grazing resistance trait (Litchman et al 2010) and phytoplankton species that produce toxins lower the water quality and negatively affect higher trophic levels (Litchman & Klausmeier 2008).

2.3.7 Size

For individual cells phytoplankton size can range from 1 µm to 1 mm, suggesting a highly diverse selection pressure (Litchman et al., 2009). Phytoplankton with smaller cell sizes sinks slower, have higher rates of nutrient acquisition, and higher maximum growth rates but have limited nutrient transport due to smaller diffusion boundary layer (Litchman et al., 2010), and are more prone to grazing (Thingstad et al., 2005). Moreover, body size and distribution in phytoplankton communities can give insights into many environmental factors such as trophic state, and predation (Litchman et al., 2010). Consequently, size is considered a “master trait” for phytoplankton since it maintains various physiological and morphometric features (Weithoff & Beisner, 2019).

Size data used in this study was taken from Erdoğan (2016)

2.3.8 Motility

The motility trait allows phytoplankton to migrate into favorable paths in the water column and oppose sedimentation (Weithoff, 2003). Motility can also decrease grazing pressure on phytoplankton (Margalef, 1978). In the study, the motility trait was investigated under two different traits as having flagella and the presence of gas vesicles.

2.3.9 Mixotrophy

Mixotrophic phytoplankton can combine both autotrophic and heterotrophic modes of nutrition (Jones, 1994). Mixotrophy is a generalist strategy that gives a competitive advantage under low nutrient conditions (Troost et al., 2005) and many phytoplankton that have the ability for mixotrophy are poor competitors for inorganic nutrients (Laybourn-Parry et al., 2005). In the construction of species-trait matrix, the phytoplankton genus was considered as mixotrophic if there is evidence in the literature for its ability of phagotrophy.

2.4 Community Weighted Mean (CWM) and Rao's Q as a measurement for Functional Diversity

Many researchers claimed that the most appropriate way to relate community structure to ecosystem functioning comes from the range and distribution of single trait measurements (e.g., Garnier et al., 2004; Lepsˇ et al., 2006; Lavorel et al., 2008; Ricotta & Moretti, 2010). CWMs (Garnier et al., 2004) and Rao coefficient (Leps et. al., 2006) are two methods suggested as an efficient functional diversity index for ecological research. Ricotta & Moretti (2011) discussed that these two measurements are complementary to each other and represent different aspects of functional traits within a community as “mean” and “dispersion” of a trait value, respectively. They suggest that within a community, while CWMs measure the weighted mean of single trait values and summarize the shifts between traits, Rao coefficient Q quantifies and summarizes the trait divergence/dispersion.

Rao’s Q or Rao coefficient gained importance as an efficient index for functional diversity because it is easy to understand and applies to various dissimilarity measures (Lepš et al., 2006). Rao coefficient estimates functional diversity as:

$$Q = \sum_{ij}^{S} d_{ij} \times p_i \times p_j$$

Where Q is Rao coefficient, d_{ij} is the dissimilarity between species i (i = 1, 2, 3, …, S) and j (j = 1, 2, 3, …, S), p_i and p_j are the relative abundances of species i and j, respectively. In this study, not species but genera were used as a unit.

CWM, proposed by Garnier et al. (2004), measures the distribution of a single trait value in an assemblage. CWM can be calculated by the formula as follows:

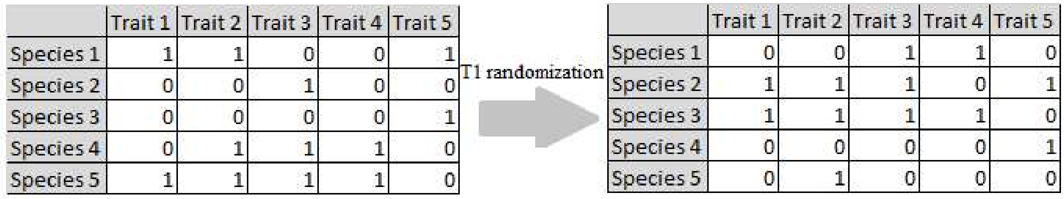
$$CWM = \sum_{i=1}^{S} p_i \times x_i$$

Where CWM is the weighted mean of the trait value, p_i is the relative abundance of the species i (i = 1, 2, 3, …, S), and x_i is the trait value for species i. For single trait measurements, CWM for a binary trait is simply the abundance of the given species (x_i = 1).

In this study, CWMs and Rao coefficient were used simultaneously. CWM is used when investigating trait distributions and Rao coefficient is used when investigating trait divergence or convergence. All measurements for the Rao coefficient and trait CWMs were conducted in the R environment. CWMs were calculated with functomp function in package *FD*. Q calculated with Rao.diversity function in the *SYNCSA* package.

2.5 Null Models

Any chosen functional diversity (FD) metric is correlated to the species richness (SR) of a given community. This is because the addition of a new species to the community will increase FD or have no effect on it while SR of that community will always increase with the addition of a new species. Comparing two communities with any given metric of FD, if they have very different FD values, one can not make sure if the difference is arising from communities having very different SR values or if the difference is really a result of different functional properties of the community. Even FD metrics that are based on pairwise calculations which are designed to be independent of SR such as Rao’s Q, somewhat have bias related to SR values (Swenson, 2014). Thus, instead of using raw values of Rao’s Q, standardization is needed. That standardization can be made using a null model approach.



	Trait 1	Trait 2	Trait 3	Trait 4	Trait 5
Species 1	1	1	0	0	1
Species 2	0	0	1	0	0
Species 3	0	0	0	0	1
Species 4	0	1	1	1	0
Species 5	1	1	1	1	0

	Trait 1	Trait 2	Trait 3	Trait 4	Trait 5
Species 1	0	0	1	1	0
Species 2	1	1	1	0	1
Species 3	1	1	1	1	0
Species 4	0	0	0	0	1
Species 5	0	1	0	0	0

Figure 2. 2 Schematic representation of T1 randomization (Götzenberger et al. 2016) procedure.

Here, the randomization method used in the study becomes an important decision. Many different randomizations are used in community assemblage studies using null models with functional traits. In this thesis, the T1 randomization (see Figure 2.3) algorithm suggested by Götzenberger et. al. (2016), was used for the null model construction. In T1 randomization only trait values are randomized across species while species richness and abundances are fixed between communities. This randomization method allows the detection of both trait convergence via environmental filtering and trait divergence via limiting similarity (Götzenberger et al., 2016).

During the null model construction with T1 randomization, the first 999 communities assembled randomly. Phytoplankton abundance data instead of presence-absence data was used in randomization. Since the calculation of functional diversity from multiple traits can create a variety of complications (Mason et al., 2013), and habitat filtering and limiting similarity may cause traits to respond differently to those processes with convergence or divergence in their values (Lhotsky, 2016) functional diversity (Rao's Q) for 999 randomized communities is calculated separately for each trait.

For each trait, a standardized effect size (SES) is calculated from the randomized null communities. Since the distribution of the Rao's quadratic entropy is often highly right-skewed (Lhotsky et al., 2016), SES values are calculated as suggested for skewed data by Swenson (2014) as follows:

$$SES = \frac{observed - median(null)}{sd\ (null)}$$

Where SES is the standardized effect size and is calculated by dividing the difference between the observed value and median of the expected null value by the standard deviation of the null model. To understand assembly processes in phytoplankton calculated SES values are used instead of raw Rao's Q values.

Significant departures from 0 in trait SES values are tested with the Wilcoxon test since the distribution of SES values was generally non-normal in the dataset. Here, positive departures from 0 indicate trait divergence (limiting similarity) while negative departures indicate trait convergence (environmental filtering). Then, since the dominant assembly rule can change along with environmental gradients, trait SES values are plotted against environmental variables. To reveal the direction of changes in SES values, linear regression models were used.

2.6 Exploring Trait-Environment Relationships with Redundancy Analysis

Ordination is a collective term for multivariate analyses which arrange sites as points along with two-dimensional space. Species ordination in ecology aims to arrange points in a such way that points that are close to each other correspond to sites that are close to each other in species composition. The resulting diagram is a summary of data in two dimensions (two axes).

In this study, ordination methods are used to reveal the relationship between different environmental variables and trait compositions (CWMs). A detrended correspondence analysis (DCA) was conducted on environmental data to decide which ordination method to use. Since DCA axis lengths are <3, an RDA with CWMs and environmental variables is used. Colinearity was tested using the variance inflation factor (VIF). Model selection was made with backward and forward selection using the ordiR2step function from the vegan package in R. The first two axes of RDA are used to study trait distribution patterns (CWMs) and trait SES values using linear regression. DCA and RDA are conducted using the functions in the vegan package in R.

CHAPTER 3

RESULTS

3.1 Phytoplankton Taxonomic Composition

A total of 85 different genera were recorded in 44 lakes. Lakes were grouped as mesotrophic (6), eutrophic (32), and hypereutrophic (6) according to the trophic state index (TSI) classification (Carlson, 1977; Carlson & Simpson, 1996).

Seven main phyla with the abundances of genera in each lake are presented in *Figure 3.1*. In total, *Cyanobacteria* abundance contribution was high in eutrophic and hypereutrophic lakes. However, there were a small number of eutrophic and hypereutrophic lakes that are dominated by *Cryptophyta*, *Chlorophyta*, or *Bacillariophyta* instead of cyanobacteria (i.e. Lake Seyfe). Also, some mesotrophic lakes have high *Cyanobacteria* contribution in abundance (i.e. Lakes B. Akgol, Poyrazlar) (Figure 2.1).

Seven main phyla with the number of occurring genera in each lake are presented in *Figure 3.2*. Diatoms and green algae were the most diverse phyla in terms of the number of genera in mesotrophic lakes. In eutrophic and hypereutrophic lakes, *Cyanobacteria* as an addition to the former two groups were seen as diverse in genera. However, the most diverse phyla in terms of several genera are not always the most abundant phyla too (Figure 3.2).

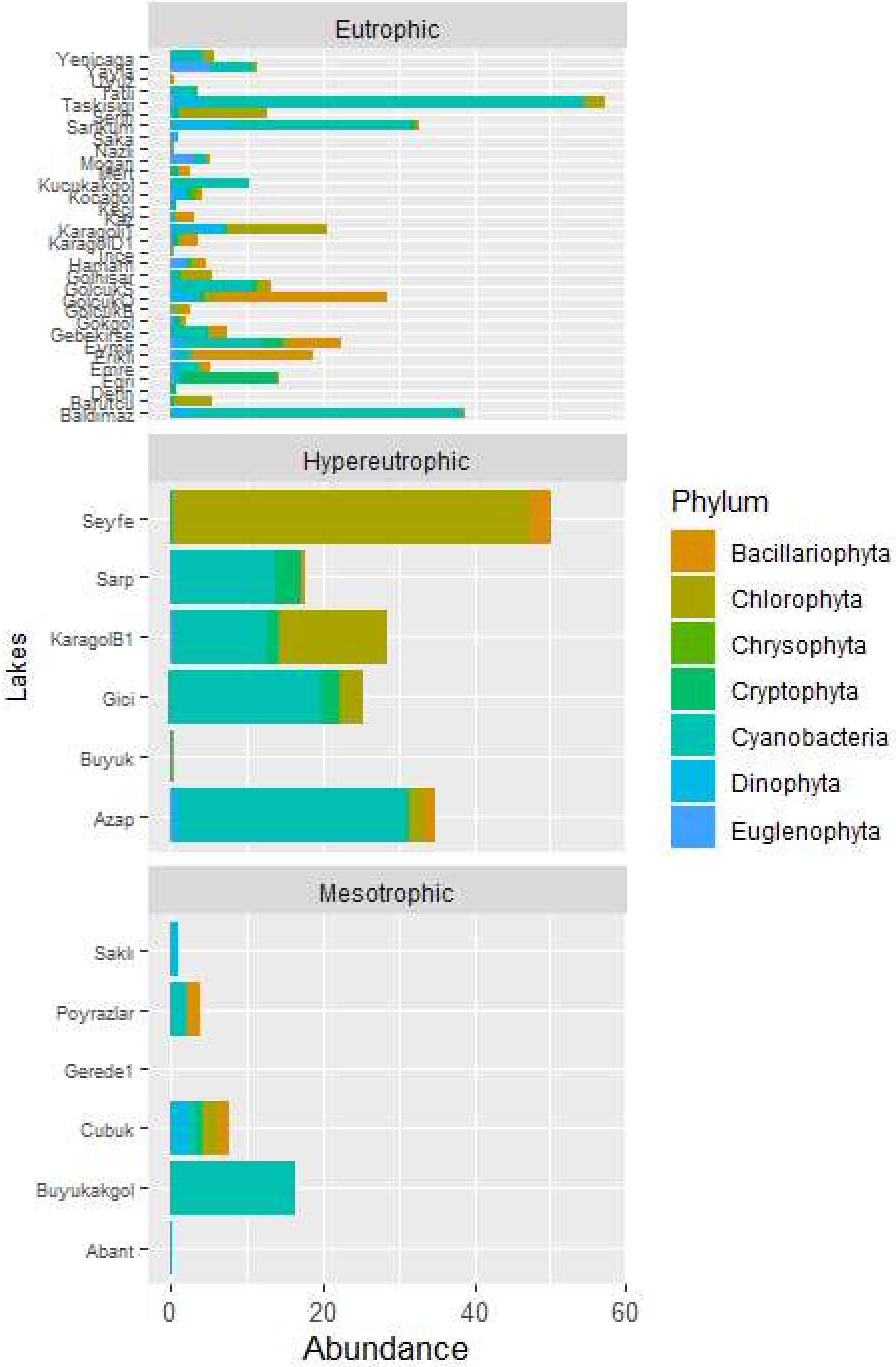


Figure 3. 1 Abundance distributions of phytoplankton phyla in studied lakes grouped by productivity

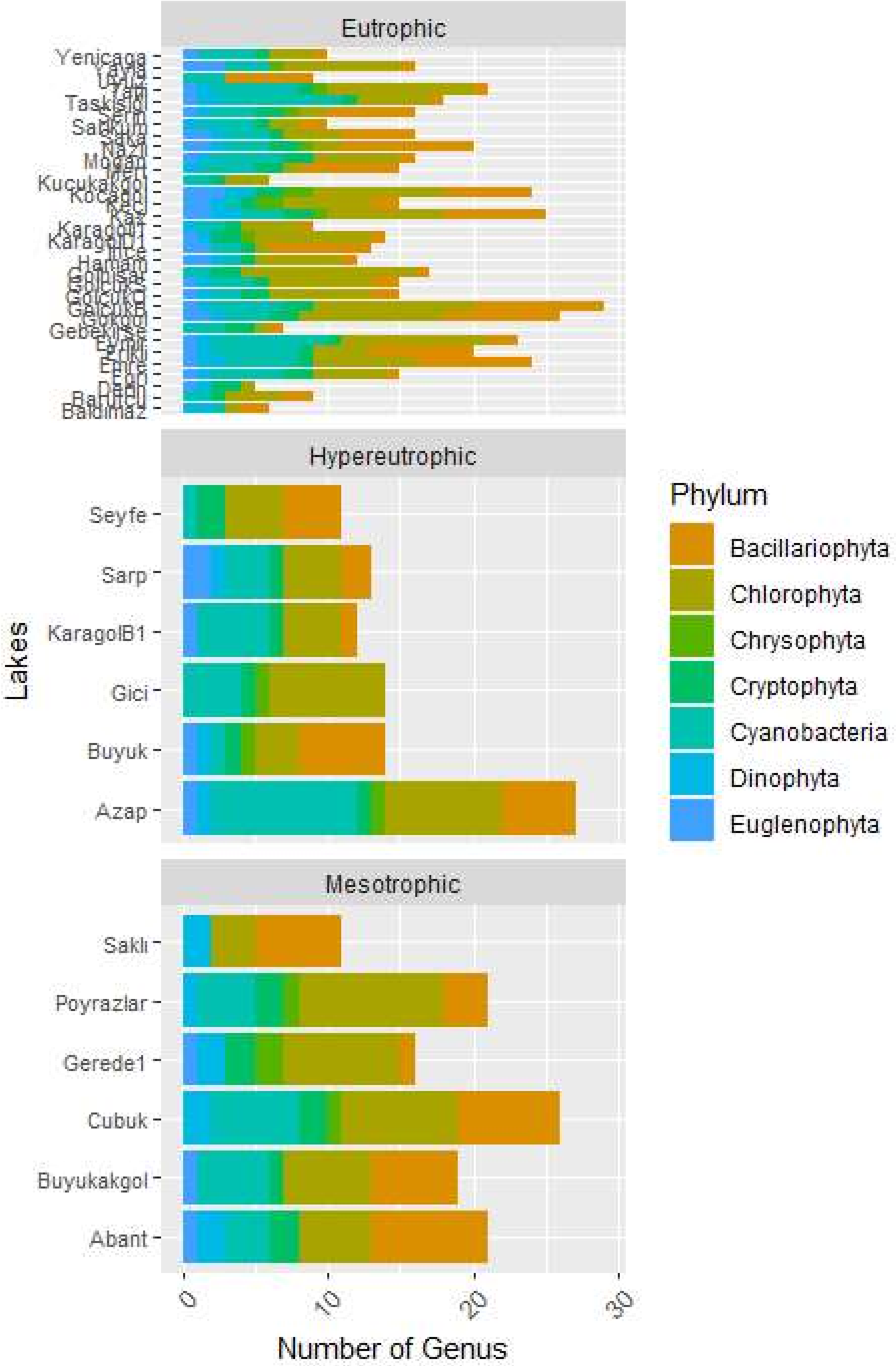


Figure 3. 2 Number of genera distribution of the phyla among the lakes grouped by productivity

3.2 Dispersal

The results of the Mantel test show no significant correlation between community distances (Bray-Curtis dissimilarity matrix) and geographic distances (Mantel statistic R= 0.025, p-value = 0.333). To further support the Mantel test results, a multiple regression on two distance matrices (community distance matrix and geographic distance matrix) was applied. The result of the regression supported the results of the Mantel test (R-squared = 0.0008, p-value = 0.542) on insignificant decay in similarities with increasing geographic distance. Therefore, like lakes, hence phytoplankton communities became geographically more distant, and communities in corresponding lakes didn't become more dissimilar (Figure 3.3). In other words, dispersal in studied lakes is not a limiting factor in the similarity between communities.

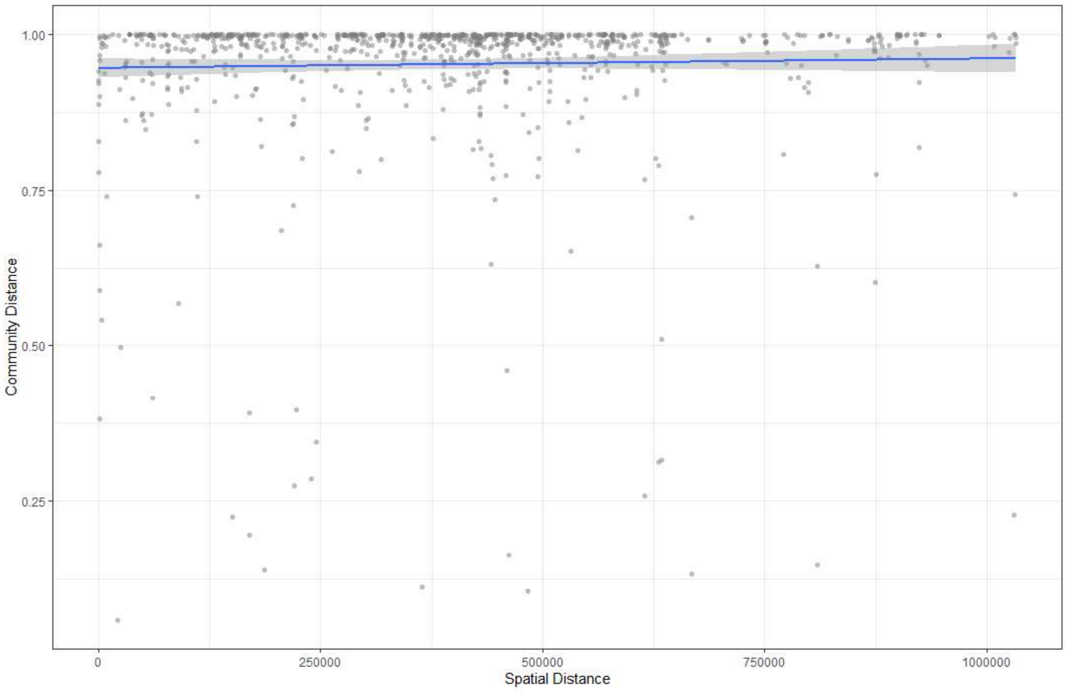


Figure 3. 3 Results of Mantel test between community dissimilarity(Bray-Curtis dissimilarity) and spatial distance(km). Each point represents a pairwise distance between lakes. The blue line indicates the linear regression line (r = 0.025, p = 0.325).

3.3 Phytoplankton Trait Distribution

Percentage distributions of trait values can be seen in Table 3.1.

Among the binary traits, the most abundant ones in the dataset were unicellularity with a 61.2% distribution followed by the presence of mucilage (58.4%) and the formation of colonies (47.1%). The least abundant binary traits were the ability to fix nitrogen (10.7%), the presence of gas vesicles (11.9%), and the presence of flagella (14.3%).

Length trait ranged between 2.5 – 335.6 micrometers with a mean of 66.9 micrometers, width trait ranged between 1.5 – 115.7 micrometers with a mean of 13.5 micrometers.

Table 3. 1 Trait distributions in dataset

Traits		Distribution of the trait values in dataset (%)
Life form	**Unicellular**	61.2
	Filament	27.1
	Colonial	47.1
Silica demand		32.9
Nitrogen fixation		10.7
Mucilage		58.4
Sexual reproduction		46.4
Toxin production		14.6
Size	**Length**	-
	Width	-
Motility	**Flagella**	14.3
	Gas vesicles	11.9
Mixotrophy		15.3

3.4 Distribution of Standardized Effect Sizes (SES) Compared to Null Model

Results of the Wilcoxon test showed that except for the traits related to filament formation, having the ability to reproduce sexually, and the width of phytoplankton, SES values were significantly different than 0 ($p<0.05$) compared to the null model, indicating non-random distribution (Table 3.2, Figure 3.4).

Table 3. 2 Distribution and significance levels of the trait standardized effect size (SES) values calculated from the null model.

Traits		Distribution of the SES values			
		Mean	Distribution of negative values (%)	Distribution of positive values (%)	Level of significance (Wilcoxon test)
Life form	**Unicellular**	-0.376	**65.9**	34.1	**0.029**
	Filament	-0.263	56.1	43.2	0.154
	Colonial	-0.349	**63.6**	36.4	**0.031**
Silica demand		-0.466	**68.2**	29.5	**0.012**
Nitrogen fixation		0.695	25.0	**68.2**	**0.001**
Mucilage		-0.330	**68.2**	29.5	**0.005**
Sexual reproduction		-0.229	63.6	36.4	0.203
Toxin production		0.435	38.6	**59.1**	**0.037**
Size	**Length**	-0.378	**63.6**	36.4	**0.014**
	Width	0.047	54.5	45.5	0.894
Motility	**Flagella**	0.690	22.7	**72.7**	**0.000**
	Gas vesicles	0.491	43.2	**52.3**	**0.047**
Mixotrophy		0.658	27.3	**65.9**	**0.000**

For the traits unicellularity (-0.376), formation of colonies (-0.349), having a demand for silica (-0.466), presence of mucilage (-0.330), and length of phytoplankton (-0.378) all have a negative SES means with a higher distribution of negative values (65.9%, 63.6% 68.2%, 68.2%, and 63.6%, respectively), referring to a higher probability of convergence in those traits, indicating environmental filtering is the main force acting on community assemblage. The traits of ability to fix nitrogen (0.695), capability to produce toxins (0.435), having flagella (0.690) and gas vesicles (0.491), and mixotrophy (0.658), all have positive SES means with a higher distribution of positive values (68.2%, 59.1%, 72.7%, 52.3%, and 65.9% respectively), indicating a higher probability of trait divergence, and thus competitive forces are the main driver in the community assemblage.

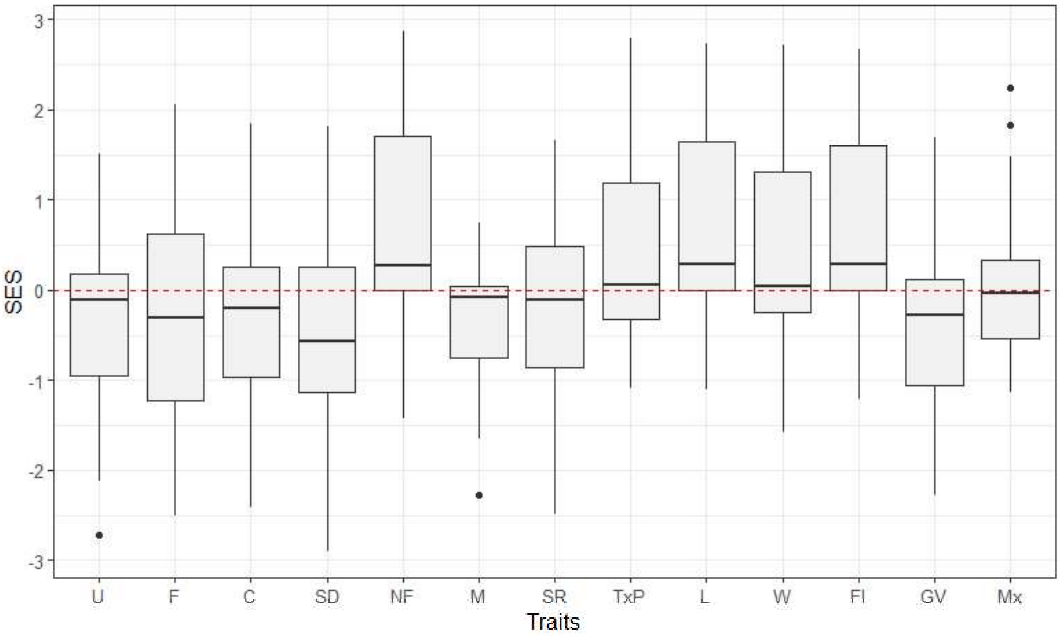


Figure 3. 4 SES distributions of phytoplankton functional traits. The Red line indicates SES=0.

3.5 Trait Community Weighted Means (CWMs) Relationships with Environmental Variables

Results of RDA are shown in Figure 3.3. Overall selected model was significant (Pseudo-F = 4.32, p = 0.001). The first axis was also significant (Pseudo-F = 17.02, p = 0.001), while the second axis was not. The selected best RDA model contained pH, alkalinity, salinity, and TN as explanatory variables that explain variability in response variables.

The first canonical axis (eigenvalue = 3.718, see Table 3.3) describes variation in trait community weighted means (CWMs) approximately at 28.6% (Table 3.3). This axis was negatively associated with TN and pH and positively associated with salinity and alkalinity. Traits that are mostly associated with cyanobacteria (colony formation, nitrogen fixation, toxin production, using gas vesicles as motility apparatus, and presence of mucilage) all positively while unicellularity, mixotrophy, and presence of flagella were negatively correlated to this axis.

Table 3. 3 Summary table of RDA results. Total variation is 13.000, explanatory variables account for 32.5%.

Statistic	RDA1	RDA2
Eigenvalues	3.718	0.366
Explained variation (proportion %)	28.60	2.81
Explained fitted variation (proportion %)	87.99	8.65
Permutation test results		
Global	Pseudo-F = 4.315, p = 0.001	
First axis	Pseudo-F = 17.07, p = 0.001	

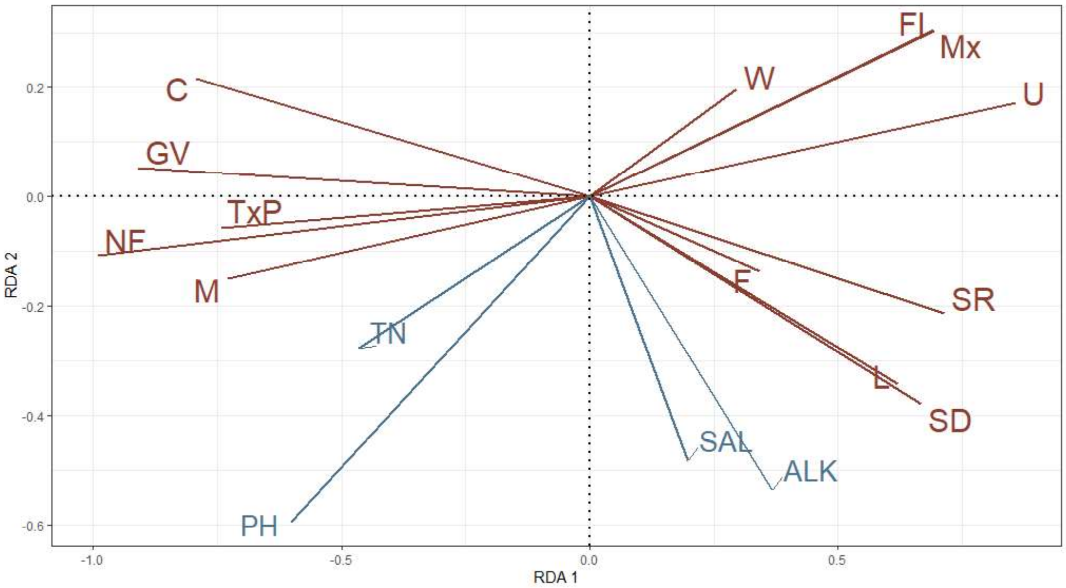


Figure 3. 5 RDA biplot displaying relationships between CWMs of traits and environmental variables. Red arrows represent traits and blue arrows represent environmental variables. For trait; U unicellular, F filament, C colony, SD silica demand, NF nitrogen fixation, M mucilage, SR sexual reproduction, TxP toxin production, L length, W width, Fl flagella, GV gas vesicles, Mx mixotrophy. For environmental variables; TN total nitrogen (µg L-1), PH pH, SAL salinity, ALK alkalinity.

The second axis (eigenvalue = 0.366, see Table 3.3) is uncorrelated with the first axis and explains variation in trait CWM distributions approximately at 2.81%.

Traits coloniality, gas vesicles, flagella, mixotrophy, width, and unicellularity are positively correlated to the second axis. Oppositely, all other traits are negatively correlated with this axis (Table 3.3).

3.6 Standardised Effect Sizes Along Canonical Axes and Environmental Variables

Standardized effect size (SES) values showed various distribution patterns along two canonical axes (Appendix B). Only the SES value of the silica demand trait showed a significant distribution pattern along the first axis. The second axis, however, showed no significant trend. Moreover, permutation test performed on canonical axes showed that the second axis was in fact insignificant.

Figure 3.6 shows selected trait SES values along two canonical axes. Regression lines (see Table 3.4) to show general trends along those axes further supported the null model results on trait divergence or convergence. Unicellularity was highly positively associated with the first RDA axis and regression lines always stayed in the negative region, suggesting the trait convergence along the first canonical axis for the unicellularity trait. Most of the traits highly associated with the first axis were traits that suggested divergence (i.e. nitrogen fixation, toxin production, flagella, gas vesicles, mixotrophy). Trend lines for nitrogen fixation and gas vesicles traits were also in the positive region, further supporting divergence for those traits.

Sexual reproduction, which is one of the three traits that did not show significant deviance from the null model showed a decreasing trend along the first axis. However, the trend line started in the positive region but passed into the negative region at higher values of the axis.

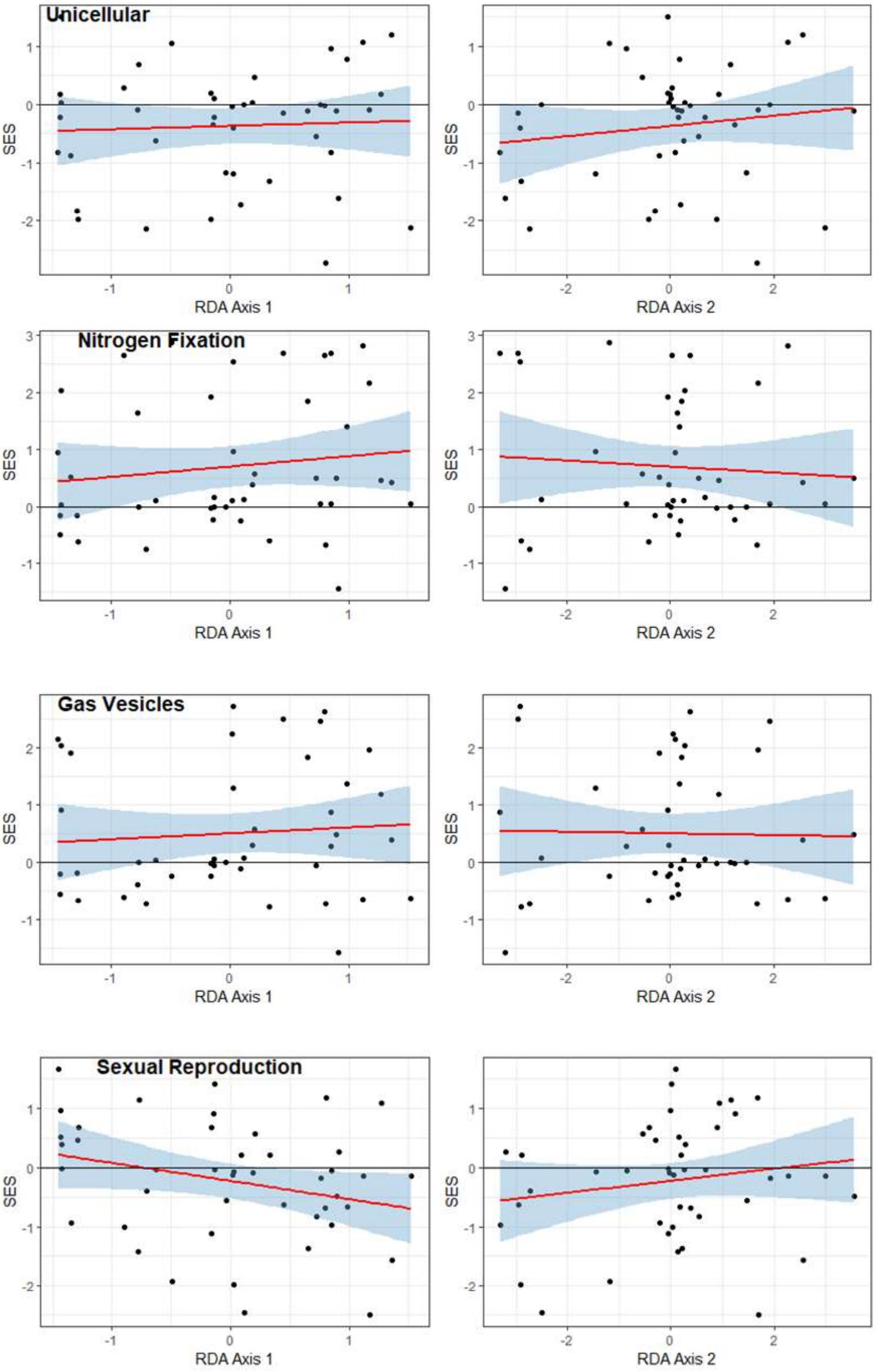


Figure 3. 6 Standardised effect size (SES) values of selected trait trends along two canonical axes. The thin black line indicates SES = 0. Values below this line indicate trait convergence while the above points indicate trait divergence. Each blue dot represents the SES value of the sampled lake. Red trend lines are based on linear regression models. The blue color shows 95% confidence intervals.

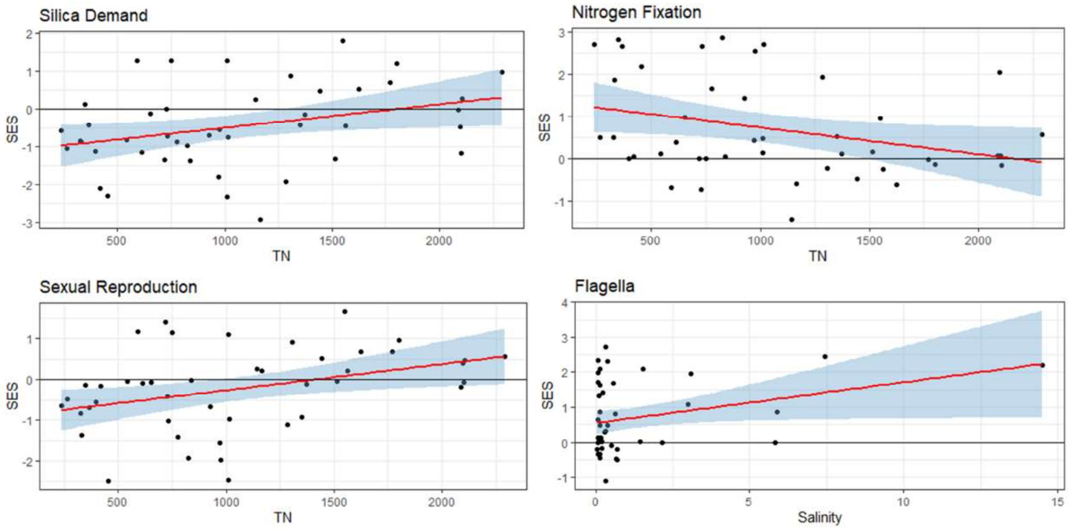


Figure 3. 7 Significant regression lines of trait SES values along with environmental variables

SES value distributions along with environmental variables were also studied. However, even though some environmental variables were correlated with the canonical axes, most of the trait distributions did not display significant trends along with those environmental variables when they were modeled separately (Table 3.6, Appendix C).

Significant SES values along environmental variables are presented in Figure 3.7. All the other regressions are presented in Appendix C. Silica demand trait along TN gradient showed an increasing trend that passes from negative region to positive region. Nitrogen fixation, on the other hand, showed a decreasing trend along the TN gradient. Sexual reproduction showed an increasing trend along with TN as it did along the first canonical axes. Again, a trend started from the negative region but passed to the positive region with increasing TN concentrations. Another significant trend line was of flagella trait along the salinity gradient.

Table 3. 4 Summary table of linear regressions along environmental gradients and canonical axes. Significant results are written in bold.

Traits	**TN**		**pH**		**ALK**		**SAL**		RDA1		RDA2	
	Adj R2	p-value	Adj R2	p-value	Adj R2	p-value	Adj R2	p-value	Adj R2	p-value	Adj R2	p-value
Unicellular	-0.022	0.802	-0.029	0.669	-0.012	0.480	-0.010	0.454	-0.021	0.740	-0.003	0.351
Filament	-0.024	0.999	-0.022	0.761	0.027	0.145	-0.022	0.785	-0.023	0.876	0.019	0.181
Colony	0.015	0.208	0.022	0.168	0.044	0.092	-0.017	0.597	0.018	0.187	-0.021	0.719
Silica demand	**0.090**	**0.0272**	-0.018	0.629	-0.024	0.954	-0.008	0.424	**0.072**	**0.044**	-0.019	0.649
Nitrogen fixation	**0.078**	**0.0372**	-0.023	0.892	0.013	0.219	-0.009	0.444	-0.004	0.368	-0.018	0.633
Mucilage	--0.016	0.564	-0.023	0.833	-0.024	0.950	0.000	0.315	0.036	0.115	-0.003	0.351
Sexual reproduction	**0.117**	**0.0131**	-0.023	0.835	-0.023	0.890	-0.016	0.573	0.053	0.072	0.005	0.280
Toxin production	0.000	0.323	-0.016	0.573	-0.012	0.485	-0.008	0.416	-0.019	0.678	0.004	0.284
Flagella	-0.022	0.764	-0.023	0.861	-0.002	0.344	**0.071**	**0.044**	0.008	0.250	-0.023	0.854
Gas vesicles	-0.024	0.917	-0.016	0.569	-0.023	0.835	-0.021	0.748	-0.017	0.599	-0.023	0.891
Mixotrophy	-0.019	0.657	-0.024	0.966	0.005	0.279	0.002	0.304	-0.015	0.558	-0.023	0.876
Length	0.030	0.135	-0.024	0.983	-0.017	0.597	-0.019	0.654	0.018	0.189	-0.017	0.600
Width	0.006	0.266	-0.021	0.755	-0.013	0.497	-0.005	0.378	0.044	0.093	-0.007	0.408

CHAPTER 4

DISCUSSION

4.1 Is dispersal a limiting factor in Turkish shallow lakes for phytoplankton assemblages?

The role of dispersal in the assemblage of communities is especially recognized in metacommunity theory (Leibold et al., 2004). In the metacommunity concept, communities are assembled with the effect of two groups of factors that are operating on different scales. Here, dispersal is the regional factor determining the species' coexistence in local communities. At low rates, dispersal becomes a limiting force on species assembly for local communities, preventing species occurrence in available suitable habitats in a region (Ozinga et al., 2005). However, when dispersal rates are higher, the species sorting perspective in the metacommunity concept becomes effective in the assembly of local communities. According to the species sorting perspective, local processes (i.e. environmental filtering, limiting similarity) are the main forces acting on community assembly when dispersal rates are higher.

According to the Mantel test in this study, with increasing distance between lakes, differences in species compositions did not show a meaningful increase. If dispersal was more of importance, the occurrence of species on the sampled lakes should be best explained by their dispersal abilities. Here, the results mean that phytoplankton species in study lakes are not limited by their dispersal abilities. Therefore, the famous saying "everything is everywhere but the environment selects" for microbial taxa (Baas-Becking, L. G. M. 1934) applies to the dataset used in this study. Here, the claim "everything is everywhere" suggests that microorganisms have such immense dispersal capabilities that past evolutionary and ecological events become insignificant in species coexistence and spatial differentiation is prevented.

4.2 Trait divergence and convergence compared to null models

Several theories have been proposed about the possible processes that determine species composition in a community from the global species pool with a series of filters (Keddy 1992; HilleRisLambers et al. 2012). Those processes can be listed as dispersal limitation, environmental suitability, and interactions between coexisting species (Lhotsky et al., 2016).

In our study, dispersal limitation was not a factor that constrains the species' coexistence. This implies that abiotic conditions might be the main driver of which species from the regional species pool can establish, survive and reproduce in the actual community. In this community, species are filtered according to their functional trait values that were adapted to persist in the given habitat. In other terms, abiotic conditions are the limiting factors for possible trait values that can endure in coexisting species in the actual community. This process causes trait convergence in the community and it is called environmental filtering (Keddy 1992).

On the other hand, however, species with the same functional trait ranges, hence overlapping niches, use the same resources in a similar way. According to the competitive exclusion principle (Gause, 1934) species with highly overlapping niches can not coexist in a stable manner. Thus, the interspecific competition inhibits the coexistence of species with highly similar trait values. This limitation causes divergence in trait values is called limiting similarity (MacArthur & Levins 1967).

In this study, standardized effect size (SES) values of most of the traits significantly differed from 0 according to the Wilcoxon test, which indicates convergence and/or divergence of functional traits. SES values significantly lower than zero supported a higher probability of environmental filtering while SES values significantly higher than 0 supported a higher probability of limiting similarity.

The results showed that competitive traits (nitrogen fixation, mixotrophy, motility, and toxin production) successfully showed trait divergence, in other means limiting similarity or competition were dominant assembly rules in phytoplankton communities.

Lakes in the dataset are mostly eutrophic and hypereutrophic, they had high concentrations of phosphorus. In highly productive lakes like those, nitrogen can become the main limiting nutrient instead of phosphorus (Paerl et al. 2016; Shatwell & Köhler, 2018). Under these circumstances, the ability to fix atmospheric nitrogen creates a competitive advantage over the species that don't have this ability (Reynolds et al., 2014).

In his overview of mixotrophy in planktonic protists, Jones (2000) divided them into four groups based on their behavior. In his classification, one group is mainly autotrophic but uses phagotrophy under light-limited conditions. Also, he classifies one more group that takes the benefit of phagotrophy under light-limited conditions but this time different than the first group, they ingest their prey at a very slow rate. The examples each group with *Dinobryon* and *Cryptomonas* species respectively, which were mostly present in the studied lakes. In the dataset used in this study, mixotrophy was found to be under the force of limiting similarity by trait divergence further supports the fact that mixotrophy can provide competitive advantages under certain circumstances like a light limitation. Since most of the studied lakes were under eutrophic conditions, light limitation caused by algal growth might have provided a competitive advantage to *Dinobryon* and *Cryptomonas* species which have the mixotrophic ability.

Both of the motility traits (flagella and gas vesicles) also showed a higher probability of trait divergence. The ability to move upwards or downwards in the water column is available for both modes of motility and it allows phytoplankton species to use light efficiently (Klais et al., 2017). Having flagella additionally provides active movement to phytoplankton and species with flagella can move in other directions in the water column. They can move towards patches with high nutrient amounts or avoid predation by movement. Therefore, both modes of motility provide a competitive advantage over others and both traits show divergence in SES values.

Recent studies show that toxin production in many phytoplankton populations can cause high amounts of toxins to release during an algal bloom (Yu et al, 2017). Moreover, there are several experimental studies showing toxins are causing mortality in non-toxic phytoplankton (Schmidt & Hansen 2001, Windust et al. 1996, Peace et al. 2016). Those studies can imply that toxin production in phytoplankton might give competitive advantages over non-toxic species. In this study, toxin production is one of the traits that showed divergence in trait values. This implies that toxin-producing species may in fact under the effect of limiting similarity during community assemblage.

The presence of silica in the cell wall differentiates diatoms and silicaflagellates from other groups (Litchman & Klausmeier, 2008; Vogt et al. 2010). Since these groups rely on the silica resources available in lakes, it is expected to get the results of convergence for this trait. This result means that the environment acts as a filter when it comes to the species that require silica such as diatoms that were not abundant in most of the studied lakes (Figure 3.1).

Unicellularity, coloniality, and the presence of mucilage can all be considered as traits that provide benefits to species against sinking and resistance to predation. All of those traits were found to be convergent in their trait values, indicating environmental filtering was the acting force in community assembly. Species that bear those traits are filtered in due to the presence of the traits.

Length can be considered as a representation of size trait and it showed convergence in trait values. Acevedo-Trejos et al. (2015) found that size structure in phytoplankton might be related to nutrient uptake, zooplankton grazing and phytoplankton sinking. Size trait being under the effect of environmental filtering implies for the studied communities size traits were not providing a competitive adventage in terms of nutrient uptake, grazing and sinking.

In their study, Borics et al. (2020) discussed that some traits might not give significant results because same traits might be possesed by several algal groups and putting all those groups under the same trait category can couse oversimplification for that trait. The fact that sexual reproduction did not show significant divergence from zero might be because sexual reproduction in phytoplankton can happen in different forms and putting all sexual reproduction forms in the same category might be causing oversimplification.

4.3 Trait Distributions Along Canonical Axes

Among the traits that indicated convergence compared to null distribution, only silica demand showed a significant trend along canonical axes. Other traits indicated convergence i.e. unicellularity, coloniality, presence of mucilage and length showed random distribution along both canonical axes. These result does not directly imply that those traits are neutral. Random distribution along canonical axes might indicate the fact that environmental filtering and limiting similarity can simultaneously act on the same traits and can compensate for each other (Borics et al, 2020) therefore they still might be affected by environmental filtering or limiting similarity. Moreover, recent studies show that competetive interactions, especially intransitive competition, can cause more than convergence in trait values depending on the number of resources that are limiting species fitness (Gallien et al., 2017). In other words, if different phytoplankton are competing over more than one resource (e.g. nutrients and light), competetive interactions might cause convergence or divergence in the functional trait values at the same time. Thus, random distribution of trait values might indicate more complex competitive interactions in the phytoplankton community assembly.

In this study, except for traits length and width were binary traits, meaning that the distance between species can be either 1 or 0. Reducing the variation between trait values to only two values between species can cause oversimplification of the traits. For example, toxins produced by two different species might vary in terms of lethality, but both species get the same trait value, 1, for toxin production rate. Another shortcoming with this method is that, if trait distribution is at 50%, trait divergence can not be distinguished and if the distribution in the dataset is highly unequal, the same can be said for convergence (Borics et al., 2020). Trait distribution of nitrogen fixation, toxin production, flagella, gas vesicles, and mixotrophy was lower than 20% (Table 3.1). For those traits, which all can be counted as competitive traits, divergence was successfully identified compared to the null model. On the other hand, the model simply could not be able to show convergence due to low trait distribution. Moreover, among the traits that showed a close distribution of 50%, that are sexual reproduction (47.1%) and coloniality (46.4%), sexual reproduction did not show a significant difference from the null model (Table 3.2). Here, sexual reproduction, which can also be considered as a competitive trait since it creates genetic variability that can provide a competitive advantage to individuals, might actually be a divergent trait but the model was not able to give significant results because the trait distribution was around 50%.

Most of the SES values did not show significant trends along canonical axes. However, that does not mean those traits are neutral along environmental gradients. Environmental filtering and limiting similarity can act simultaneously on traits and compensate for each other. Therefore, the research question still can be answered.

4.4 Trait Distributions Along Environmental Gradients

Results of the RDA somewhat reflected the eutrophic and hypereutrophic lake domination in the dataset. It is known that in eutrophic lakes, phytoplankton community composition is mostly dominated by cyanobacteria (T. Dokulil et al., 1998). Results of RDA also reflected this domination. If the RDA biplot is evaluated in two parts as left and right (see Figure 3.6), traits on the left side (coloniality, presence of mucilage, toxin production, nitrogen fixation, and movement with gas vesicles) can be associated with cyanobacteria while traits in the left side can be associated with dinoflagellates, euglenoids, cryptophytes and chrysophytes (unicellularity, mixotrophy -by phagotraphy-, movement by flagella) and diatoms (silica demand, sexual reproduction). Cryptophytes and chrysophytes have high metabolic activity and generally prefer to live in oligotrophic environments (Phillips et al., 2013). Dataset used in this study does not have any oligotrophic lakes but Cryptophytes and Chrysophytes were mostly present in the studied lakes (Figure 3.1)

Although freshwater phytoplankton is mostly limited by phosphorus in growth, in lakes with TP > 30 μg l^{-1} and TN: TP < 14 nitrogen limitation occurs frequently (Downing & McCauley, 1992). In the studied database TN: TP ratios varied between 2.75 and 71.11 with a mean of 14.77 and the number of lakes with TP > 30 μg l^{-1} and TN: TP < 14 is 25 out of 44 (Appendix D). This refers to a possible N limitation in the dataset. The nitrogen fixation trait trend decreased significantly along the TN gradient. This implies that with increasing TN concentration the effect of limiting similarity decreases in community assembly. Thus, with increasing TN, the nitrogen fixation trait loses its competitive advantage. The trend line just passes through the SES = 0 value at the end of the gradient (Figure 3.7) which means at higher levels of TN nitrogen fixation starts to get affected by environmental filtering. Along the TN gradient, there were two more significant regression lines. The SES values of silica demand and sexual reproduction were both significantly increased with increasing TN concentration. Both traits started from the negative region and passed through the positive region, meaning the dominant force acting on community assembly in lower TN concentrations is environmental filtering but limiting similarity becomes the main force at higher concentrations.

CHAPTER 5

CONCLUSIONS

In this thesis, first, the effect of dispersal in phytoplankton community assembly was assessed and dispersal limitation was found insignificant in the assembly of local species pool from regional species pool. Then, trait convergence and divergence in phytoplankton assembly were studied with a null model approach using functional diversity as a measure of biodiversity. From the null models constructed, out of 13 phytoplankton traits, 5 of them were found to be under the effect of environmental filtering, 5 of them were under the effect of limiting similarity, and 3 of the traits were found to be not affected by both of the processes. Among the traits under the environmental filtering, most of the traits were associated with *Cyanobacteria*, and traits under the effect of limiting similarity were the traits that provide competitive advantages to phytoplankton species. When the relationships between traits and environmental gradients are studied separately, it is found that traits may be under the effect of different assembly rules or different assembly rules may act on the same traits simultaneously.

This study further supported to idea that functional diversity is a useful method to measure biodiversity and explain processes like community assembly. Studying biodiversity patterns with a functional approach might provide scientists a better understanding and this understanding can be crucial to predicting future communities and conservation approaches under a changing climate.

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APPENDICES

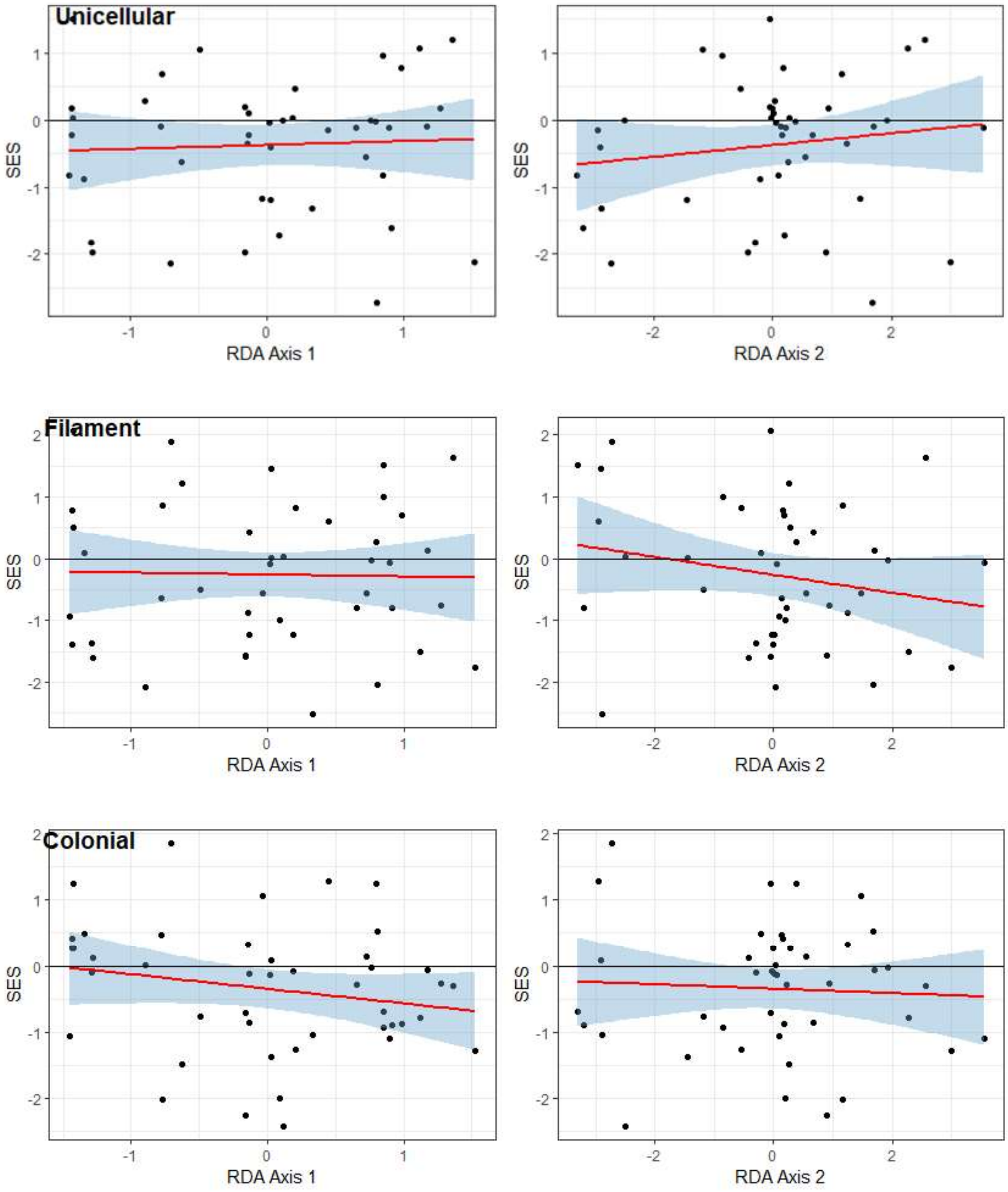
A. Species-Traits Matrix

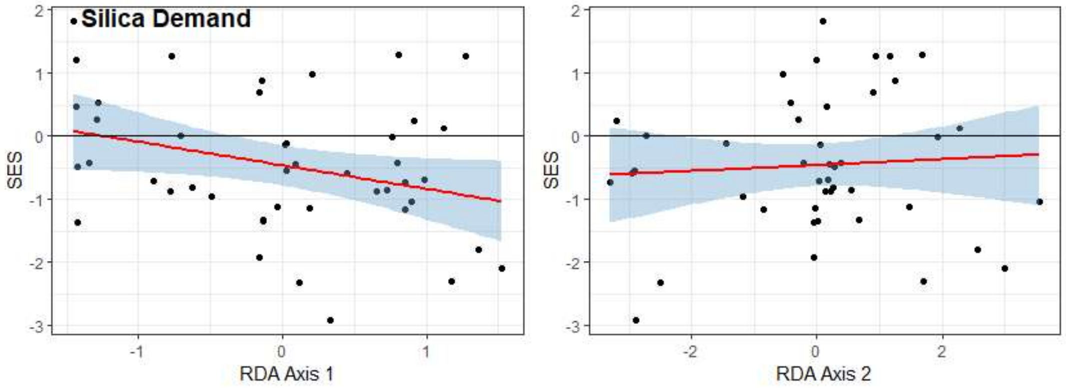
	U	F	C	SD	NF	M	SR	TxP	L	W	Fl	GV	Mx
Achnanthidium	1	0	0	1	0	0	1	0	0.045	0.022	0	0	0
Actinastrum	0	0	1	0	0	1	0	0	0.056	0.035	0	0	0
Amphora	1	0	0	1	0	0	1	0	0.108	0.145	0	0	0
Anabaena	0	1	1	0	1	1	0	1	0.484	0.041	0	1	0
Anabaenopsis	0	1	0	0	1	1	0	1	0.218	0.025	0	1	0
Aphanizomenon	0	1	1	0	1	1	0	1	0.503	0.022	0	1	0
Aphanocapsa	0	0	1	0	0	1	0	0	0.093		0	0	0
Arthrospira	1	0	0	1	0	0	1	0	1.000	0.044	0	0	0
Asterionella	0	0	1	1	0	1	1	0	0.230	0.012	0	0	0
Attheya	1	0	1	1	0	0	1		0.259	0.135			0
Aulacoseria	0	1	1	1	0	0	1	0	0.196	0.049	0	0	0
Boreozonacola	1	0	0	1	0	0	1	0	0.072	0.064	0	0	0
Botryococcus	0	0	1	0	0	1	0	0	0.409	1.000	0	0	0
Caloneis	1	0	0	1	0	0	1	0	0.259	0.199	0	0	0
Carteria	1	0	0	1	0	0	1	0	0.037		0	0	0
Ceratium	1	0	0	0	0	0	1	0			1	0	1
Chlamydomonas	1	0	0	1	0	1	1	0	0.017		1	0	1
Chlorella	1	0	0	0	0	1	0	0	0.000		0	0	0
Chroococcus	1	0	1	0	1	1	0	0	0.031		0	1	0
Closterium	1	0	0	0	0	0	1	0	0.357	0.061	0	0	0
Cocconeis	1	0	0	1	0		1	0	0.065	0.117	0	0	0
Coelastrum	0	0	1	0	0	1	0	0	0.072		0	0	0
Cosmarium	1	0	0	0	0	1	1	0	0.063	0.164	0	0	0
Crucigenia	0	0	1	0	0	1	0	0	0.016	0.053	0	0	0
Crucigeniella	0	0	1	0	0	1	0	0	0.006	0.014	0	0	0
Cryptomonas	1	0	0	0	0	1	0	0	0.066	0.097	1	0	1
Cyclotella	1	1	0	1	0	0	1	0	0.045		0	0	0
Cymbella	1	0	0	1	0	1	1	0	0.202	0.152	0	0	0
Diatoma	0	0	1	1	0	0	1	0	0.127	0.124	0	0	0
Dictyosphaerium	0	0	1	0	0	1	1	0	0.013		0	0	0
Dinobryon	1	0	1	1	0	0	1	0	0.052	0.063	1	0	1
Epithemia	1	0	0	1	0		1	0	0.152	0.122	0	0	0
Euastrum	1	0	0	0	0	0	1	0	0.048	0.131	0	0	0
Euglena	1	0	0	0	0	0	1	0	0.248		1	0	1
Fragilaria	0	0	1	1	0	0	1	0	0.666	0.137	0	0	0

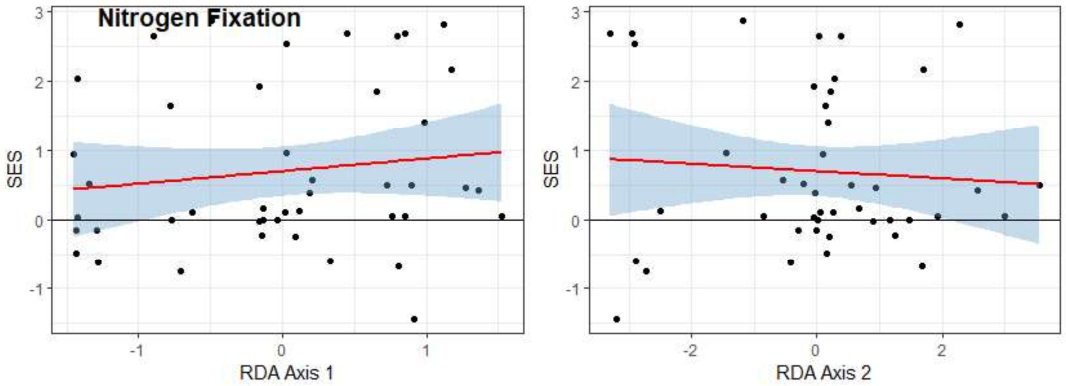
Glaucospira	0	1	0	0	0	1	0	0	0.102	0.007	0	0	0
Gloeocystis	1	0	1	0	0	1	0	0	0.040	0.117	0	0	0
Golenkinia	1	0	0	0	0	1	0	0	0.034		0	0	0
Gomphonema	1	0	0	1	0	1	1	0	0.106	0.090	0	0	0
Gomphosphaeria	1	0	1	0	0	1	0	0	0.035	0.047	0	0	0
Gonatozygon	1	1	0	0	0	1	1	0	0.644	0.058	0	0	0
Gymnodinium	1	1	1	0	0	0	1	1	0.116	0.283	1	0	1
Gyrosigma	1	0	0	1	0		1	0	0.471	0.172	0	0	0
Jaaginema	0	1	0	0	0	1	0	1	0.492	0.006	0	0	0
Kirchneriella	1	0	1	0	0	1	0	0	0.024	0.014	0	0	0
Komvophoron	0	1	1	0		1	0		0.137	0.008	0	0	0
Lagerheimia	1	0	1	0	0	1	0	0	0.023	0.040	0	0	0
Leptolyngbya	0	1	1	0	0		0		0.289	0.000	0	0	0
Limnotrix	0	1	0	0	0			0	0.543	0.004	0	0	0
Lyngbya	0	1	1	0	1	0	0	1	0.803	0.102	0	0	0
Mallomonas	1	0	0	1	0	0	1	0	0.060	0.077	1	0	1
Melosira	0	1	1	1	0	1	1	0	0.390	0.061	0	0	0
Merismopedia	0	0	1	0	1	1	0	0	0.007	0.021	0	0	0
Micractinium	0	0	1	0	0	1	0	0	0.014		0	0	0
Microcystis	0	0	1	0	1	1	0	1	0.025		0	1	0
Monoraphidium	1	0	0	0	0	0	0	0	0.143	0.007	0	0	0
Navicula	1	0	0	1	0		1	0	0.138	0.083	0	0	0
Nitzschia	1	0	1	1	0	1	1	1	0.181	0.028	0	0	0
Oocystis	1	0	1	0	0	1	0	0	0.031	0.066	0	0	0
Oscillatoria	0	1	1	0	1	0	0	1	0.643	0.053	0	1	0
Pediastrum	0	0	1	0	0	0	0	0	0.081	0.241	0	0	0
Peridiniopsis	1	0	0	0	0	1	1	0	0.095	0.233	1	0	1
Peridinium	1	0	0	0	0	0	1	0	0.086	0.227	1	0	1
Phacus	1	0	0	0	0	0	0	0	0.129	0.280	1	0	1
Phormidium	0	1	1	0	1	1	0	1	0.617	0.024	0	1	0
Planctonema	0	1	0	0	0	1	0	0	0.252	0.040	0	0	0
Planktolyngbya	0	1	0	0	0	1	0	0	0.228	0.005	0	0	0
Planktothrix	0	1	0	0	0	0	0	1	0.650	0.043	0	1	0
Pseudoanabaena	0	1	1	0	0	1	0	0	0.247	0.004	0	1	0
Rhodomonas	1	0	0	0	0	0	0	0	0.026	0.041	1	0	1
Rhopalodia	1	0	0	1	0	0	1	0	0.208	0.167	0	0	0
Scenedesmus	1	0	1	0	0	1	0	0	0.038	0.056	0	0	0
Schroederia	1	0	0	0	0	0	0	0	0.183	0.026	0	0	0
Spirulina	1	0	1	0	0	0	0	0	0.211	0.001	0	0	0
Staurastrum	1	0	0	0	0	1	1	0	0.052	0.129	0	0	0
Stephanodiscus	1	1	0	1	0		1	0	0.033		0	0	0
Surirella	1	0	1	1	0		1	0	0.535	0.862	0	0	0

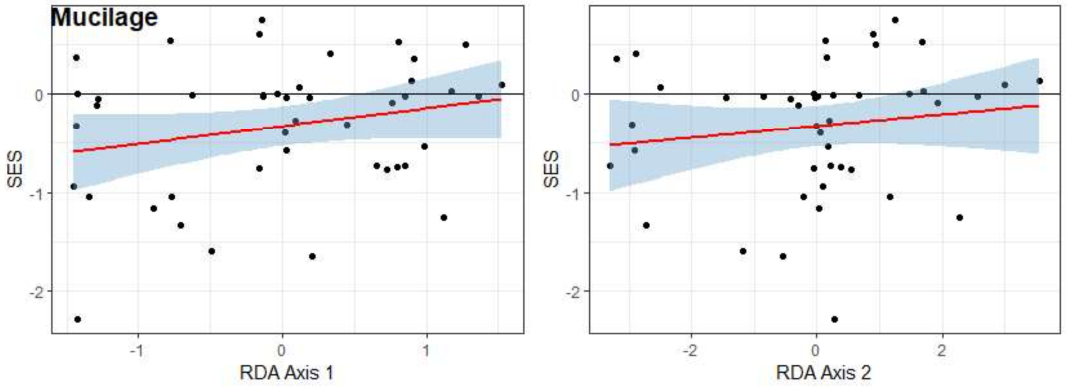
Synechococcus	1	1	0	0	0	1	0	0	0.021	0.008	0	0	1
Synedra	1	0	0	1	0	1	1	0	0.567	0.043	0	0	0
Tabellaria	0	1	1	1	0	1	1	0	0.112	0.183	0	0	0
Tetraedron	1	0	0	0	0	0	0	0	0.021		0	0	0
Tetrastrum	0	0	1	0	0	1	0	0	0.025		0	0	0
Trachelomonas	1	0	0	0	0	0	0	0	0.039		1	0	1
Treubaria	1	0	0	0	0	0	0	0	0.040	0.117	0	0	0
Woronichinia	1	0	1	0	0	1	0	1	0.021	0.053	0	1	0

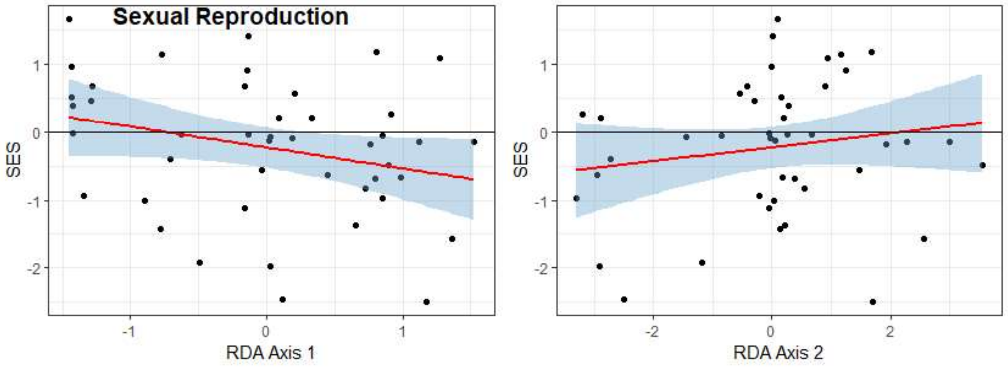
B. SES Values Along Canonical Axes

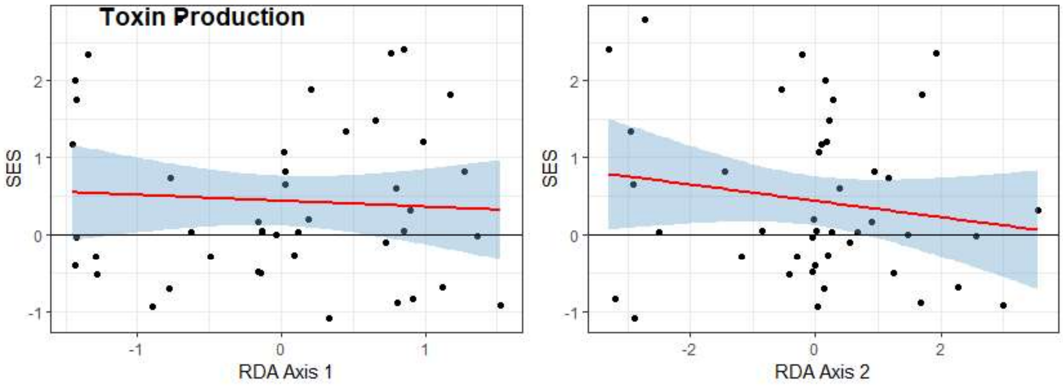


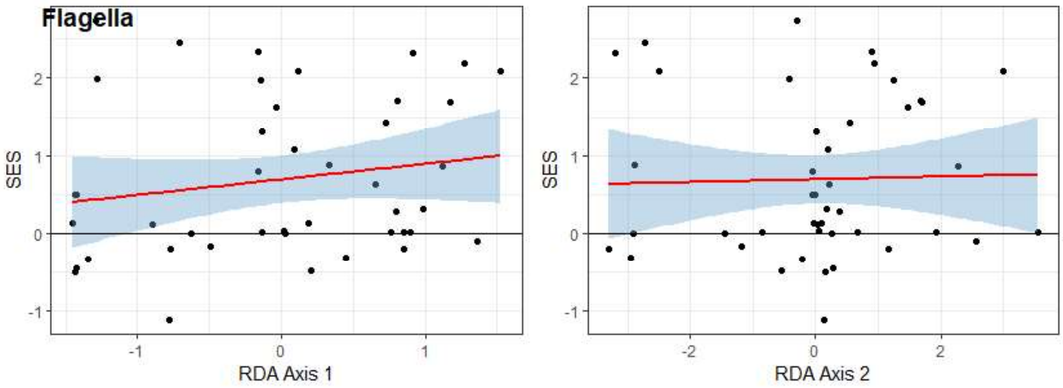

Silica Demand
SES
2
1
0
-1
-2
-3
-1
0
1
RDA Axis 1
2
1
0
-1
-2
-3
-2
0
2
RDA Axis 2

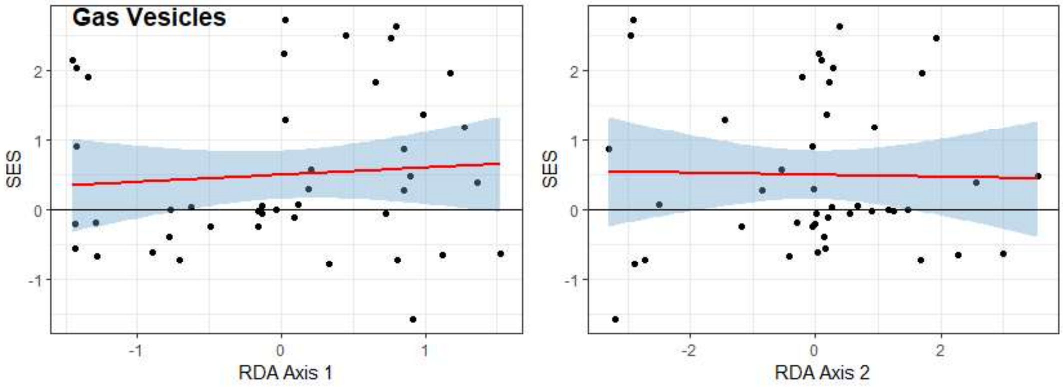

Nitrogen Fixation
SES
3
2
1
0
-1
-1
0
1
RDA Axis 1
3
2
1
0
-1
-2
0
2
RDA Axis 2

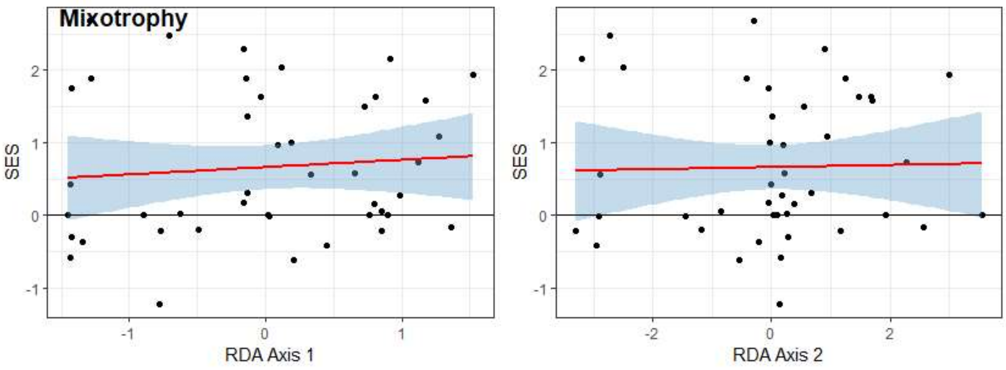

Mucilage
SES
0
-1
-2
-1
0
1
RDA Axis 1
0
-1
-2
-2
0
2
RDA Axis 2

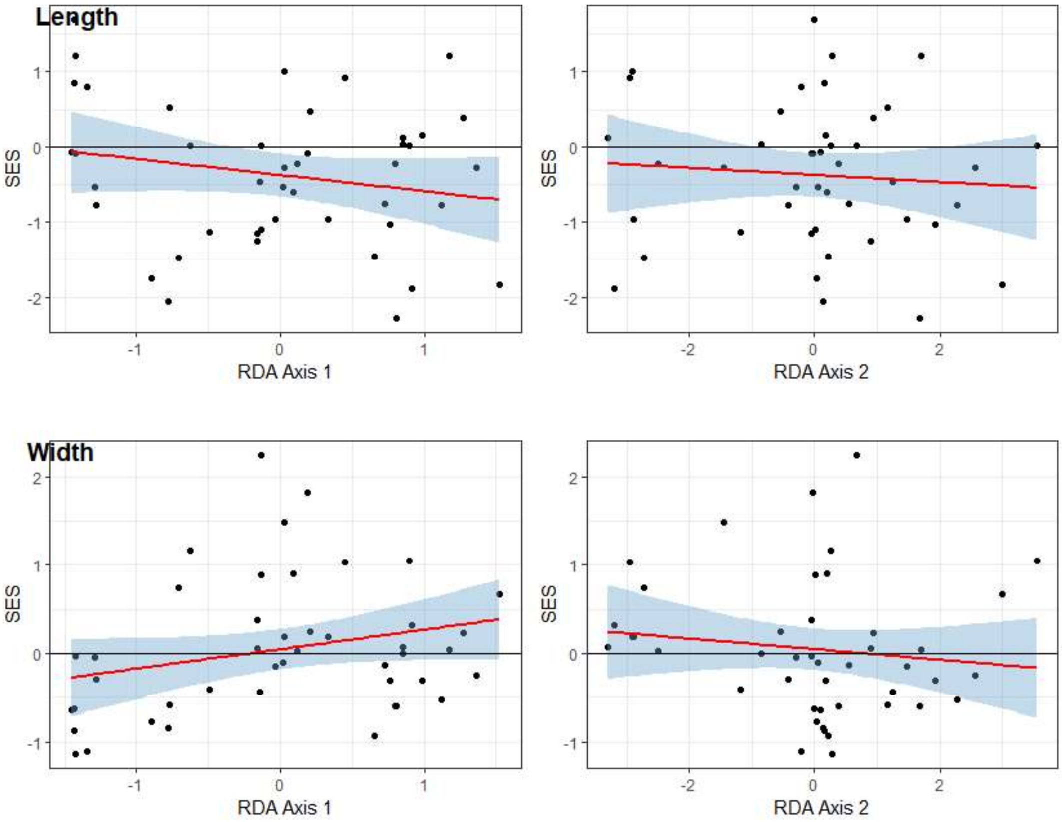

Sexual Reproduction
SES
1
0
-1
-2
-1
0
1
RDA Axis 1
1
0
-1
-2
-2
0
2
RDA Axis 2


Toxin Production
SES
2
1
0
-1
-1
0
1
RDA Axis 1
-2
0
2
RDA Axis 2


Flagella
SES
2
1
0
-1
-1
0
1
RDA Axis 1
-2
0
2
RDA Axis 2

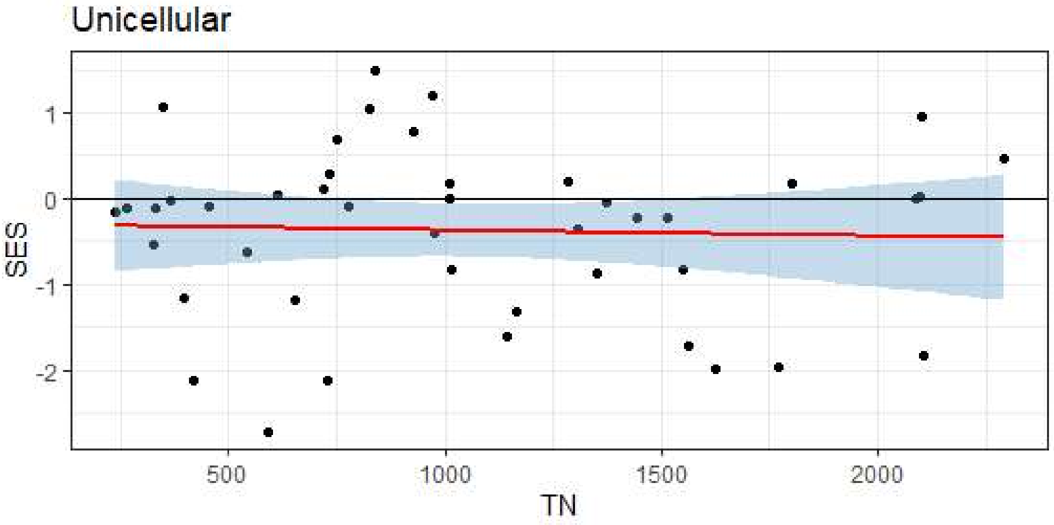

Gas Vesicles
SES
2
1
0
-1
-1
0
1
RDA Axis 1
-2
0
2
RDA Axis 2

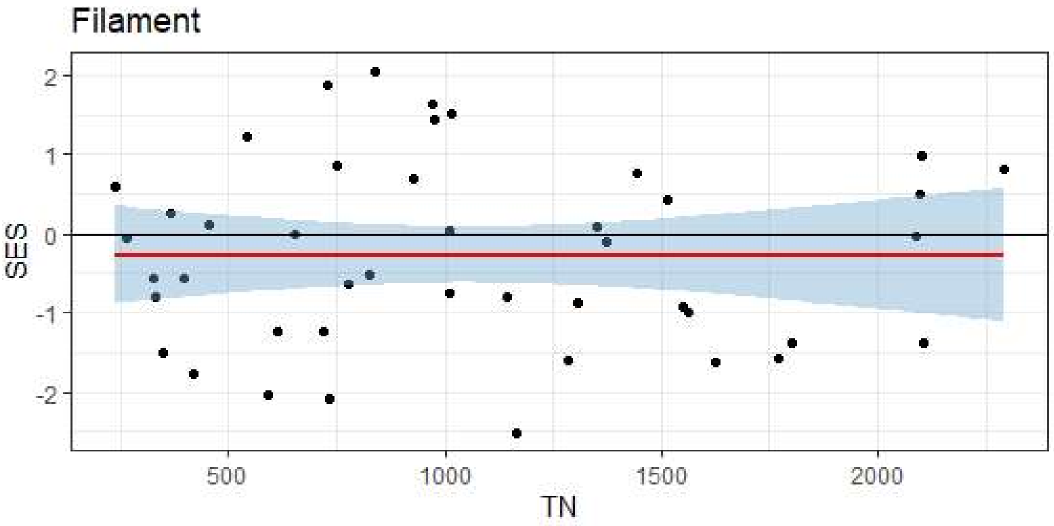

Mixotrophy
SES
2
1
0
-1
-1
0
1
RDA Axis 1
-2
0
2
RDA Axis 2

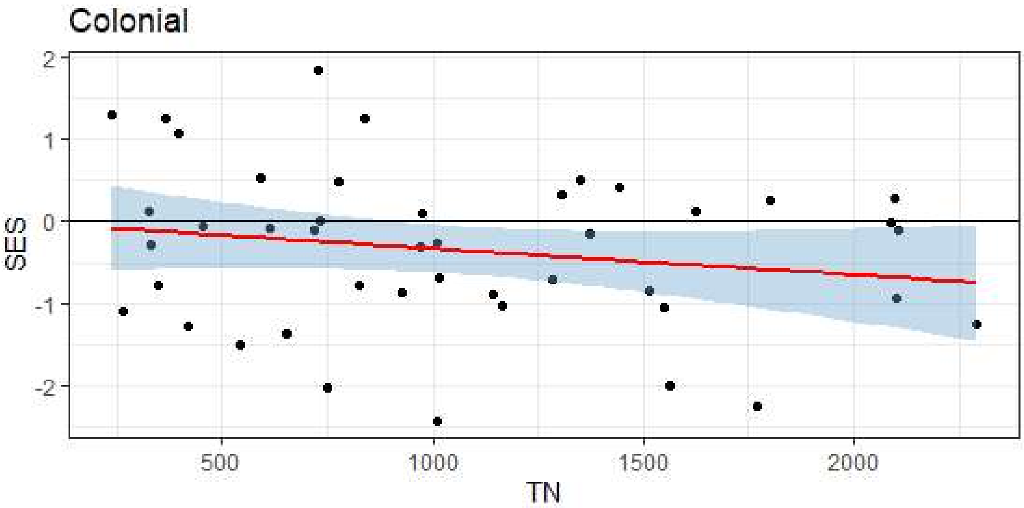

Length
SES
1
0
-1
-2
-1
0
1
RDA Axis 1
SES
1
0
-1
-2
-2
0
2
RDA Axis 2
Width
SES
2
1
0
-1
-1
0
1
RDA Axis 1
SES
2
1
0
-1
-2
0
2
RDA Axis 2

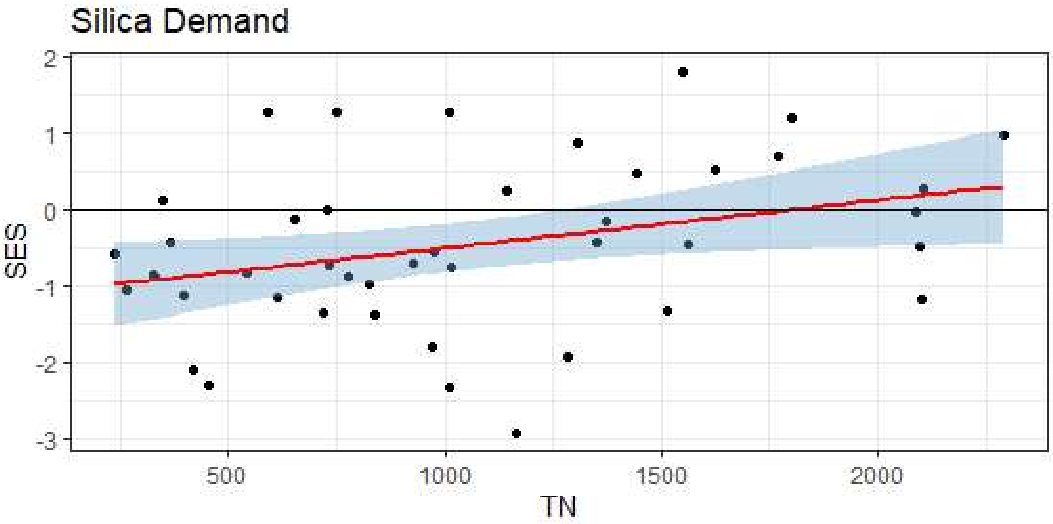
C. SES Values Along Environmental Gradients

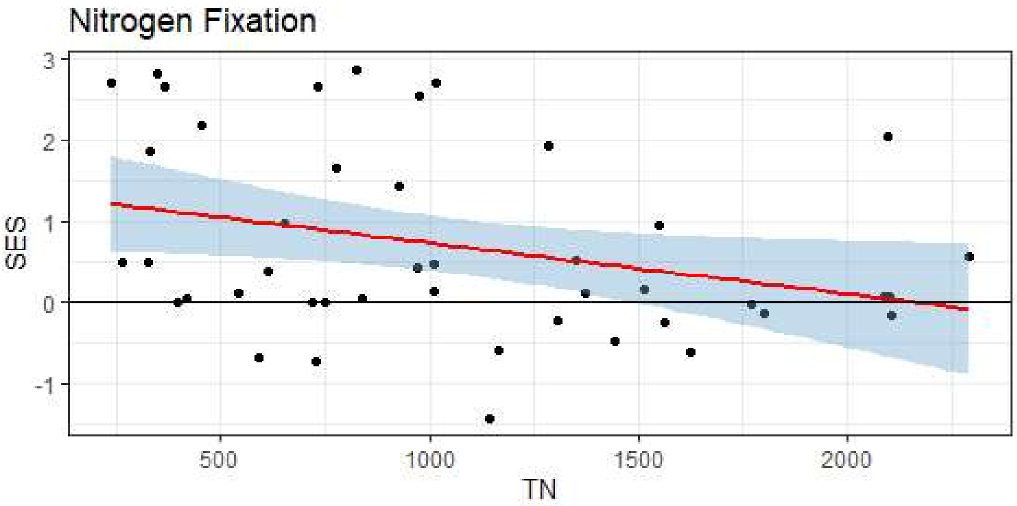
a. TN

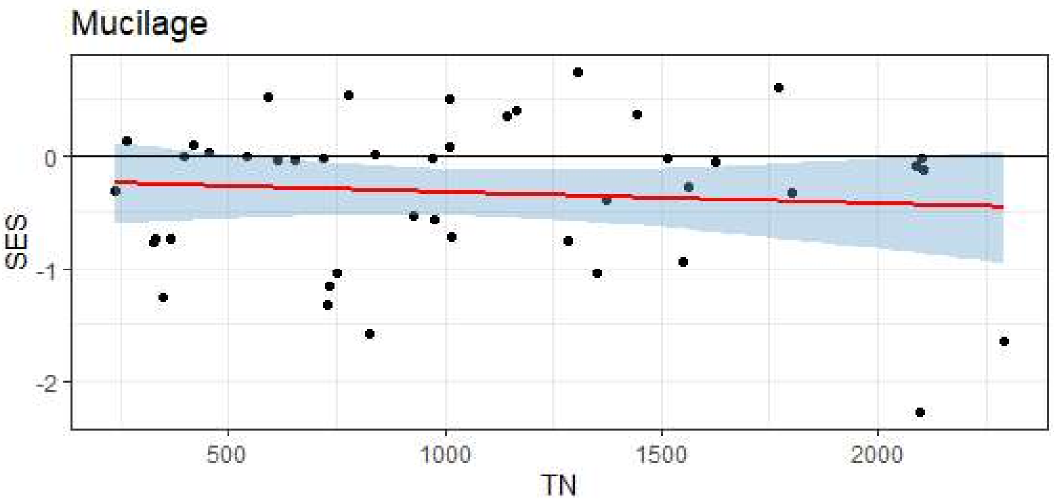


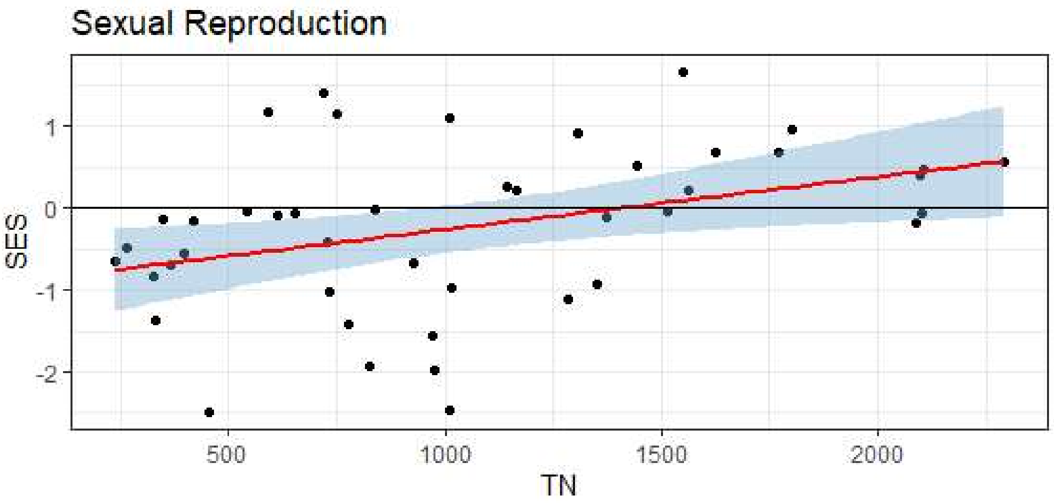


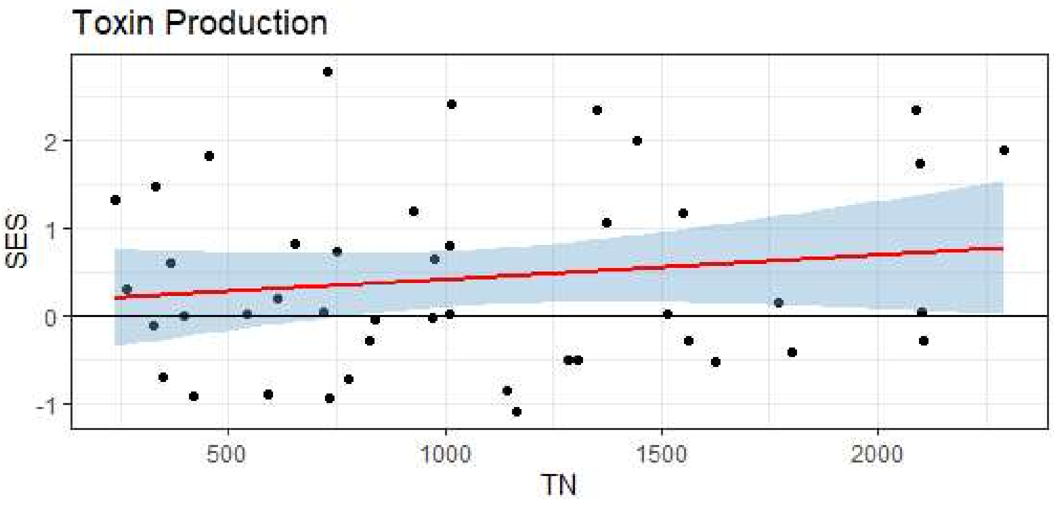

Colonial

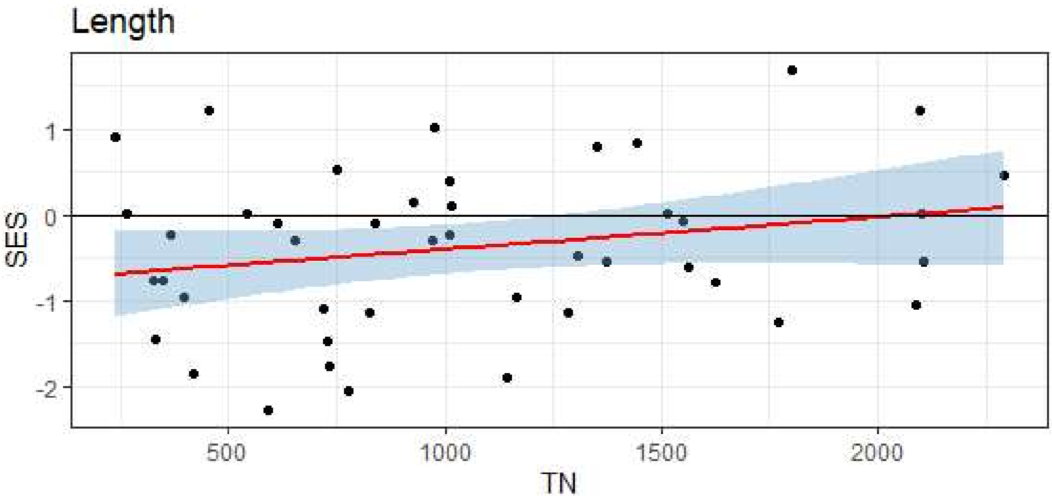

Silica Demand

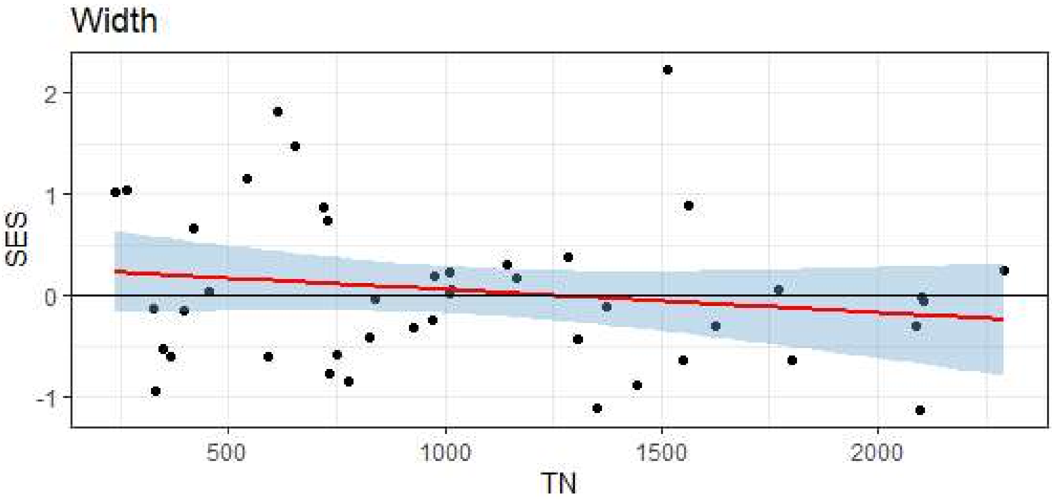

Nitrogen Fixation

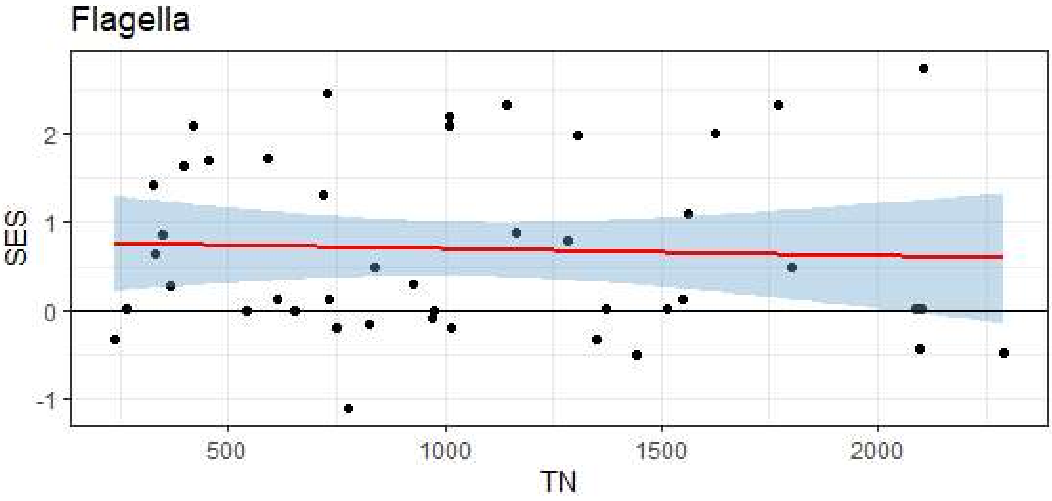

Mucilage
SES
0
-1
-2
500
1000
1500
2000
TN

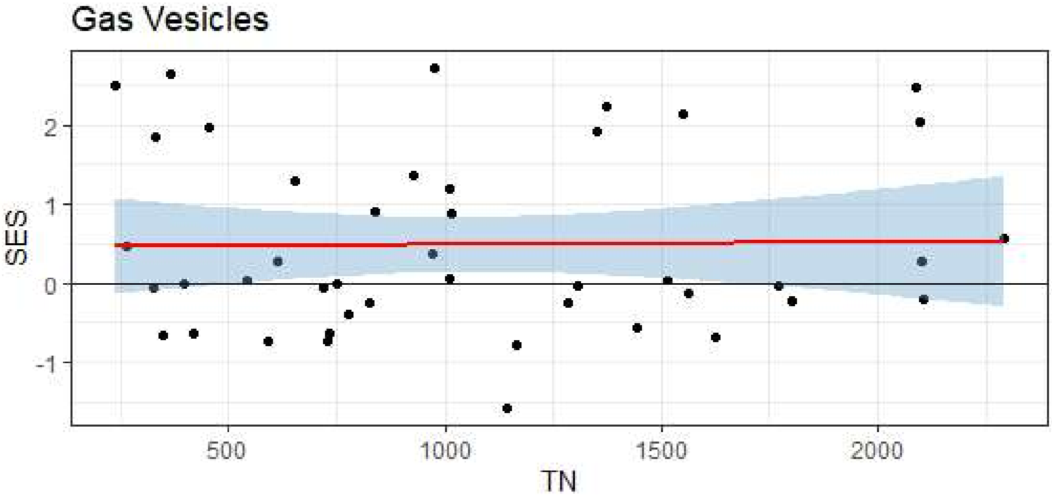

Sexual Reproduction
SES
1
0
-1
-2
500
1000
1500
2000
TN

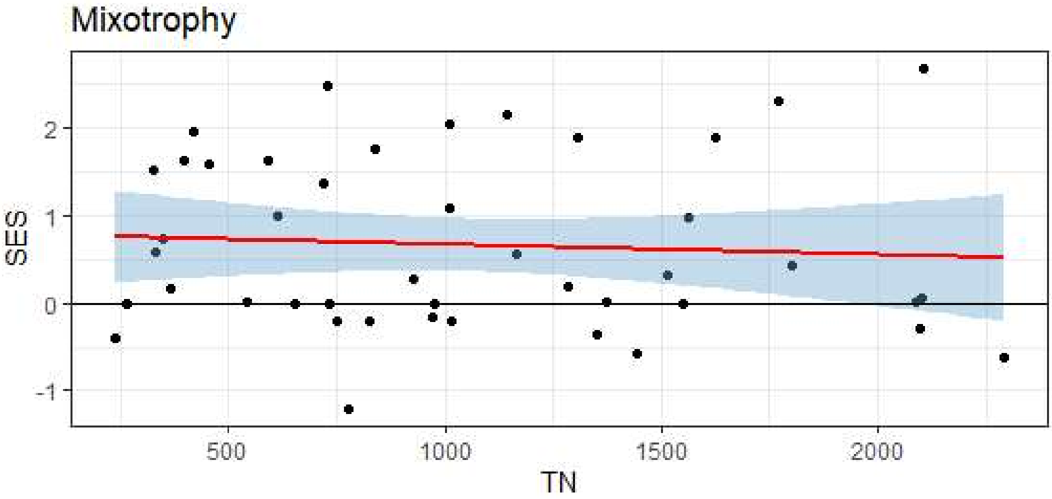

Toxin Production
SES
2
1
0
-1
500
1000
1500
2000
TN


Length
SES
1
0
-1
-2
500
1000
1500
2000
TN

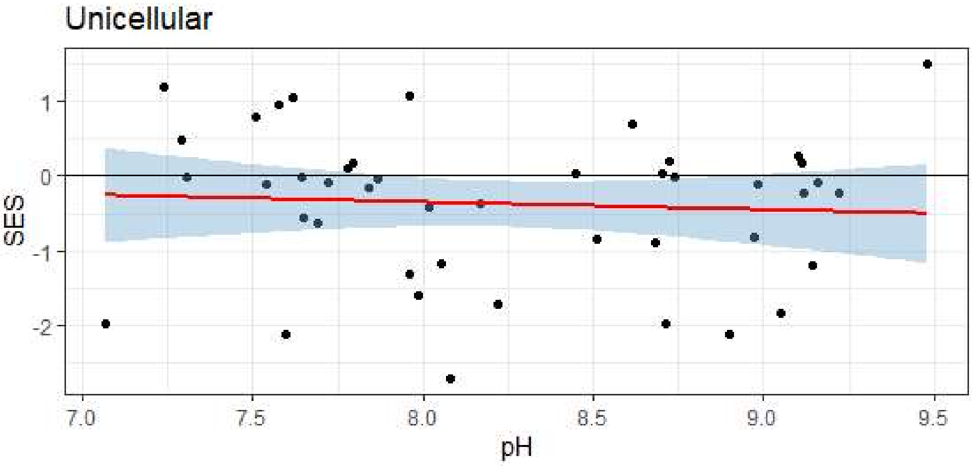

Width
SES
2
1
0
-1
500
1000
1500
2000
TN

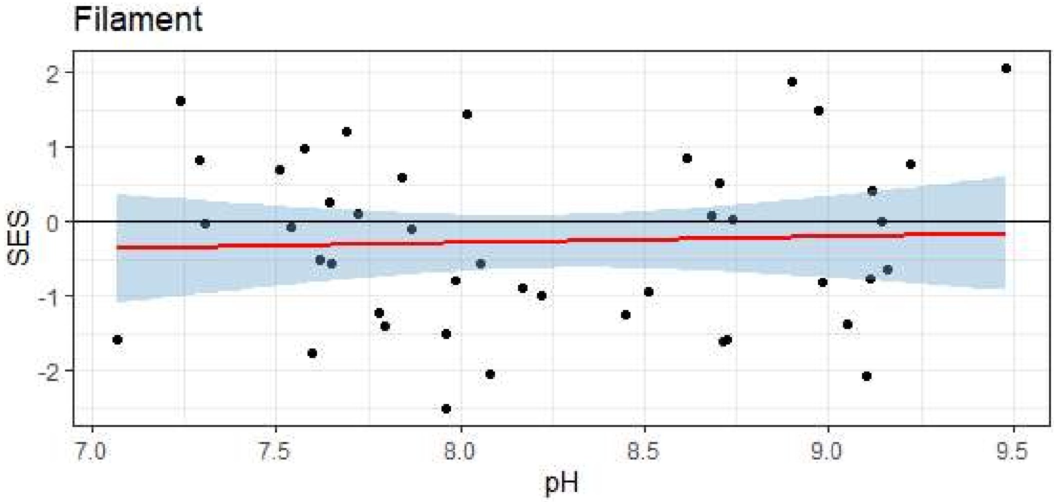

Flagella
SES
2
1
0
-1
500
1000
1500
2000
TN

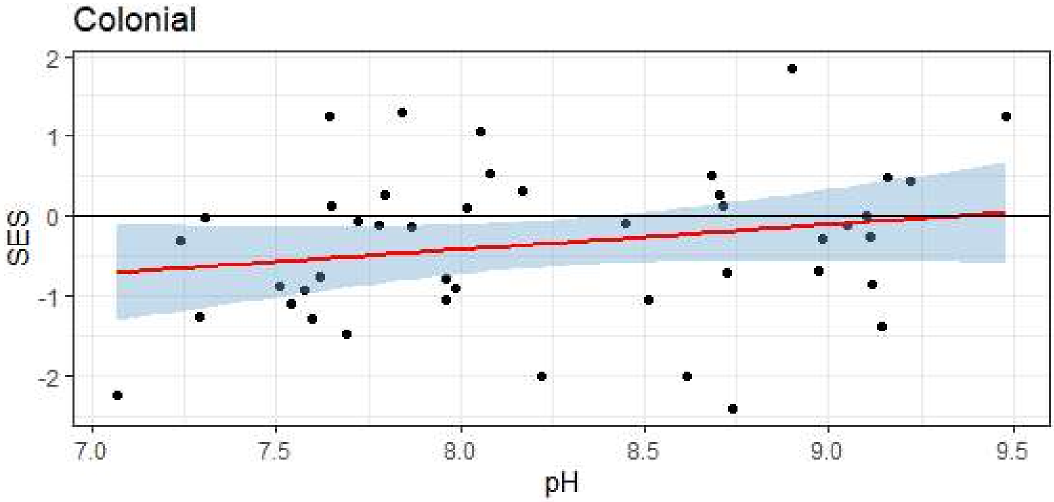

Gas Vesicles
SES
2
1
0
-1
500
1000
1500
2000
TN

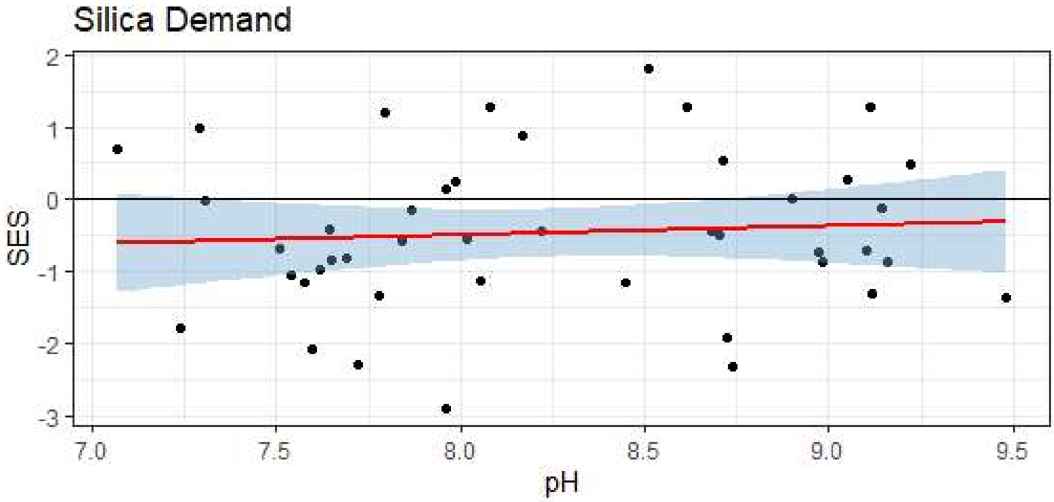

Mixotrophy
SES
2
1
0
-1
500
1000
1500
2000
TN

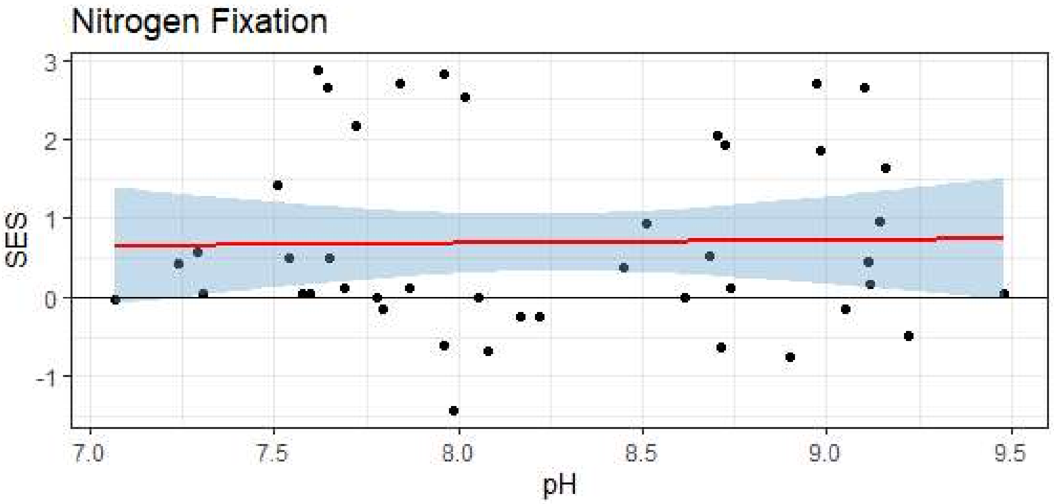
b. pH

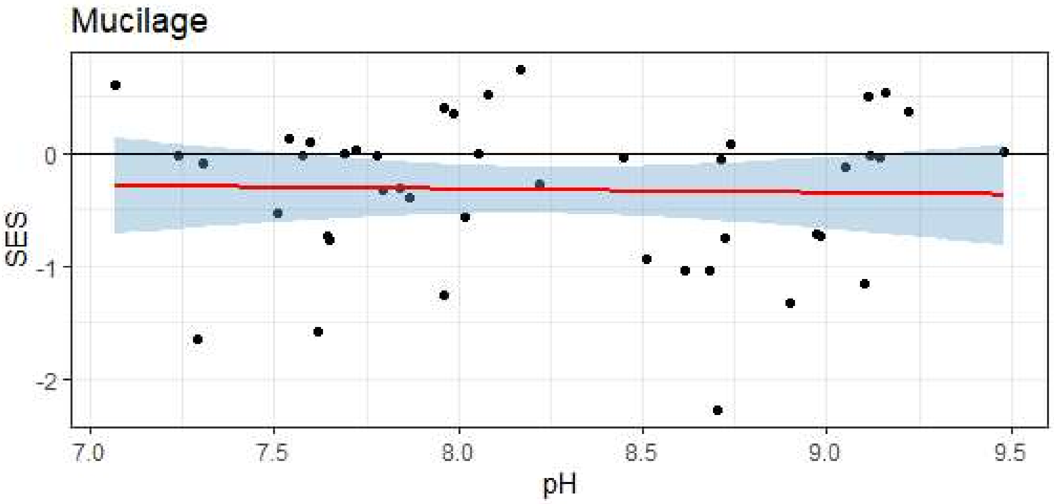

Unicellular
SES
1
0
-1
-2
7.0
7.5
8.0
8.5
9.0
9.5
pH

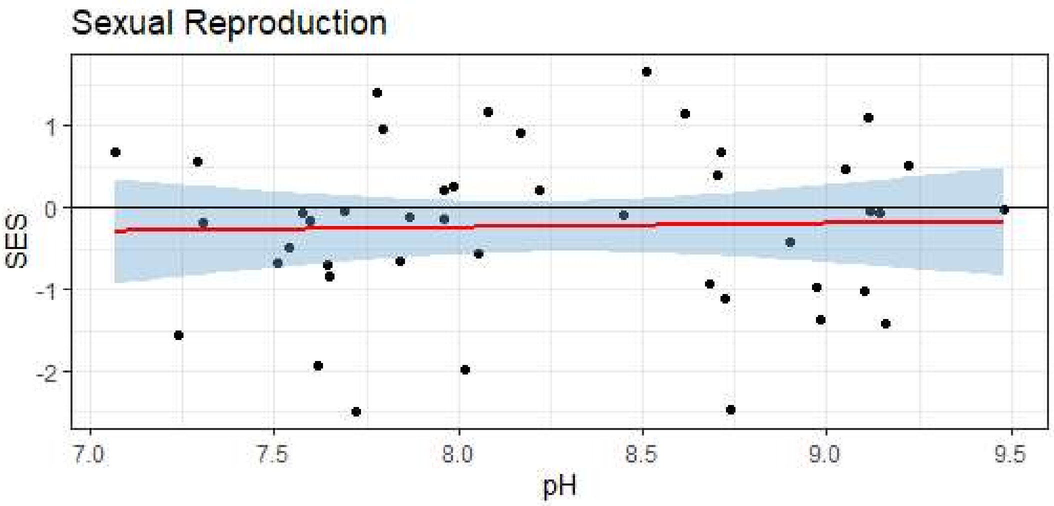

Filament
SES
2
1
0
-1
-2
7.0
7.5
8.0
8.5
9.0
9.5
pH

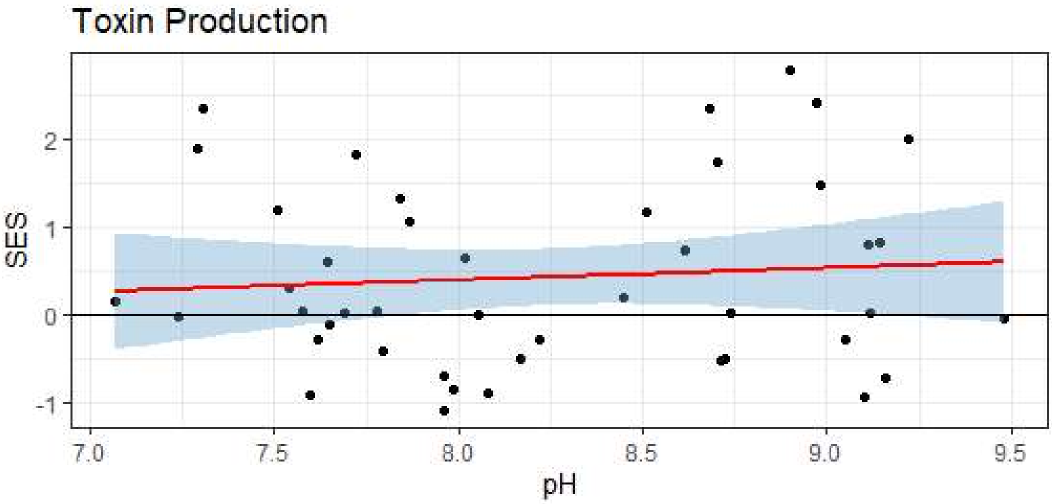

Colonial
SES
2
1
0
-1
-2
7.0
7.5
8.0
8.5
9.0
9.5
pH

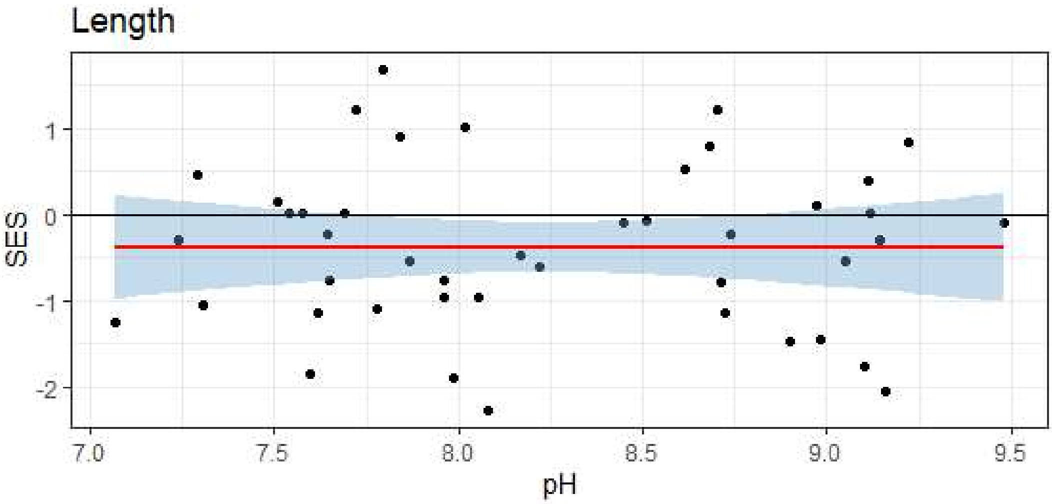

Silica Demand
SES
2
1
0
-1
-2
-3
7.0
7.5
8.0
8.5
9.0
9.5
pH

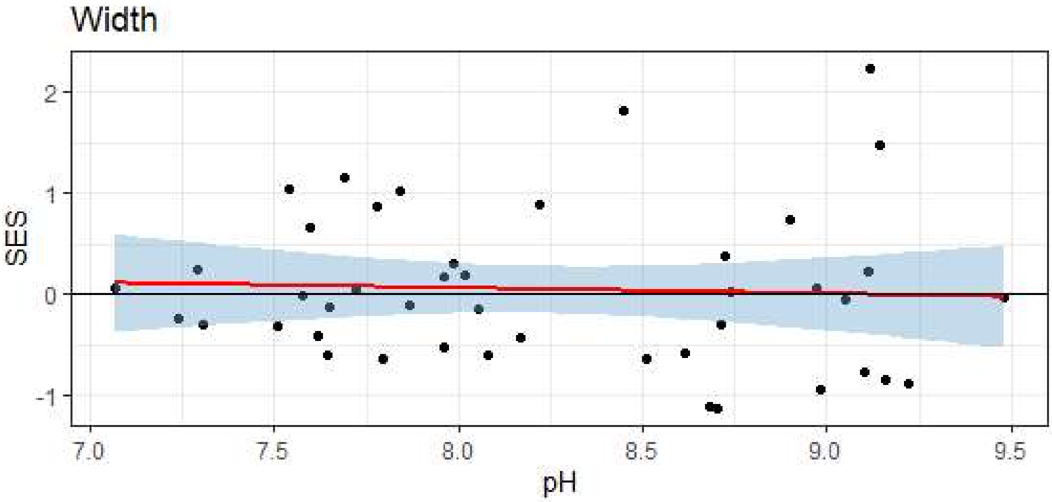

Nitrogen Fixation
SES
3
2
1
0
-1
7.0
7.5
8.0
8.5
9.0
9.5
pH

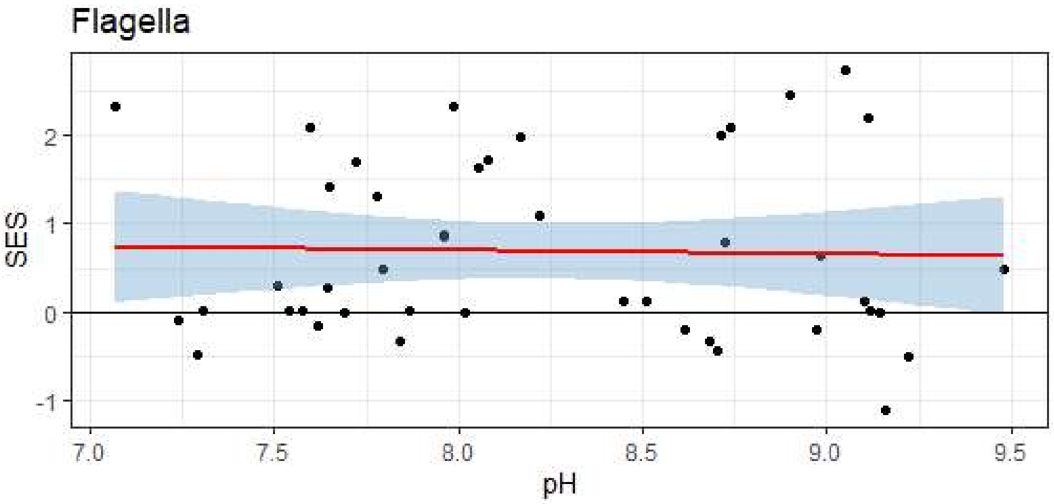

Mucilage
SES
0
-1
-2
7.0
7.5
8.0
8.5
9.0
9.5
pH

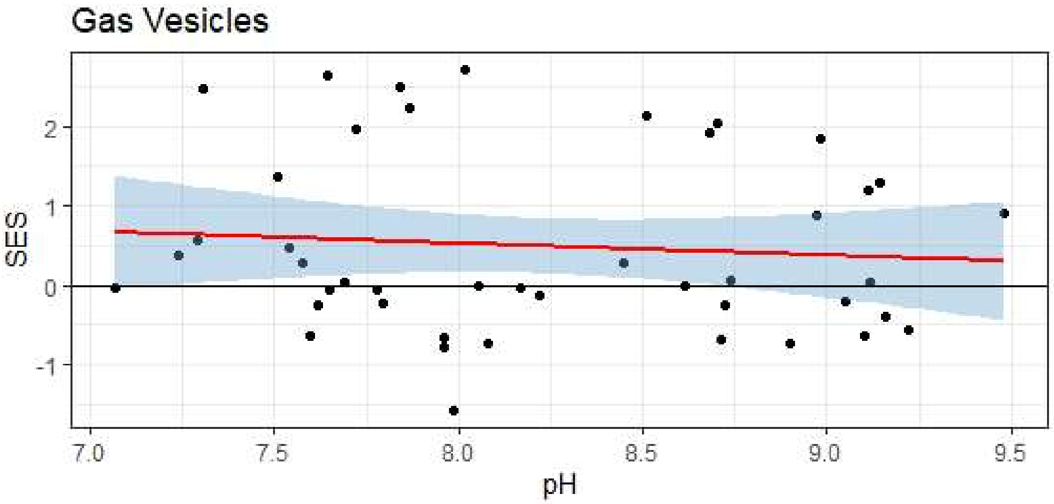

Sexual Reproduction
SES
1
0
-1
-2
7.0
7.5
8.0
8.5
9.0
9.5
pH

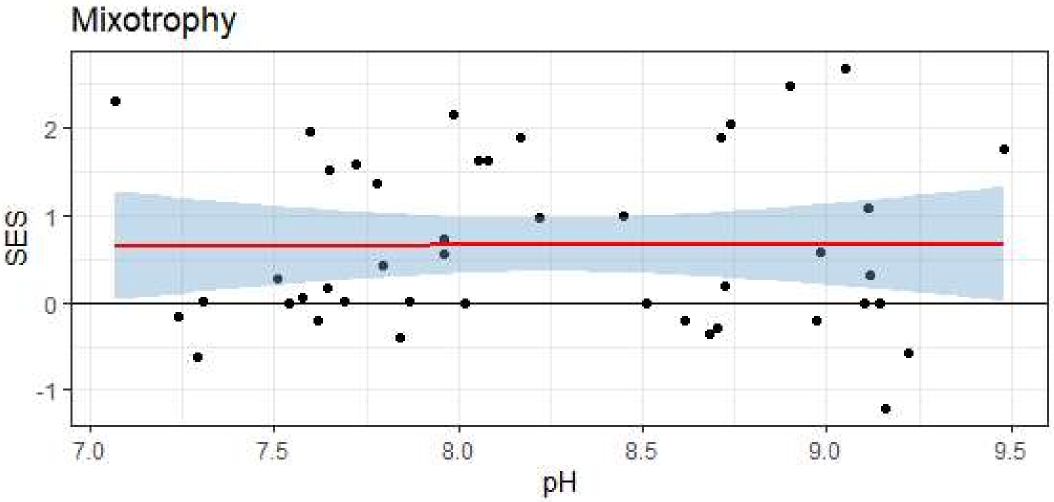

Toxin Production


Length

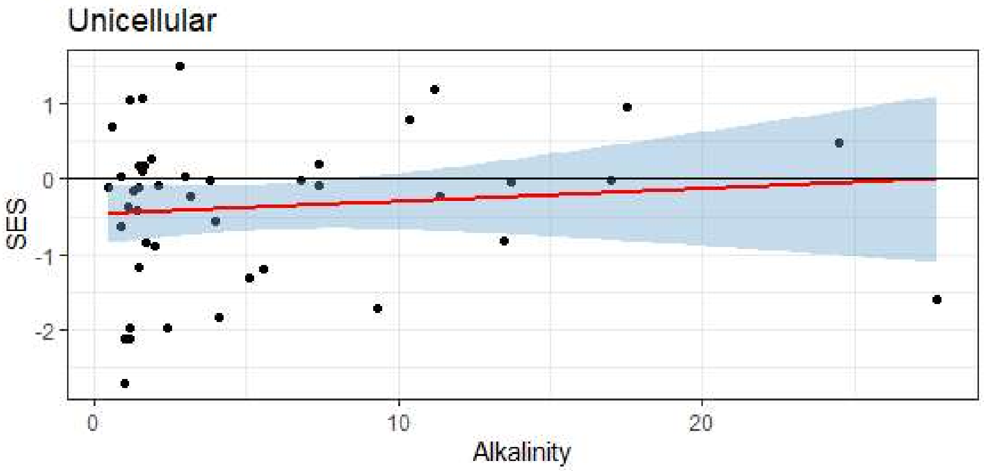

Width

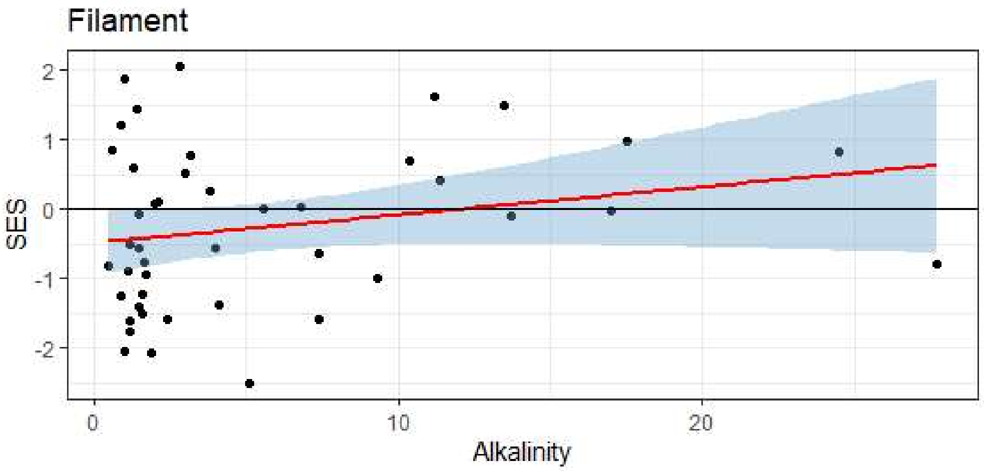

Flagella
SES
2
1
0
-1
7.0
7.5
8.0
8.5
9.0
9.5
pH

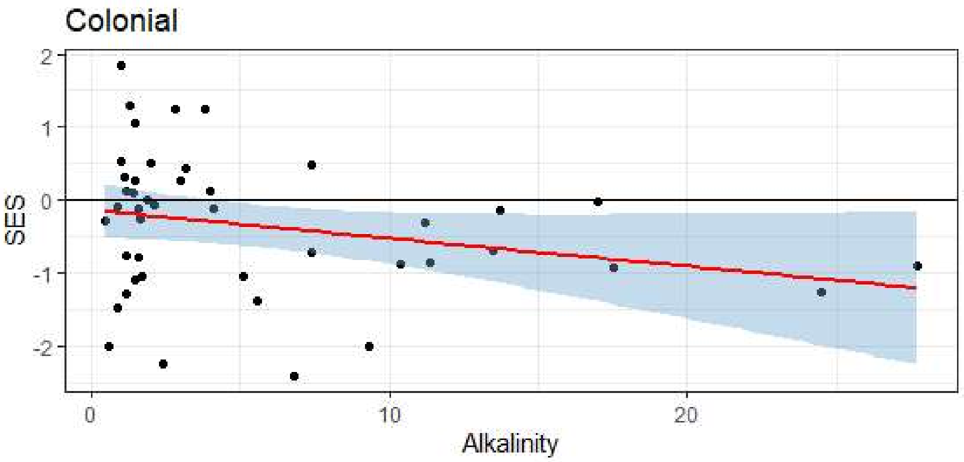

Gas Vesicles
SES
2
1
0
-1
7.0
7.5
8.0
8.5
9.0
9.5
pH

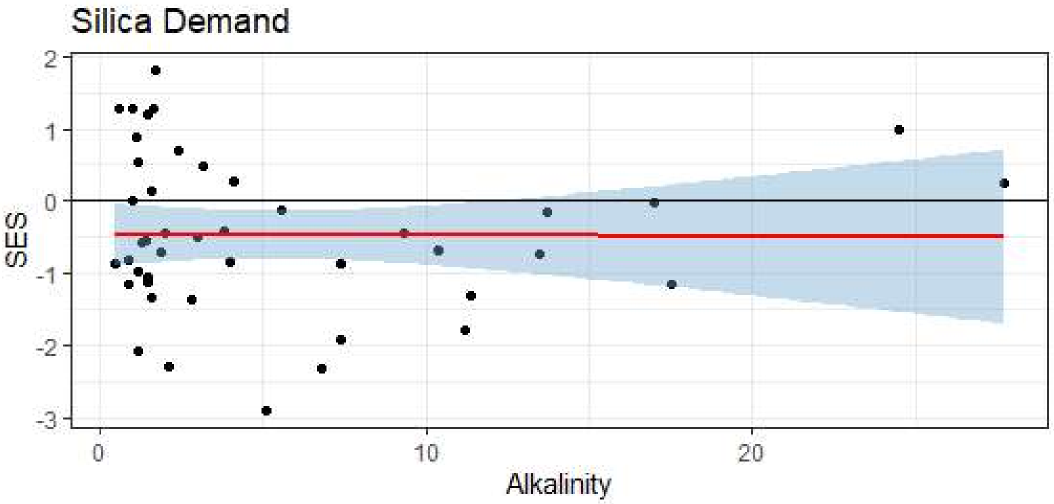

Mixotrophy
SES
2
1
0
-1
7.0
7.5
8.0
8.5
9.0
9.5
pH

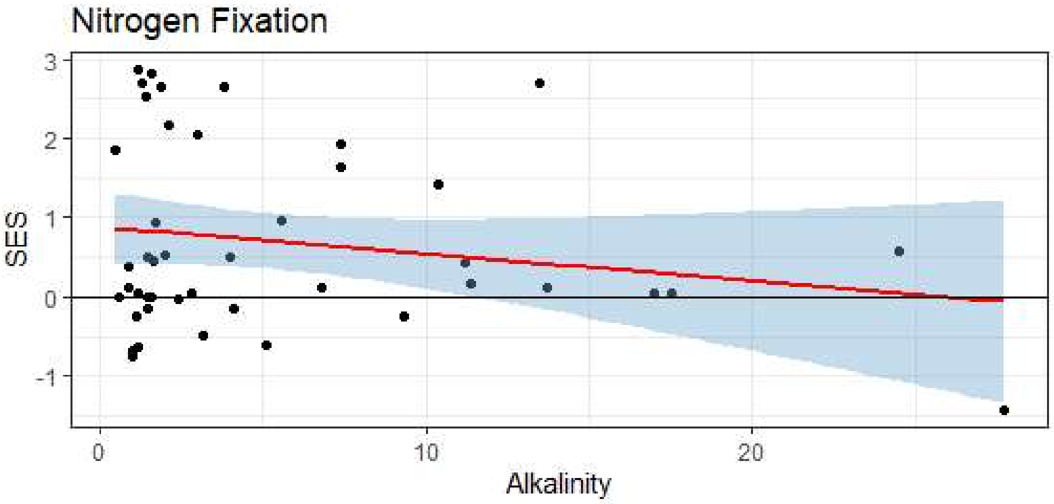
c. Alkalinity

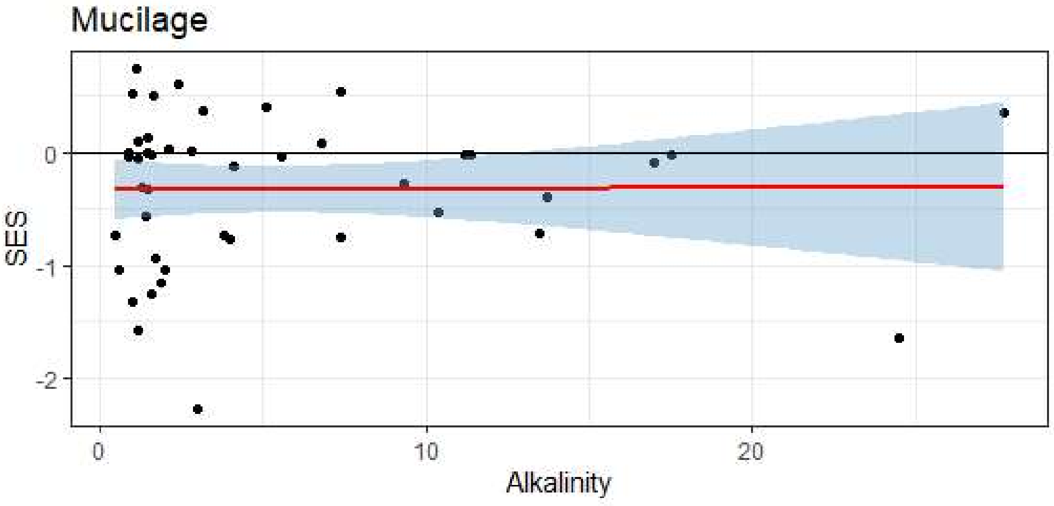


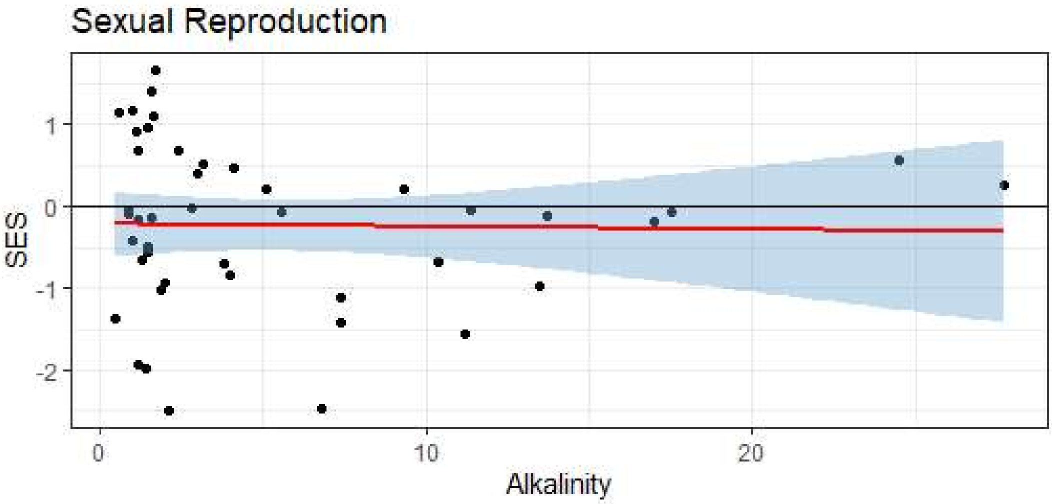


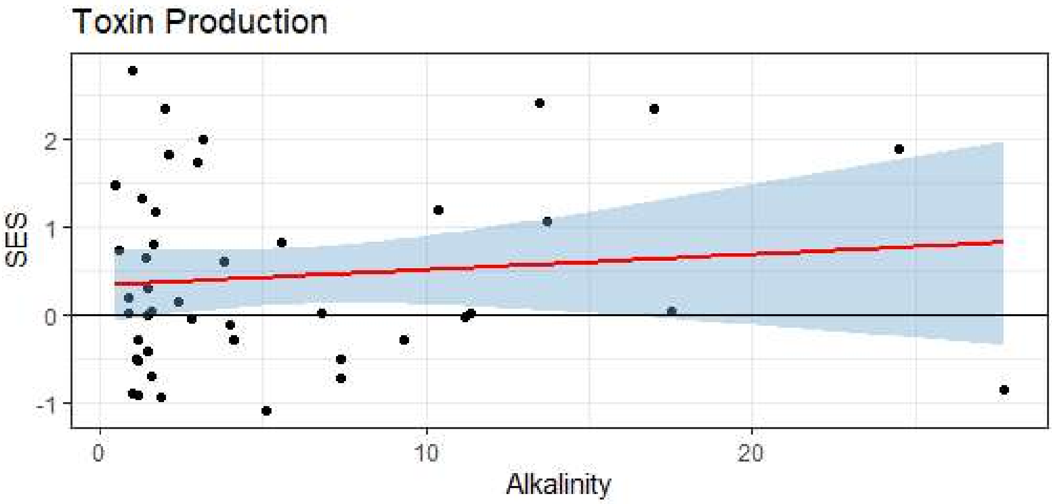


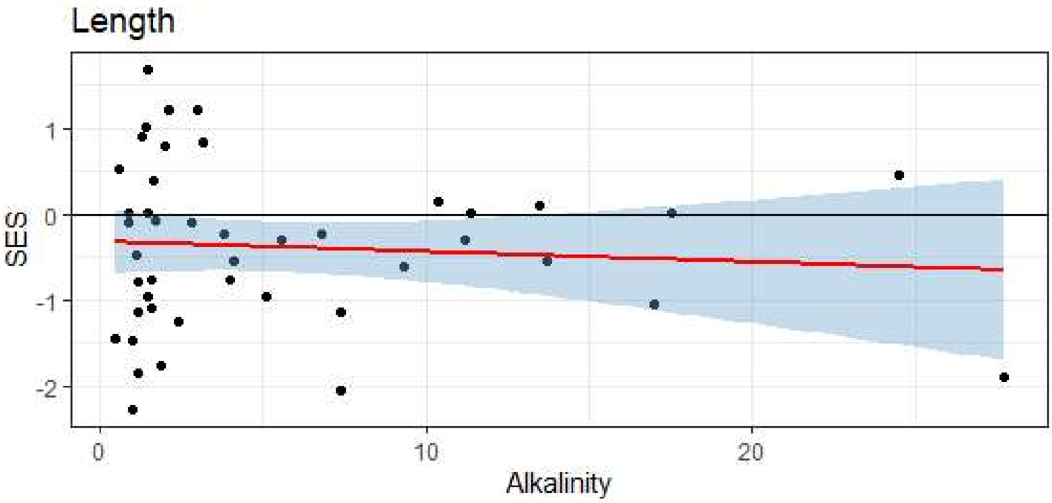

Silica Demand

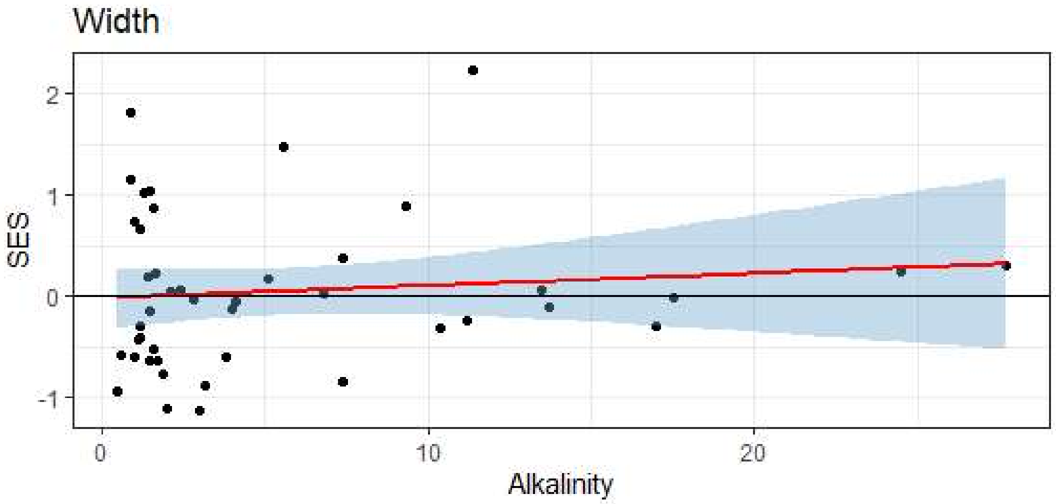

Nitrogen Fixation

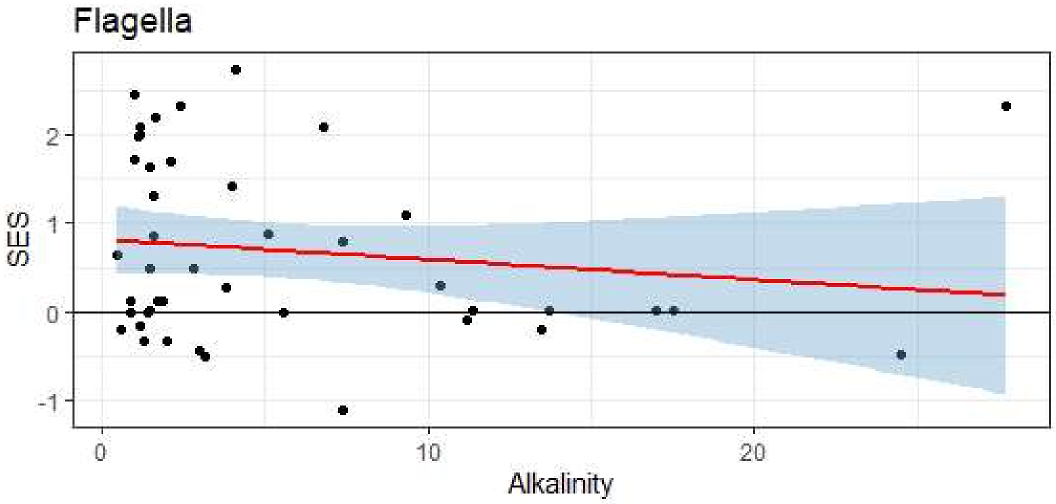

Mucilage

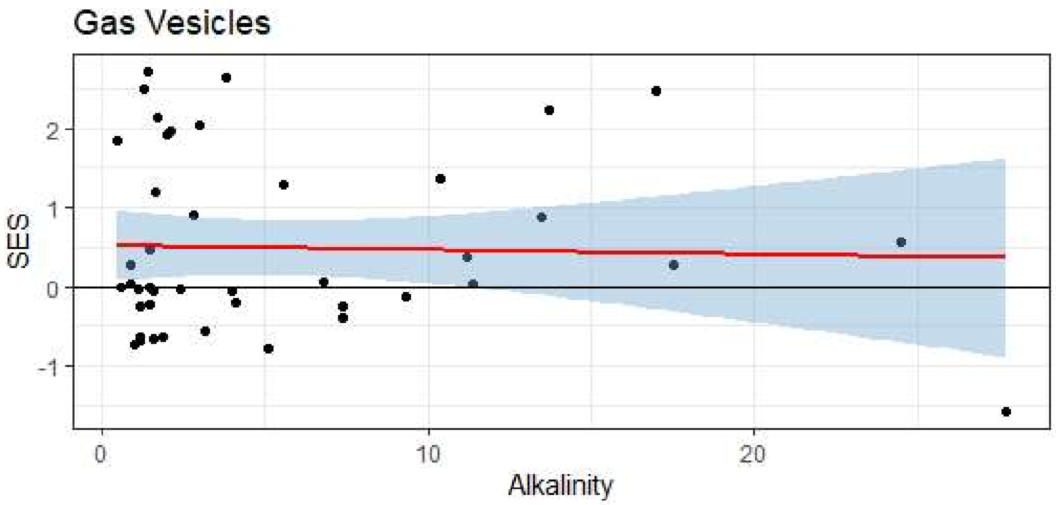

Sexual Reproduction
SES
1
0
-1
-2
0
10
20
Alkalinity

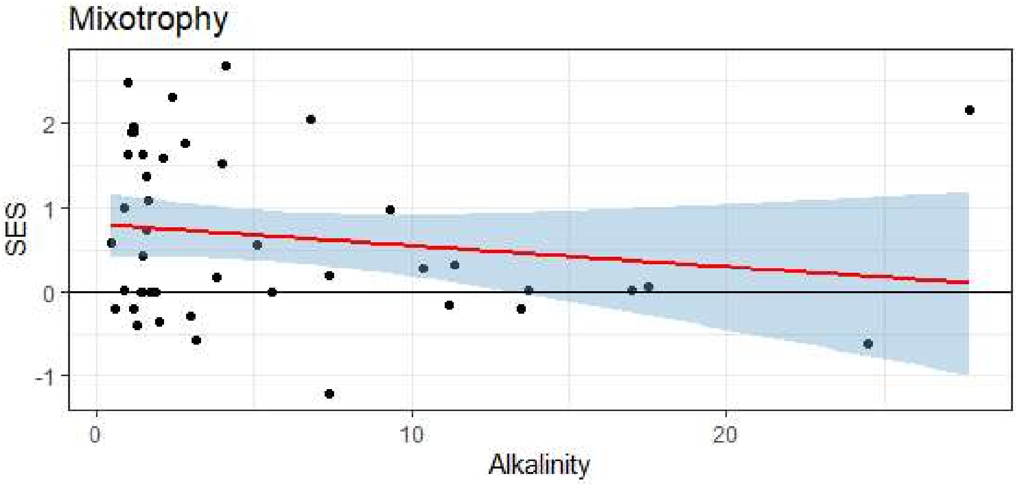

Toxin Production
SES
2
1
0
-1
0
10
20
Alkalinity


Length
SES
1
0
-1
-2
0
10
20
Alkalinity

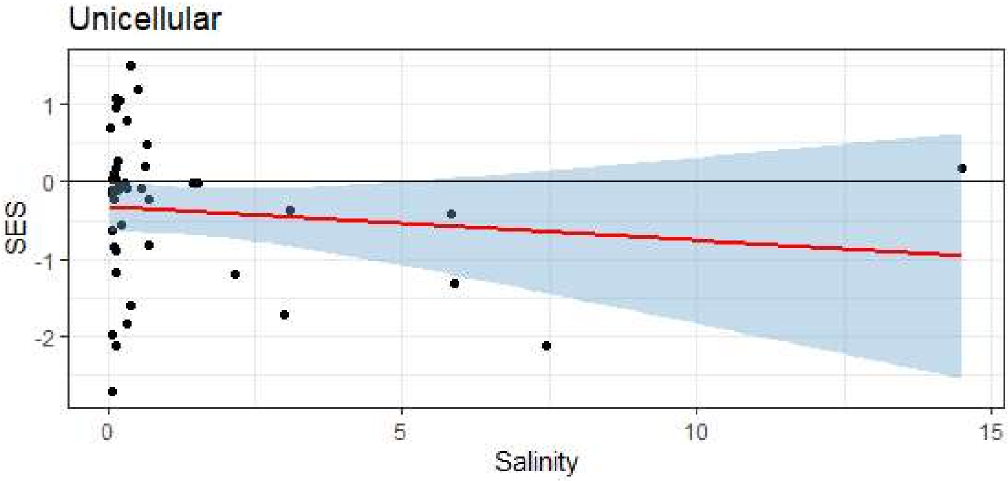

Width
SES
2
1
0
-1
0
10
20
Alkalinity

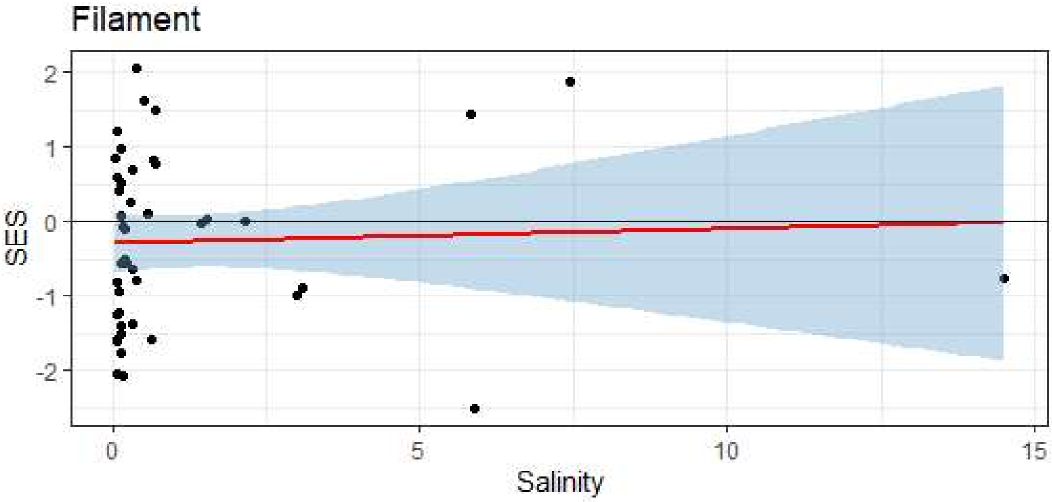

Flagella
SES
2
1
0
-1
0
10
20
Alkalinity

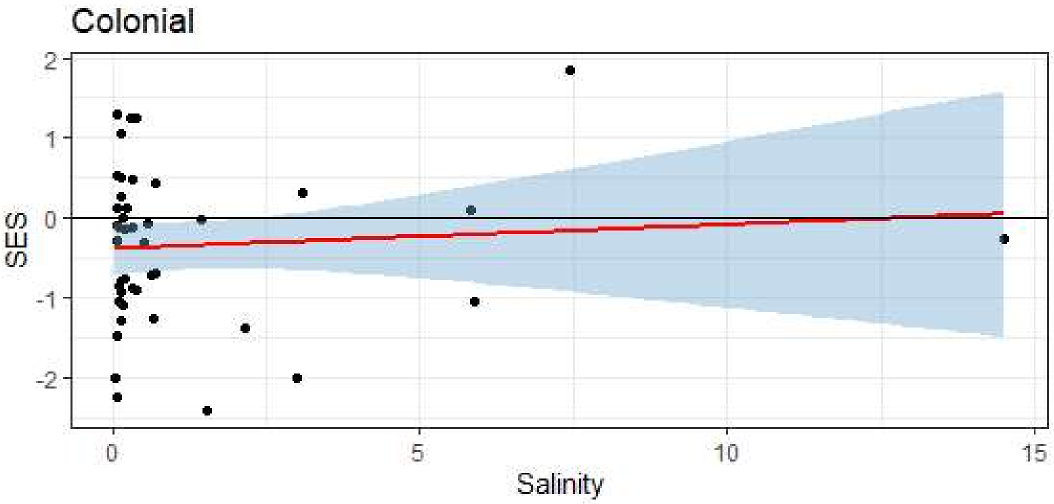

Gas Vesicles
SES
2
1
0
-1
0
10
20
Alkalinity

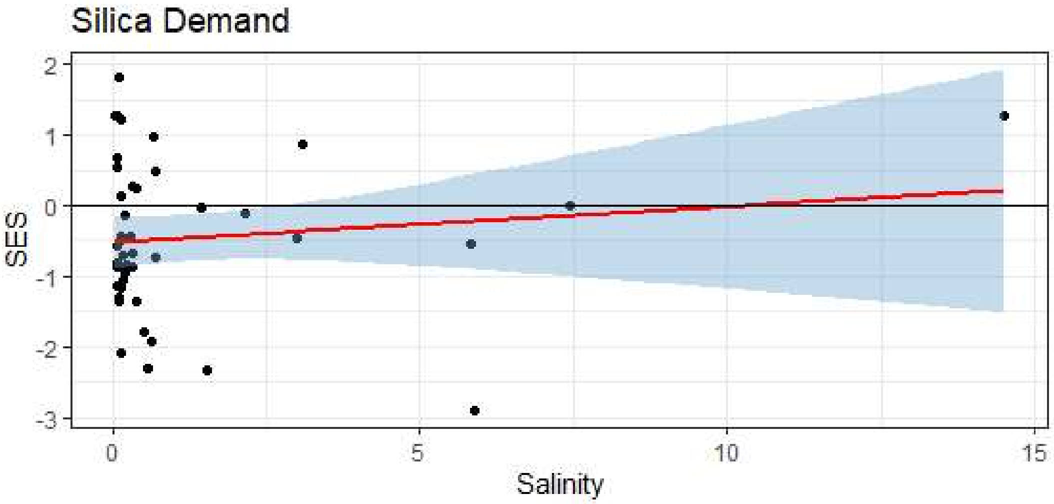

Mixotrophy
SES
2
1
0
-1
0
10
20
Alkalinity

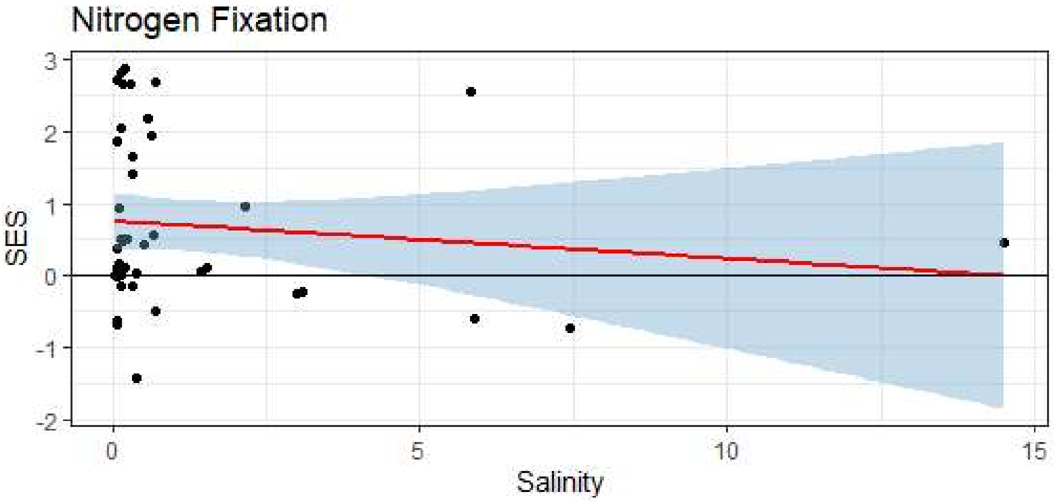
d. Salinity

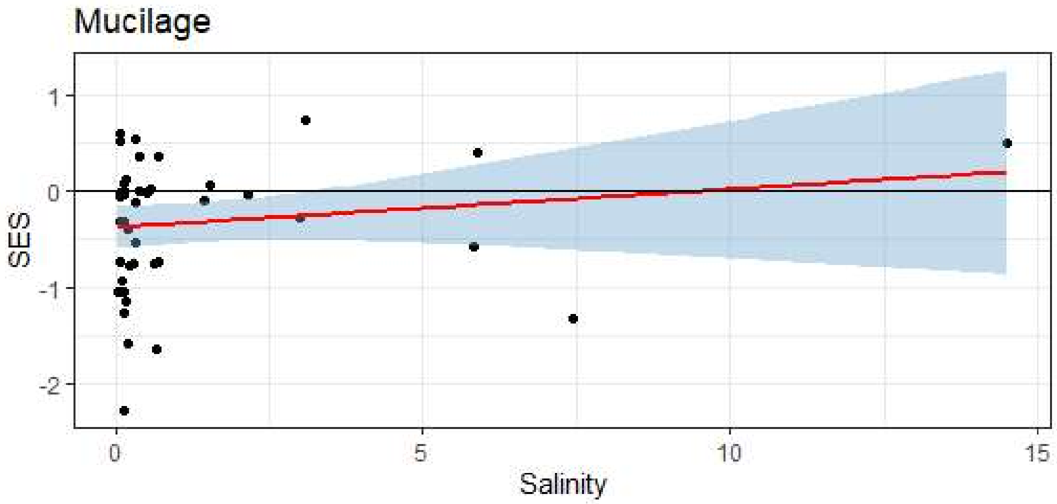

Unicellular
SES
1
0
-1
-2
0
5
10
15
Salinity


Filament
SES
2
1
0
-1
-2
0
5
10
15
Salinity

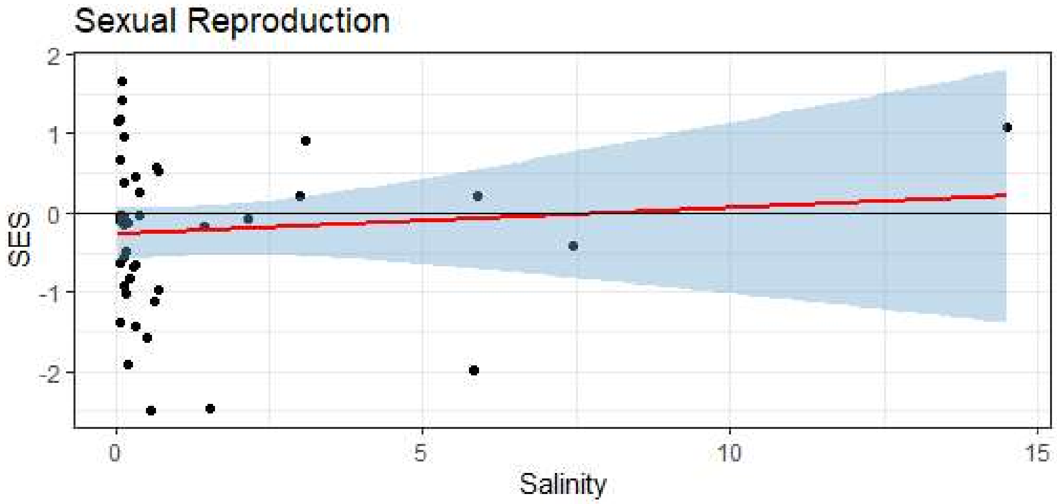

Colonial


Silica Demand

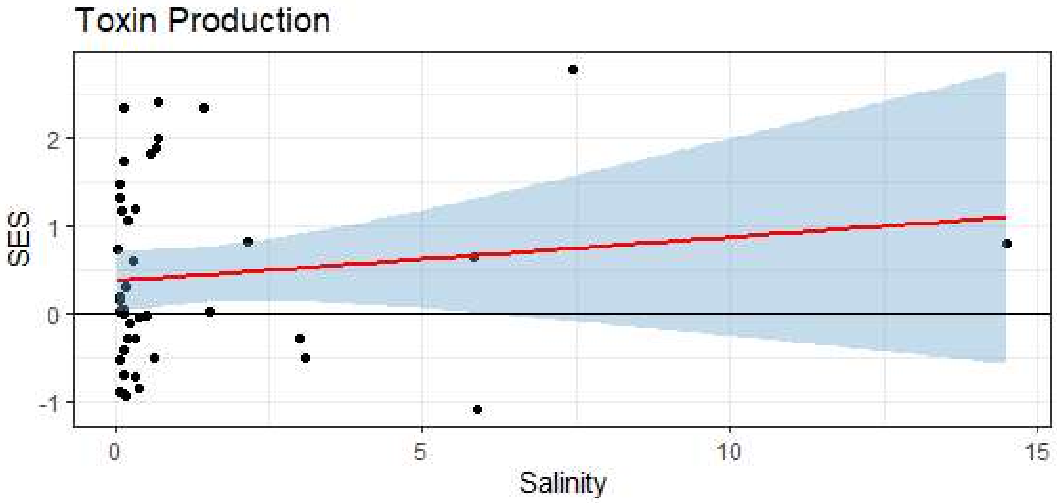

Nitrogen Fixation



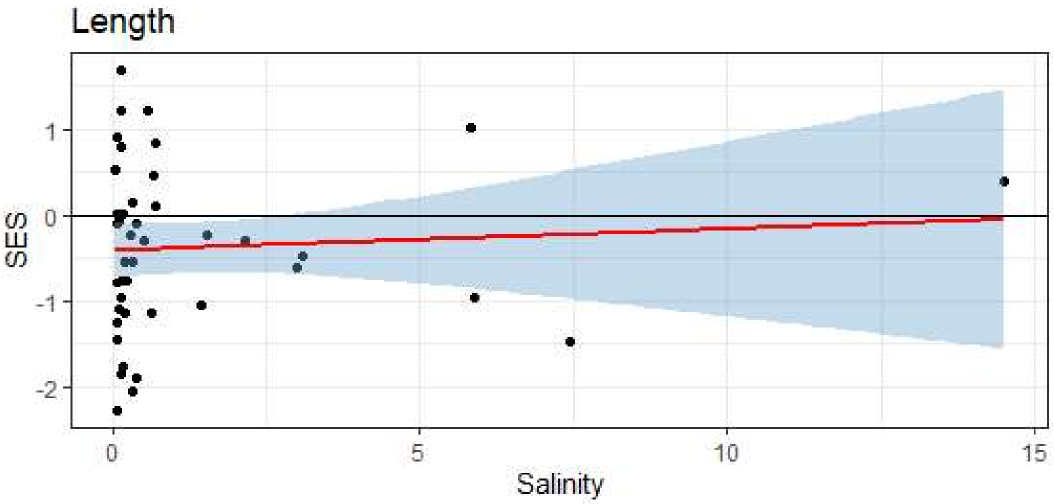
Mucilage



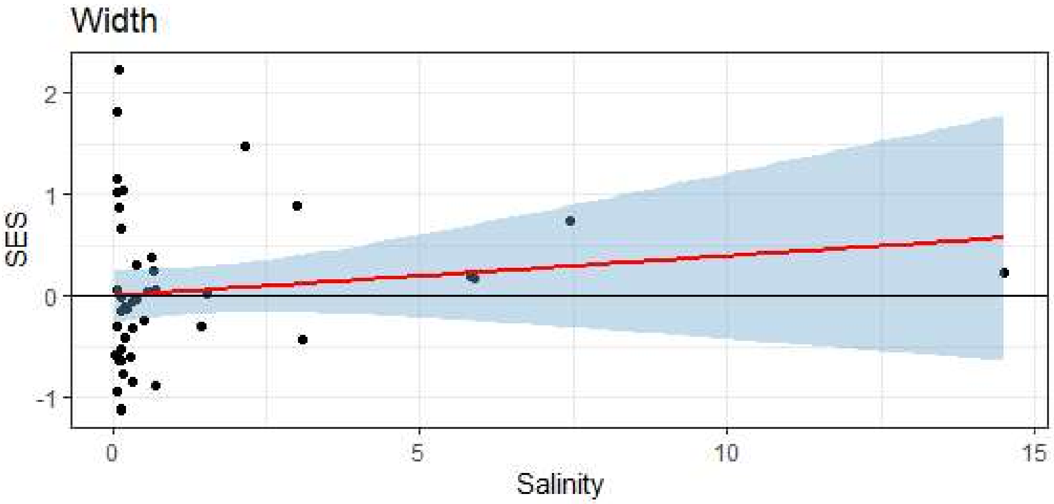
Sexual Reproduction



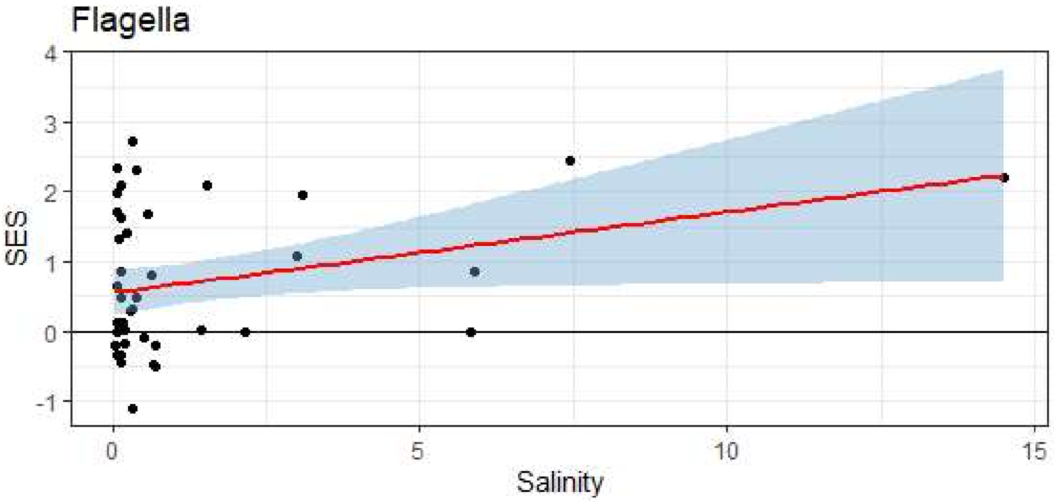
Toxin Production



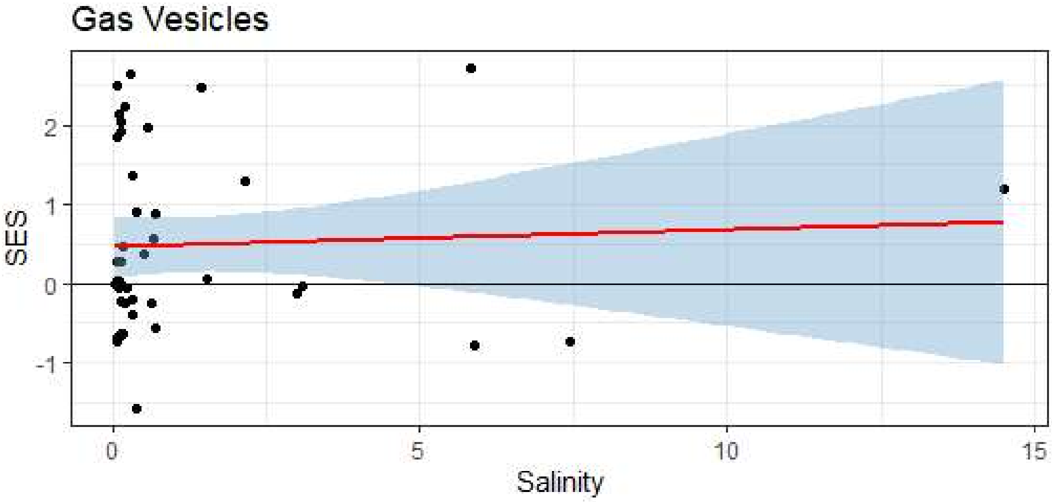
Length



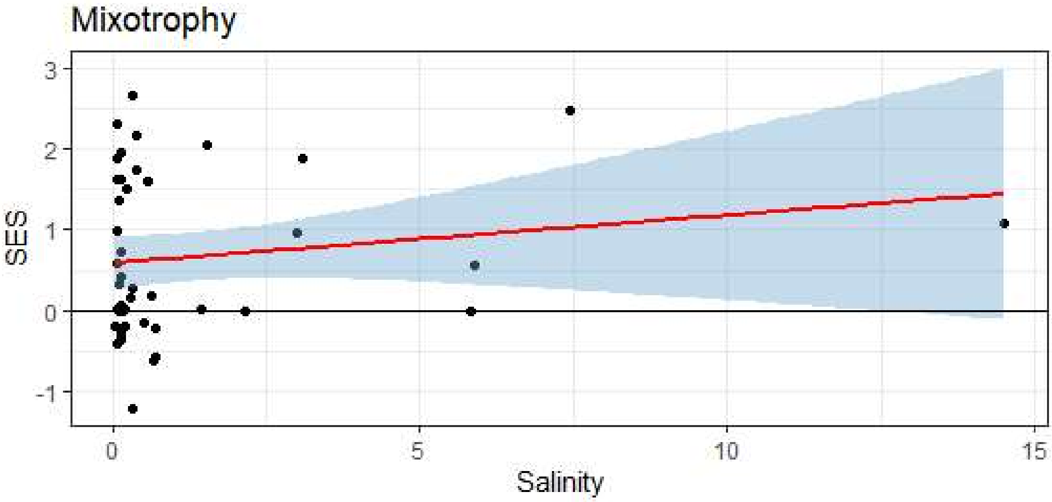
Width



Flagella

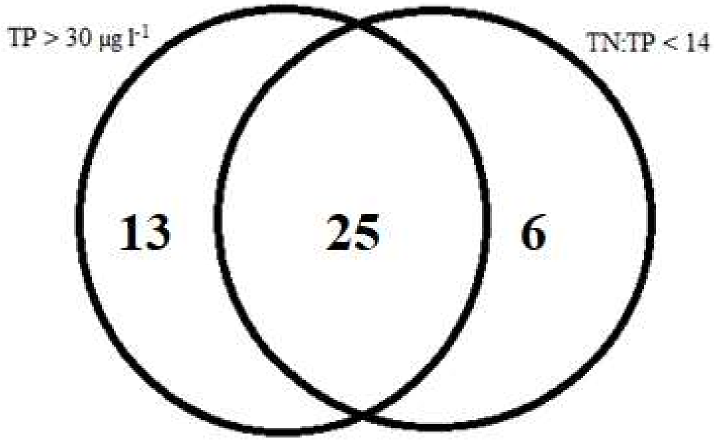


Gas Vesicles



Mixotrophy

D. TN and TP distribution in the dataset



TN:TP	
Minimum	2.75
Median	11.45
Mean	14.77
Maximum	71.11