Spatio-temporal co-occurrence patterns of marine molluscan taxa and their potential drivers

A Thesis

Submitted towards the partial fulfillment of
BS-MS dual degree programme by

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October, 2023

under the guidance of

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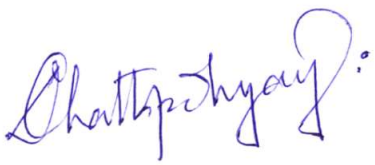
Certificate

This is to certify that this dissertation titled "Spatio-temporal co-occurrence patterns of marine molluscan taxa and their potential drivers" towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents work carried out by Amita Prajna Mallik at IISER Pune under the supervision of Dr. Devapriya Chattopadhyay (Professor, Earth and Climate Sciences) during the academic year 2022-23.



Dr. Devapriya Chattopadhyay

This thesis is dedicated to my parents, family and friends.

Declaration

I hereby declare that the matter embodied in the report entitled "Spatio-temporal co-occurrence patterns of marine molluscan taxa and their potential drivers" are the results of the work carried out by me at the Department of Earth and Climate Sciences, Indian Institute of Science Education and Research, Pune under the supervision of Dr. Devapriya Chattopadhyay, and the same has not been submitted elsewhere for any other degree.

Acknowledgements

I would like to express my sincere gratitude to the following individuals and groups for their invaluable support, guidance, and encouragement throughout the journey of completing this thesis:

- My supervisor, Dr. Devapriya Chattopadhyay and expert, Dr. Gyana Ranjan Tripathy: I am deeply thankful for your unwavering support, mentorship, and the wealth of knowledge and expertise you shared with me. Your guidance has been instrumental in shaping this work and my academic growth.
- Earth and Climate Sciences, IISER Pune: I extend my appreciation to the department for providing me with a stimulating academic environment and the necessary resources to carry out my research.
- The best-labmates-ever: Your camaraderie and collaborative spirit have been essential in making the research process enjoyable and productive, not to mention the countless moments of joy and laughter we shared together.
- My dearest friends, and family: To my family and friends, both near and far. Your belief in me kept me going through the ups and downs.

This thesis would not have been possible without the collective support of these wonderful individuals and groups. Thank you for being a part of this significant chapter in my academic and personal life.

Contents

List of Figures

List of Tables

Abstract

Ecological communities are complex, often shaped by a multitude of biotic interactions and environmental controls. Competition, which is the interaction among individuals contesting for a finite shared resource, plays a crucial role in determining the composition of these communities. However, a comprehensive understanding of the extent of competitive interactions in marine communities and their environmental drivers still eludes us. In this study, we use modern-day occurrence records and a suite of statistical approaches to gauge the evolutionary outcomes of competition in marine molluscs. We seek to explore the effect of abiotic environmental factors on competition, and propose a new metric to test the extent of competitive interactions using the mean taxonomic distinctness among co-occurring species pairs. This robust metric is not influenced by the sample size or species/genus richness of the studied population. Our key findings show that competition among marine molluscs did not result in the segregation of closely related species over time. While the effect of abiotic factors on competition were found to be context-dependent and inconsistent across classes; Depth, Sea Surface Temperature and Dissolved O_2 exerted a considerable control on competition. The cascading effects of climate change warrant further explorations to assess the impact of these factors on competition, owing to their important consequences on biodiversity and community structure.

Chapter 1

Introduction

Elements of biotic interactions like predation, mutualism, competition are resource-intensive and profoundly influence survival and reproductive outcomes [Kozłowski 1992]. Studies done on living ecological communities demonstrates the substantial and enduring impacts of these biotic interactions on the participating organisms [Thompson 2005].

In both marine and terrestrial ecosystems, competition plays a crucial role in determining the composition of biological communities [Tilman 1987]. Competition is generally described as the interaction among individuals contesting for a finite shared resource. However, more broadly, competition can be considered as the indirect or direct interplay within organisms that results in a change in their fitness when they vie for the same finite resource. If the demand for a resource by organisms within an ecosystem is substantial, it results in a reduction in the resource's abundance or concentration. When the resource's concentration dwindles to a critical threshold, it can become insufficient to meet the minimum requirements of a species, thus limiting the proliferation of that species.

The critical resource concentration at which net population growth is sustained, with uptake rates by the population and supply rates by the environment in equilibrium, is referred to as R* [Tilman 1985]. If a_j is the rate at which species j consumes the resource and d denotes the death rate of species j,

$$R_j^* = d/a_j$$

Assuming that all species vie for the same limited resource, the species possessing the lowest R* is expected to outcompete and predominate over other species within a community [Tilman et al. 1982]. However, natural communities often deviate from equilibrium, and the competitive outcome and diversity of a community are regulated

not solely by a species' capacity to exploit resources.

In addition to limiting resources, species diversity is governed by other significant regulatory factors, which can be classified as either biotic - factors like differential grazing pressure, parasitism or various forms of symbiotic interactions like mutualism; or abiotic - including factors like temperature, pH, depth, and salinity [Begon et al. 2006; Cloern et al. 2005]. The predictability of how environmental change affects the outcome of competition however remains uncertain, mainly due to the limited number of studies addressing this issue. The situation is further complicated by concurrent shifts in multiple abiotic factors, something often anticipated under the cascading effects of climate change. For instance, scenarios involving rising sea surface temperatures alongside alterations in nutrient inputs could present complex challenges, as these abiotic factors may interact in various ways (e.g., antagonistically or multiplicatively). Moreover, organisms might respond in manners that do not align with the responses observed when individual factors operate in isolation [Harley et al. 2017, Thomas et al. 2017].

1.1 Competitive Interactions

The principle of competitive exclusion was borne out of Georgy Gause's groundbreaking work in early 1930s, based on laboratory experiments with mixed cultures of both yeast and Paramecium species [Kneitel 2019]. It posits that two or more species sharing identical ecological niches and competing for the same set of resources cannot coexist in the same niche over an extended period of time. A dominant competitor can displace a subordinate one from the region over time, culminating in competitive exclusion [Hardin 1960]. Equations such as the Lotka-Volterra model [Volterra 1926, Lotka 1932], offer predictive insights into the outcomes of competition between two species. The ecological consequences of competition can result in a) one of the species always outcompeting the other, b) either of the species outcompeting the other, subject to ambient biotic/abiotic factors, or c) emergence of mechanisms for coexistence.

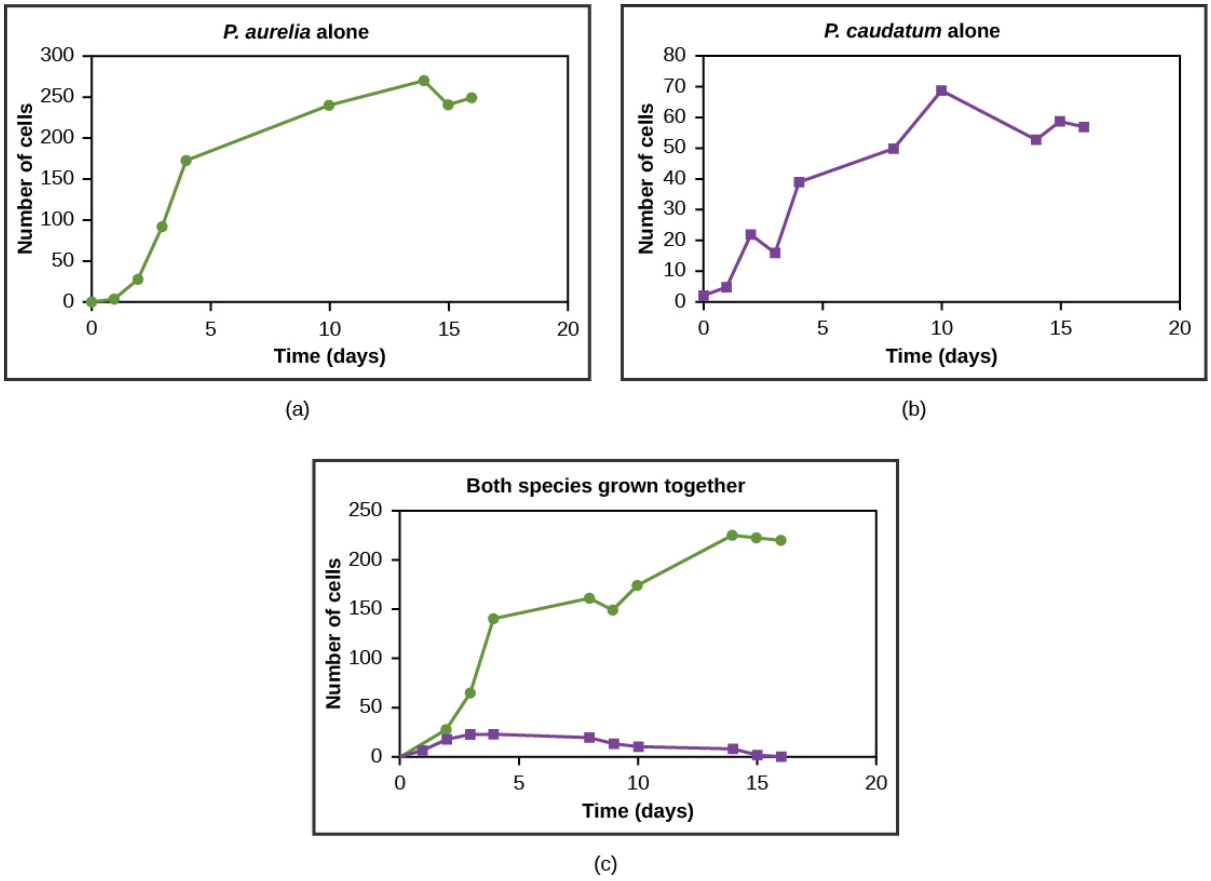


Figure 1.1: **Gause's Laboratory Experiments on Competitive Exclusion** Paramecium aurelia and Paramecium caudatum thrive when they exist separately. However, while vying for the same resources, P. aurelia surpasses P. caudatum in the competition. (Image sourced from Biology LibreTexts, with free usage permission)

Competitive exclusion may result in changes in proportions of a group within a population, or even a local extinction of one of the species from the environment in question. Consequently, quantifying competitive interactions have far-reaching implications on the stability of ecosystems and decision-making regarding biodiversity conservation [Yang et al. 2017, Lehman et al. 2000].

Multiple independent approaches have been adopted to quantify competition in marine communities, both in modern and fossil records [Peterson 1980, Link et al. 2013]. For example, it has been determined that relative differences in size can be used as a tracer for competitive interactions in encrusting bryozoans, which compete for the limiting resource of substrate space. [Liow, Di Martino, et al. 2017, Liow, Reitan, et al. 2019].

Traditionally, the assessment of competition in ecological contexts has primarily relied on experimental methodologies [e.g., Lafferty et al. 2016, Hixon et al. 2005]. Alternatively, the post-hoc analysis of time series data on species abundance has been em-

ployed, accompanied by statistical modeling to fit population dynamics [e.g., Schoener 1974, Novak et al. 2008]. These diverse approaches possess their respective strengths and limitations, and in some instances, a combination of methods have revealed congruous conclusions [King et al. 1983, Novak et al. 2010].

Yet, the precise quantification of competition and the identification of its specific determinants have remained elusive. In essence, gauging competition in natural settings, where its effects can be unequivocally attributed to this factor and stand up to rigorous scrutiny while accounting for existing ecological theory, remains a challenging endeavor. While competition has been demonstrated more readily in aquatic ecosystems such as coral reefs, intertidal zones and freshwater lakes, with many seminal theories and tests stemming from these studies [Connell 1961, Lubchenco et al. 1978, Menge et al. 1986], the resulting competition theories have often concentrated on smaller, localized spatiotemporal scales due to the nature of these investigations. Thus, the extent of competition over large spatio-temporal scales and involving a multitude of species belonging to different taxonomic groups remains underexplored.

1.1.1 Biotic and Abiotic Controls on Competition

- **Taxonomic Relatedness**: The Naturalization hypothesis [Darwin 1859] implies a reduced establishment success among closely related species, due to competition and exceedance of "limiting similarity" [Abrams 1983]. However, this is contradicted by Darwin's Naturalization Conundrum [Darwin 1859, Diez et al. 2008], which propounds higher establishment success among closely related species. This is thought to be a consequence of increased habitat suitability conferred by similar traits.

  There is yet another standpoint [Tilman 2011], which argues that the success of a species is independent of source community phylogenetic structure. In the context of marine communities, this was supported by [Klompmaker et al. 2018], who asserted that competitive interactions do not dictate community composition. Ricciardi and Mottiar [Ricciardi et al. 2006] went further to propose the pre-adaptation hypothesis, which stated that introduced species will invade regardless of existing community composition, given appropriate abiotic conditions.

- **Depth of Habitat:** Klompmaker and Finnegan [Klompmaker et al. 2018] found that competitive exclusion was rare in marine ecosystems. They attributed it to predation and disturbances, which kept the communities well below the environment's carrying capacity and thus lowered the intensity of competition between species. However, since predation pressure and disturbances strongly de-

crease with increase in depth [Harper et al. 2016], competitive interactions could indeed be significant at higher depths.

- **Sea Surface Temperature**: H. Hillebrand [Hillebrand 2011], from his microcosm experiments on benthic microalgae concluded that temperature mediates the outcome of competitive interactions. Warming was negatively correlated with the overall species richness, and contributed to a greater rate of extinction. Higher temperatures also led to changes in the dominant species and accelerated competitive displacement, thus resulting in a change in the community structure.

- **Availability of Dissolved O_2**: Previous works [Ferguson et al. 2013, Breitburg et al. 1997] have shown that the availability of dissolved oxygen in marine ecosystems plays and important role in shaping biotic interactions such as predation and competition. In certain cases, oxygen can serve as the primary limiting resource, and it is highly probable that exploitative competition for this vital resource occurs within marine communities. Changes in predator-prey interactions based on oxygen availability, and the resultant effects on the dynamics of competition can therefore be of prime importance and warrants further studies.

- **Latitude**: The existing literature [Barnes 2002, Schemske et al. 2009] points towards stronger competitive interactions at lower latitudes. Higher competition at tropics is attributed to a generally higher species richness with considerable overlap in their niches and exceedance of limiting similarity. The temperatures at lower latitudes are also higher due to increased insolation, which compound the competitive effects. In addition, studies on Bryozoans [Barnes 2002] have revealed that weaker competitors tend to experience a higher rate of failure in their interactions at higher latitudes, implying that ecological communities at the higher latitudes are primarily shaped by physical factors rather than biological (competition-related) processes. Under such a regime, complexity of the interactions are reduced and there are fewer reversal in outcomes or competitive loops (where superior competitors are defeated by inferior ones).

1.2 Co-existence of Species

1.2.1 Niche Partitioning

Nature is replete with instances where multiple closely related species manage to co-exist despite the looming shadow of competitive exclusion. This paradox is resolved through the concept of niche partitioning [Hutchinson 1957, Palmer 1994, Chesson

2000]. When seemingly similar species exhibit subtle differences in resource use, behavior, or habitat preference, they can coexist by reducing direct competition.

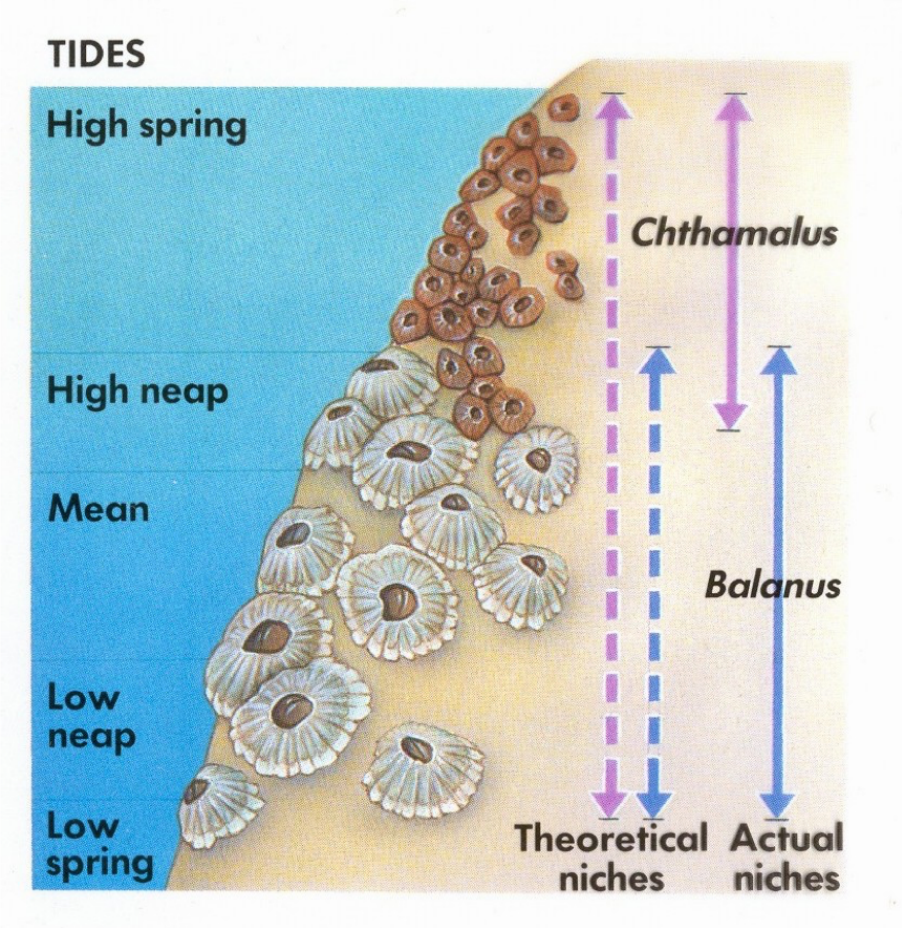


Figure 1.2: Connell's Field Experiments
Image sourced from rushinglab.github.io, with permissions for free usage.

Connell's pioneering research along [Connell 1961] the rocky intertidal zones of Scotland and Wales in the 1960s exemplified this concept. He observed two barnacle species, *Chthamalus stellatus* and *Semibalanus balanoides*, coexisting on the same substrate. Rather than engaging in head-to-head competition, these species exhibited vertical zonation, with *Chthamalus stellatus* primarily occupying the upper zone and *Semibalanus balanoides* dominating the lower zone. This spatial segregation, driven by differences in desiccation tolerance, demonstrated how niche partitioning allowed these barnacles to share the same habitat without intense competition, and highlights the significance of resource specialization in coexistence. In these experiments, barnacle species partitioned their niches vertically and displayed fluctuations in abundance over time due to factors like wave action and predation. These dynamics maintained species diversity in the ecosystem by preventing one species from completely excluding the other, offering a prime example of coexistence in action. Hence, niche partitioning strategies such as temporal segregation, spatial segregation, or dietary special-

ization allow multiple species to thrive within the same ecosystem.

1.2.2 Other mechanisms of co-existence

Coexistence of species can also be facilitated when intra-specific competition outweighs inter-specific competition. In such cases, each species curbs its own population growth before significantly impacting the competitor, thus allowing for their coexistence.

Another strategy to prevent competitive exclusion is the adoption of alternative life history and dispersal tactics, often reinforced by the forces of natural selection. Maintaining coexistence becomes feasible when disturbances take place at intervals or distances that support the persistence of the competitor which is weaker but more adept at dispersing within a habitat. When disturbances occur too frequently, the inferior competitor, which is a superior disperser, prevails. In contrast, if disturbances are rare, the superior competitor gradually outcompetes the inferior one, ultimately leading to competitive exclusion. This phenomenon is known as the intermediate disturbance hypothesis [Fox 1979, Wilkinson 1999].

1.3 Introduction to Species Co-occurrence

The concept of species co-occurrence offers a straightforward yet effective method for inferring species interactions within ecological systems, in cases where other direct indicators are unavailable or hard to measure [Morales-Castilla et al. 2015, Cazelles et al. 2016, Sander et al. 2017]. In this context, substantial spatial co-occurrence is indicative of positive or mutualistic interactions, while co-exclusion suggests negative interactions, such as competition [Faust, Lahti, et al. 2015, Fuhrman et al. 2015]. The fundamental premise of the co-occurrence approach is that if species within a community interact in ways that influence each other's abundance or presence across space, thereby shaping local community assembly patterns, they will exhibit non-random co-occurrence patterns, which can be detected through suitable sampling designs and statistical tests [Ulrich et al. 2013, Borthagaray et al. 2014].

For instance, predators might be observed more frequently with their prey, and competitors might be seen together less often than expected by random assembly. While our understanding of co-occurrence patterns and the underlying processes of community assembly has evolved beyond its initial simplicity [Chase 2010, De Bello et al. 2012, Cazelles et al. 2016], the core premise incorporates species presence-absence data and estimates their probability of occurrence at each site [Peres-Neto et al. 2001].

The patterns of interactions among community members have implications for population dynamics, species persistence, network stability, and ecological function maintenance [Allesina et al. 2008, Faust and Raes 2012]. Hence, it's crucial to grasp the extent to which species co-occurrence patterns reflect species interactions.

However, several ecological and methodological factors may obscure the translation of ecological interactions into easily discernible co-occurrence patterns. Ecological species co-occurrence analyses often involve non-trivial assumptions integrated into their design, which require scrutiny to better understand the approach's limitations in interpreting ecological dynamics.

For example, predator-prey relationships may exhibit positive correlations over specific spatial scales that allow predators to maximize prey encounters. However, at smaller scales, effective predators may eliminate prey, forcing them into refuges beyond predator reach, resulting in strong negative associations. Detecting such correlations across multi-species assemblages with fixed sampling sizes can be challenging. Moreover, species can coexist and exhibit correlations in their abundances through time or space due to the influence of a third species or a common environmental factor, even if the species pair doesn't interact directly (as in apparent competition). The complex multi-species interactions in real communities, where each species simultaneously interacts with many others in diverse ways, introduce further complications when trying to derive interaction patterns from co-occurrence data [Berlow et al. 2004, Kéfi et al. 2016; Azaele et al. 2010].

Despite these challenges, one can argue that if species interactions significantly influence species presence, non-random co-occurrence patterns should reflect this multitude of interactions, particularly when controlling for environmental effects and the indirect effects of third species [Peres-Neto et al. 2001, Azaele et al. 2010]. Co-occurrence analyses can be particularly valuable because they have the potential to unveil which species respond similarly to ecosystem conditions. Detecting significant co-occurrence patterns can highlight robust ecological interactions while screening out weaker effects.

Chapter 2

Objectives

A comprehensive understanding of the biotic and abiotic factors shaping the structure of ecological communities still eludes us. When it comes to marine communities, the picture is even murkier since they are far understudied compared to their terrestrial counterparts.

Open questions remain regarding the evolutionary outcomes of competition in marine molluscs. The current literature provides conflicting views on the links between competition and relatedness among species, and it has not been concretely established whether closely related marine species are more likely to compete. Similarly, we lack an understanding regarding the effect of abiotic environmental factors (e.g. Temperature, Availability of Dissolved Oxygen, Depth, etc.) on community assembly, and phenomena like competition or coexistence. In this study, we attempt several tests to predict the drivers of competition or coexistence in marine molluscan communities. The hypotheses are listed and detailed below:

1. **Competition and relatedness among organisms**:
    (a) **Assumption:** Species pairs with greater phylogenetic relatedness compete more intensely for resources, in tune with Darwin's Naturalization hypothesis.
    (b) **Hypothesis**: Positively co-occurring species pairs have a higher taxonomic distinctness compared to the randomly/negatively co-occurring species pairs.

2. **Depth-dependent competitive interactions**:

   (a) **Assumption**: Competitive exclusion is at higher at greater depths.

   (b) **Hypothesis**: Positively co-occurring species pairs from deeper habitats exhibit a higher mean taxonomic distinctness in comparison to co-occurring pairs from shallower depths.

3. **Temperature-regulated Competitive interactions**:

   (a) **Assumption**: Higher temperatures lead to increased competitive exclusion.

   (b) **Hypothesis**: Positively co-occurring species pairs from higher temperature regions exhibit higher mean taxonomic distinctness in comparison to co-occurring pairs from lower temperature bins.

4. **Dependence on Dissolved Oxygen:**

   (a) **Assumption**: Lower availability of dissolved Oxygen leads to increased competitive exclusion.

   (b) **Hypothesis**: Positively co-occurring species pairs from spatial bins with lower dissolved O_2 exhibit higher mean taxonomic distinctness in comparison to co-occurring pairs from higher dissolved O_2 bins.

In addition to rigorously testing these hypotheses, we seek to conduct exploratory inquiries to ascertain the impact of a community's species richness on its mean taxonomic distinctness and the environmental drivers of species richness in a community. The findings will assist us in deriving reliable conclusions on the drivers of community assembly in marine molluscan communities.

Chapter 3

Data and Methods

3.1 Data Source and Preprocessing

The source of our primary dataset for this study was the Ocean Biodiversity Information System (www.obis.org), a globally accessible and openly available web-based repository dedicated to marine biodiversity data. Within the OBIS repository, we specifically accessed and retrieved occurrence data pertaining to two prominent molluscan classes, namely Bivalvia and Gastropoda. Our study exclusively centered on occurrences within marine environments, excluding the ones from terrestrial or freshwater environments.

The dataset contained information on multiple fields, including geographical coordinates, taxonomic nomenclature (species, genus, etc.), as well as supplementary data on the depth of occurrence, method of collection, among many others. Notably, each taxonomic entry was linked to a WoRMS AphiaID entry. This association was pivotal in mitigating potential errors arising from ambiguities in nomenclature.

A series of preliminary checks were conducted to ensure the uniformity and quality of the data, and to set the stage for subsequent analyses. The key preprocessing measures are detailed below:

1. **Validation of location coordinates:** Initial data cleansing involved the removal of records with missing or incomplete location coordinates. This step was crucial to maintain data integrity and reliability.

2. **Completeness in Taxonomic Hierarchy:** Ensuring the completeness of data availability across various taxonomic levels (Species, Genus, Subfamily, Family, Superfamily, Order, Subclass and Class) was imperative for the calculation of taxonomic distinctness, as detailed in section [2.x]. Hence, rows with any missing en-

tries in these taxonomic columns were systematically excluded from the dataset.

3. **Reprojection to geographical grids:** To facilitate spatial analysis at a 0.1 x 0.1 degree resolution, the occurrence data were binned into geographical grids of the same resolution.

In addition to the molluscan occurrence data sourced from OBIS, datasets pertaining to key oceanographic variables were downloaded from World Ocean Atlas 2018, an open-access collection made available by NCEI-NOAA (US National Oceanic and Atmospheric Administration). The following datasets were retrieved:

- **Sea Surface Temperature (SST)**: The statistical mean of the sea surface temperature in degrees Celsius, over the time period of 1981-2020.

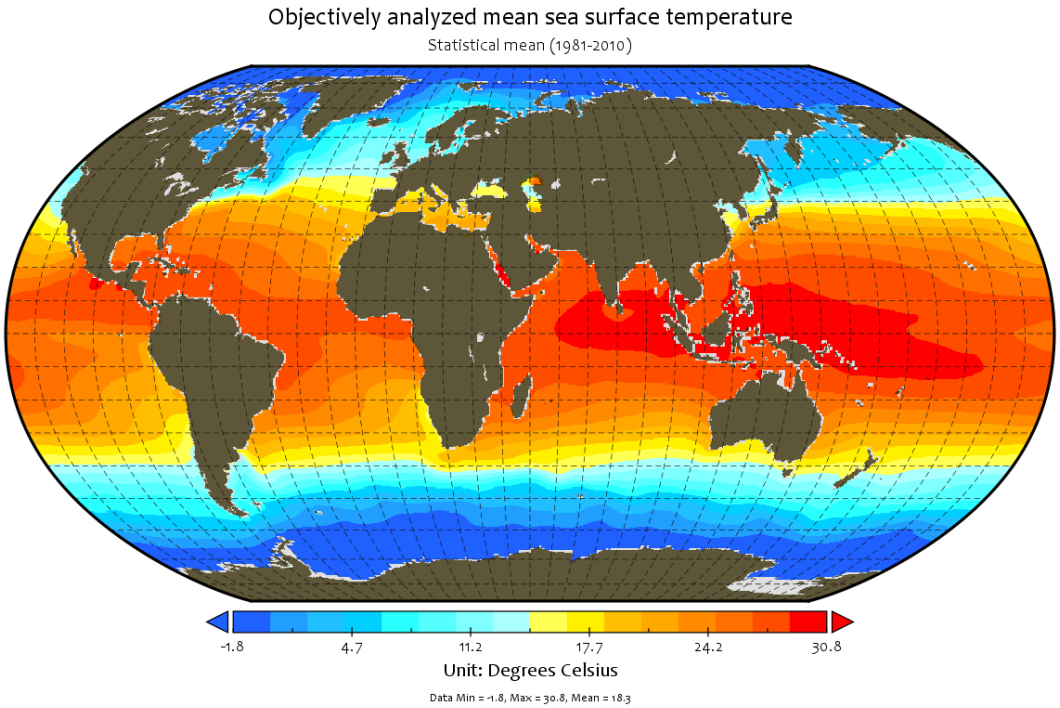


Figure 3.1: Map depicting the sea surface temperature across the world's oceans, within 1x1 degree lat-lon grids.

- **Dissolved Oxygen (dO_2)**: The statistical mean of Dissolved O_2 across all decades of available data, in µmol/kg.

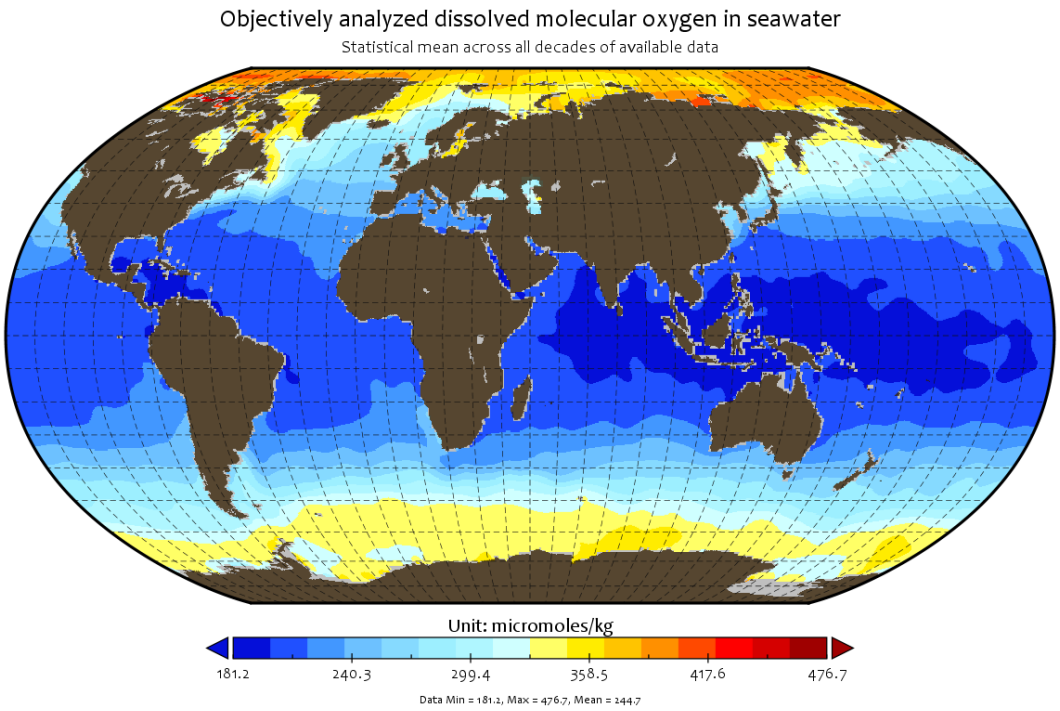


Figure 3.2: Map depicting the Dissolved O_2 in the the world's oceans, binned into 1x1 degree lat-lon grids

We then followed a systematic approach to assess the influence of environmental factors on community structure by stratifying the occurrence data into distinct subsets:

- **Latitude**: The data was categorized into latitudinal bins with a 5-degree width, spanning from 0-5 degrees to 75-80 degrees based on location coordinates given by OBIS. The northernmost latitudinal bands (80-90 degrees) were omitted from the analysis due to sparsity in the records.

- **Depth**: Utilizing the occurrence depth records, we segmented the data into depth bins, encompassing marine environments ranging from very shallow to deep. These depth bins included 0-10m, 10-20m, 20-30m, 30-40m, 40-50m, 50-200m, and >200m.

- **Sea Surface Temperature**: To account for variations in sea surface temperature across geographical grids, we divided the occurrence records into 10 subsets based on SST values at sampling sites. These subsets were determined by percentile values, spanning from the 0-10th percentile (representing the coldest 10% of sites) to 90-100th percentile (encompassing the hottest 10% of sites).

- **Dissolved Oxygen**: Similar to SST, to account for variations in Dissolved Oxygen content in the waters across the geographical grids, we divided the data into 10 subsets based on the dissolved O_2 values of the grids that the occurrence records

fall into. Again, the bins were separated by every 10th percentile, ordered from lowest to highest oxygen availability.

3.2 Species Co-occurrence Analysis

Species co-occurrence analysis is a technique that delves into the intricate relationships among species within ecosystems. This approach operates on the fundamental premise that species rarely exist in isolation but instead form complex networks of interactions in their shared environments. At its core, species co-occurrence analysis is a method that rigorously examines the patterns of species presence and absence across multiple sampling sites (or even time intervals), with the primary objective to discern whether certain species tend to co-occur more frequently or less frequently than what would be expected by random chance alone. By quantifying and statistically analyzing patterns of species co-occurrence, we can systematically evaluate hypotheses about the processes governing community assembly.

For instance, when species consistently avoid co-occurring, it suggests the potential influence of competitive interactions, where species vie for limited resources. Conversely, positive associations in co-occurrence may indicate mutualistic relationships where species benefit from each other's presence, or shared environmental preferences suggesting niche similarities.

Deciphering these intricate patterns of coexistence (or lack thereof) contributes to our broader comprehension of how biodiversity thrives and evolves within Earth's multifaceted ecosystems. To achieve this, an array of techniques have been designed to identify pairs of species that exhibit either higher or lower spatial co-occurrence than what would be expected by chance [cite packages].

However, these algorithms frequently demand huge computational resources and yield a large volume of results. This imposes a burdensome constraint in terms of both time and money, rendering such analyses to be infeasible in many cases. To address this challenge, the 'cooccur' package in R offers a streamlined and user-friendly implementation of the probabilistic species co-occurrence model, originally developed by Veech in 2013. The modified version employs a concise mathematical formulation which provides significant gains in speed and computational efficiency. As a result, this approach conserves computational resources while providing an accessible and feasible tool for ecologists that can be used for downstream analyses.

3.2.1 'cooccur' package in R

The core of the cooccur package revolves around its primary function, cooccur(). This function takes community data as input, which can be in the form of a data frame or matrix representing species presence/absence across sites (or vice-versa, i.e. sitewise presence/absence across species). When executed, cooccur() yields a comprehensive list comprising the results of pairwise species co-occurrence analyses. The analysis does not rely on any specific underlying statistical distribution.

For each of the species pairs, it also computes a precise value of probability that the species would co-occur more frequently than what is observed (p_gt) or less than what is observed (p_lt). These can be interpreted in a similar fashion as p-value, albeit without any test statistic. Therefore, for a given a species pair p_gt $\leq \alpha$ means that the species are positively co-occurring (or conversely, p_lt $\leq \alpha$ indicates that the species are negatively co-occurring). Here, α represents the chosen significance level, a threshold determined by the researcher to assess the statistical significance of the associations observed between species pairs. This approach allows for the quantification of species interactions, aiding in the identification of both positive and negative species interactions within the dataset.

To facilitate the use of 'cooccur' package in conjunction with our datasets, a few prior processing measures had to be followed to match the required input format. To this end, a new function was defined to create a presence-absence matrix, run-occur and obtain the desired output. The function accepts an occurrence dataset with latitude, longitude and species/genus name as input and creates a presence-absence matrix as output. The output results in a matrix where the 0.1 x 0.1 degree geographical grids (representing sampling sites) form the columns and the species (or genus) names form the rows. The resulting presence-absence matrix appears similar to this:

	Seymour	Baltra	Isabella	Fernandina	Santiago	Rabida	Pinzon	Santa Cruz	Santa Fe	San Cristobal	Espanola	Floreana	Genovesa	Marchena	Pinta	Darwin	Wolf
G. magnirostris	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
G. fortis	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0
G. fuliginosa	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0
G. difficilis	0	0	1	1	1	0	0	1	0	1	0	1	1	0	1	1	1
G. scandens	1	1	1	0	1	1	1	1	1	1	0	1	0	1	1	0	0
G. conirostris	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ca. psittacula	0	0	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0
Ca. pauper	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ca. parvulus	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0
P. crassirostris	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0
Ca. pallida	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0
Ca. heliobates	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ce. olivacea	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Figure 3.3: Sample presence-absence matrix

This matrix is used as an input into the 'cooccur' function, and the successful execution of the function returns all the statistics including p_gt, p_lt for each species pair. The results are stored in a CSV file for further downstream analyses.

3.3 Calculation of Taxonomic Distinctness

Taxonomic Distinctness [Clarke et al. 1998, Warwick et al. 1998] is a biodiversity metric that evaluates the evolutionary relationships by assessing the degree of similarity among species within a community. It does so by considering their placement in the hierarchical tree of taxonomic classification. For instance, a pair of species belonging to the same genus will have a lower taxonomic distinctness than a pair of species belonging to the same family but different genera.

High Taxonomic Distinctness values indicate a community comprising diverse evolutionary lineages, suggesting a broader range of ecological roles and adaptations. Conversely, low Taxonomic Distinctness values imply a community dominated by closely related species, potentially indicating ecological redundancy and a more specialized ecosystem. In theoretical studies, this metric enriches our understanding of community structure by accounting for the depth of evolutionary history, offering insights into the ecological significance of species beyond mere species counts.

Shared taxon	Path length
Species	0
Genus	1
Subfamily	2
Family	3
Superfamily	4
Order	5
Suborder	6
Class	7

Table 3.1: Path lengths assigned to taxonomic levels

3.3.1 Creation of TD Matrix

To quantify the relatedness between co-occurring species pairs, we aimed to calculate the taxonomic distinctness using the 'rdiversity' and 'vegan' packages in R programming language. To achieve this, we first defined a distance vector that assigns a path length between various levels in the Linnaean taxonomic hierarchy. The taxonomic levels and their corresponding path lengths have been outlined in table 3.1.

Then, we proceeded to create a lookup table combining the distance vector and comprehensive taxonomic information at all hierarchical levels. This table is a square symmetric matrix, where the cell (i, j) corresponds to the taxonomic distinctness between species 'i' corresponding to row 'i' and species 'j' corresponding to column 'j'. These cells contain a numeric value, with higher values naturally denoting a higher taxonomic distinctness. We will refer to this lookup table was 'Taxonomic Distinctness (TD) Matrix". Such tables were constructed for both Bivalves and Gastropods, and stored in separate CSV files.

3.3.2 Finding TD for co-occurring species pairs

We combined the ideas in Section 3.3 and 1.3 to calculate the mean taxonomic distinctness of positively co-occurring species pairs in sub-communities graded by different environmental variables. For example, the mean TD (and associated standard error) of co-occurring species pairs was calculated for gastropods falling into the 0-10m depth bin, and similarly for each depth bin. This allows us to gauge how one environmental factor can drive competitive exclusion, with the assumption that in a community, higher mean taxonomic distinctness is a consequence of competitive interactions.

3.4 Statistical Analyses

3.4.1 Correlation between Environmental Variables and Taxonomic Distinctness

The previous step provided us with arrays that contain the values of taxonomic distinctness between each co-occurring species pair, for each bin of all environmental variables. To assess the existence of any significant trend, a function was created in Python whose working is detailed below.

For a given enviromental variable, the function takes multiple arrays as input each corresponding to a specific bin and containing the taxonomic distinctness values for species pairs. We begin by calculating the mean and standard error for each array, which gives us a measure of the central tendency and variability in the data. Then a linear regression analysis is done to identify linear trends in the means across the bins, with a higher slope indicating a strong influence of the environmental factor on competitive exclusion. We also assessed monotonic relationships using the Spearman Rank Correlation coefficient and its associated p-value. This non-parametric statistic allows us to identify ordinal associations within the data.

3.4.2 Permutation Test for Mean Comparison

We employed a permutation test for comparing the means of two distributions, a statistical method used to assess whether the observed difference in means between two datasets is statistically significant. This method is particularly valuable when dealing with non-normally distributed or small sample size data, where traditional parametric tests may not be appropriate.

The created function, "**permutation_test_mean**" takes two input distributions, distribution1 and distribution2, and calculates the observed difference in means between them. It then generates a combined dataset by merging the two distributions and performs a fixed number of permutations (default is 1000) to create a null distribution of mean differences. These permutations involve random shuffling of the combined data and computing the mean difference for each permutation. The function then calculates a p-value by determining the proportion of permuted mean differences that are equal to or more extreme than the observed difference. If the p-value is less than a chosen significance level (0.05 for our analyses), the function concludes that the observed means are significantly different, and the null hypothesis of no difference between the distributions is rejected. Conversely, if the p-value exceeds the significance level,

the function fails to reject the null hypothesis, indicating that there is no statistically significant difference between the distributions.

Chapter 4

Results

4.1 Sensitivity to Sample Size

Since the mean taxonomic distinctness among species pairs in a community is being used as a quantitative measure of the extent of competition/coexistence, it is imperative to ensure that this metric is not sensitive to sample size. Hence we conducted a test by sampling (with replacement) a smaller number of individuals from a community, calculating their mean TD and repeating this process by increasing the sample size - till the maximum number is reached. This test was run for 1000 iterations to attain robust results and obtain a confidence interval.

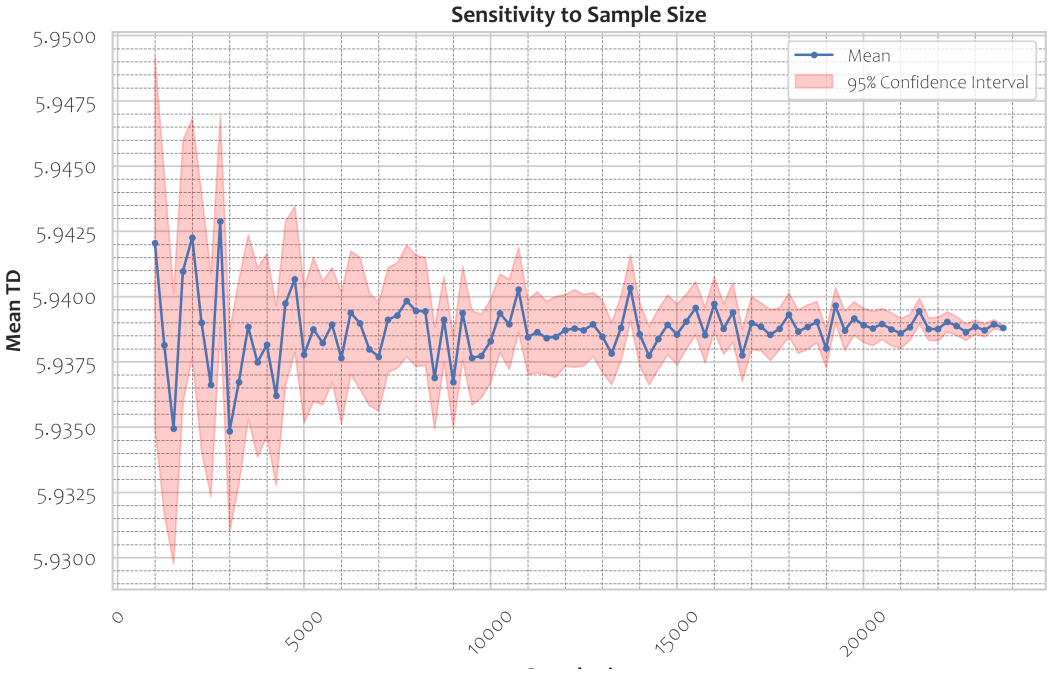


Figure 4.1: Effect of Sample Size on Mean TD

4.2 Species Richness and Taxonomic Distinctness

To assess the impact of community's species/genus richness on the mean TD among species pairs, we compared the species of communities across a gradient of different environmental factors with the mean TD observed among species pairs in that environmental bin. The normalized species (or genus) richness is calculated by ascertaining the total number of unique species/genera in a community divided by the total number of individuals to account for the differences in sample size. The results are reported in the form of Spearman Rank Correlation coefficient, and its associated p-value (<0.05 deemed as the threshold for statistical significance).

4.2.1 Bivalves

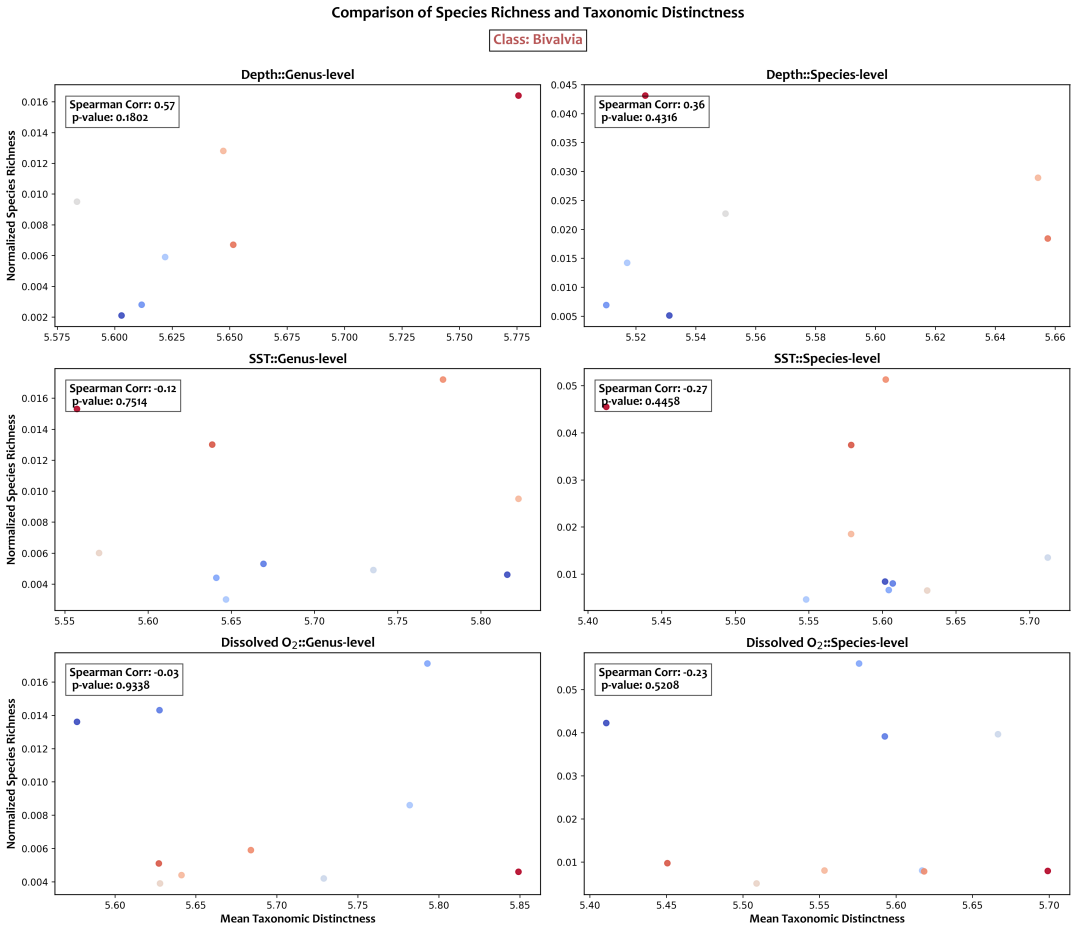


Figure 4.2: **Species Richness vs. Taxonomic Distinctness: Bivalves**
Color-coded scatter points range from Deep Blue (lower values of Depth/SST/Dissolved O_2) to Deep Red (higher values of Depth/SST/Dissolved O_2)

4.2.2 Gastropods

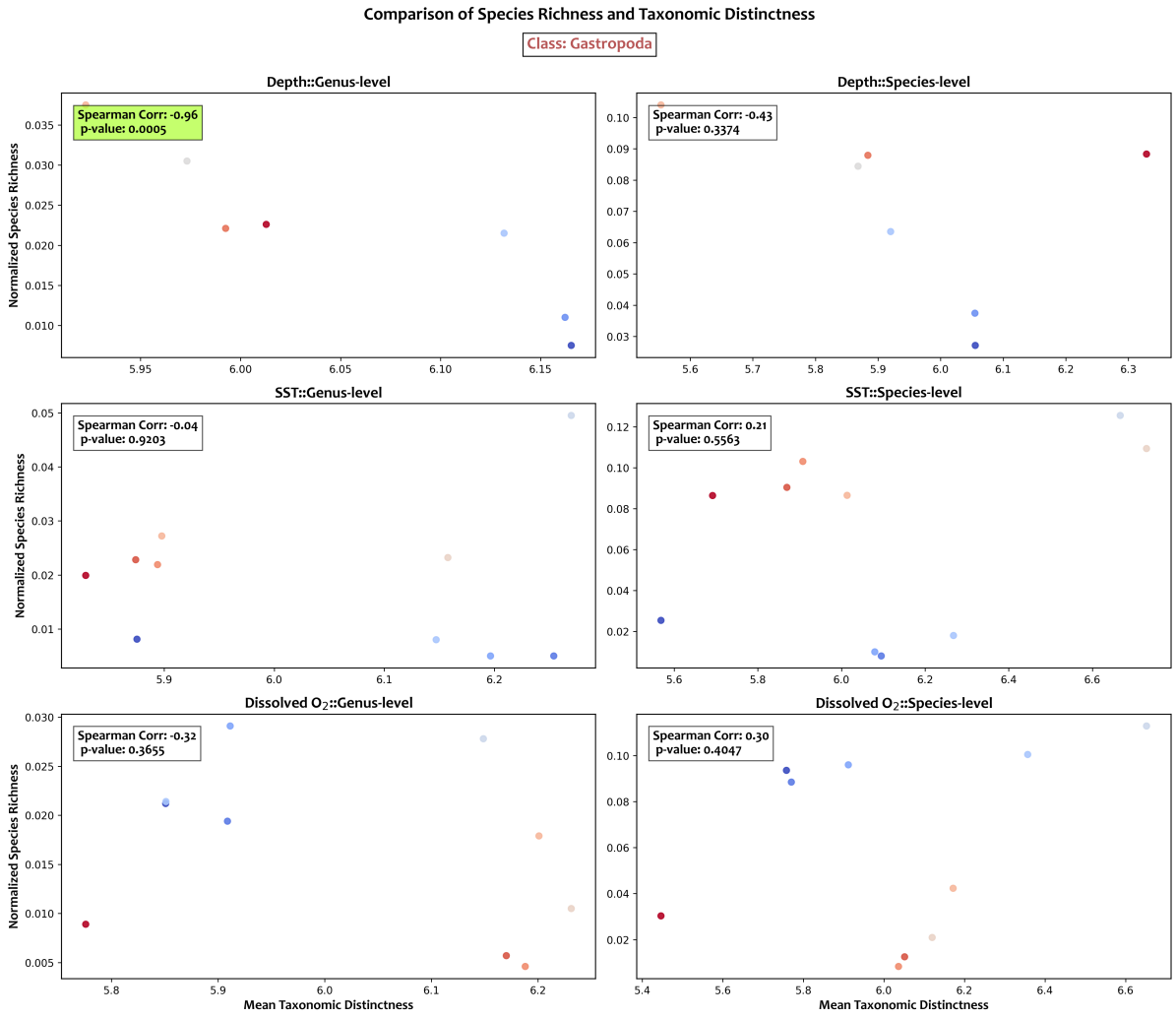


Figure 4.3: **Species Richness vs. Taxonomic Distinctness: Gastropods**

4.3 Taxonomic Distinctness of Co-occurring Species Pairs

We compared the mean TD of co-occurring and non co-occurring species/genus pairs across different environmental gradients to determine whether competition or coexistence are more dominant at a community level. The comparisons were done both at Species and Genus level for two prominent molluscan classes - Bivalvia and Gastropoda. The comparison of the distributions were done using a permutation test (as detailed in section 3.4.2). A p-value less than 0.05 suggests that the difference between the means of the distributions is statistically significant.

4.3.1 Bivalves

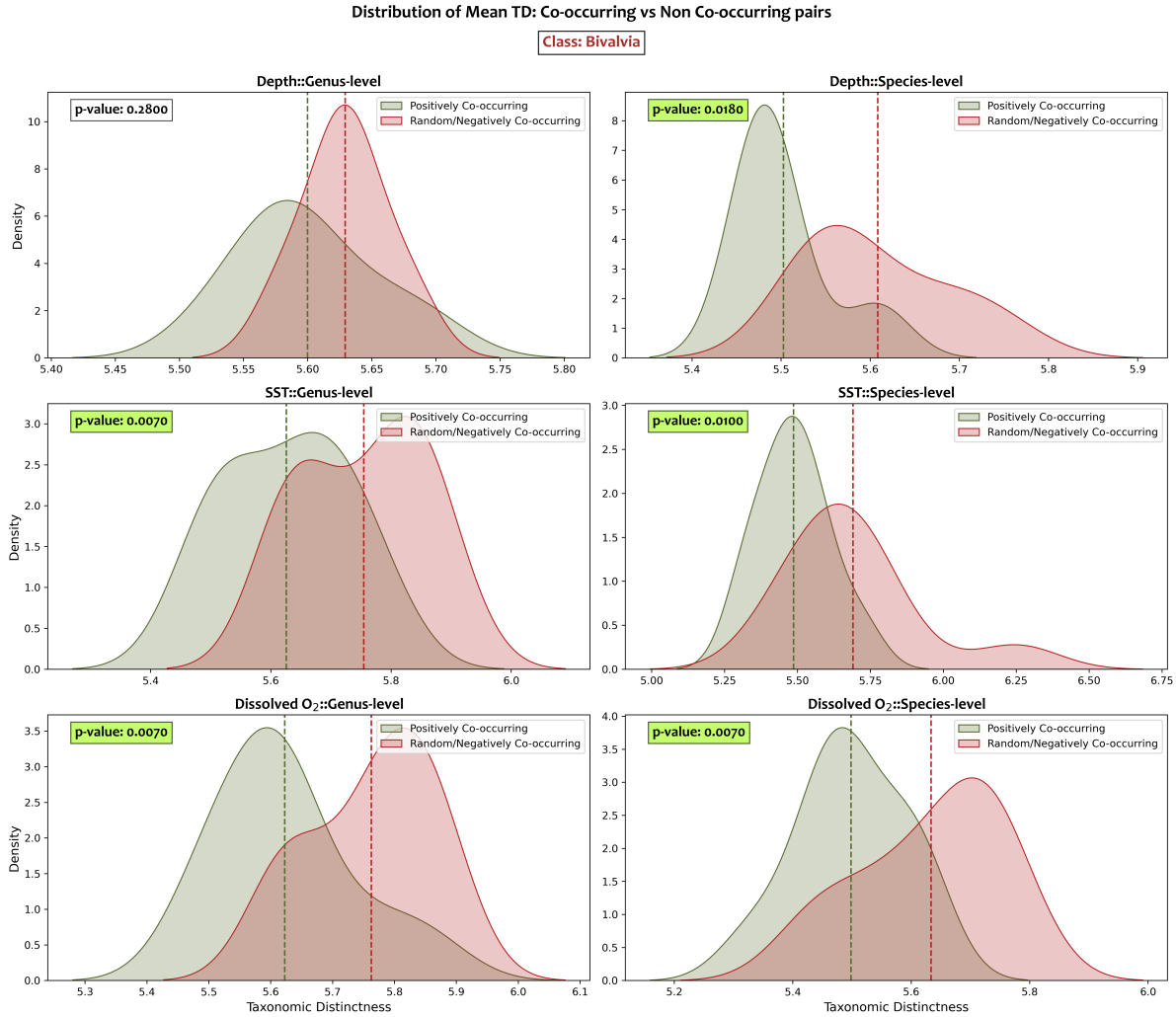


Figure 4.4: **Co-occurring vs. Non Co-occurring Pairs (Bivalves)**
The comparison of the mean TD of these two distributions serves as a proxy for detecting competition. Vertical dotted lines corresponds to the mean of the distributions.

4.3.2 Gastropods

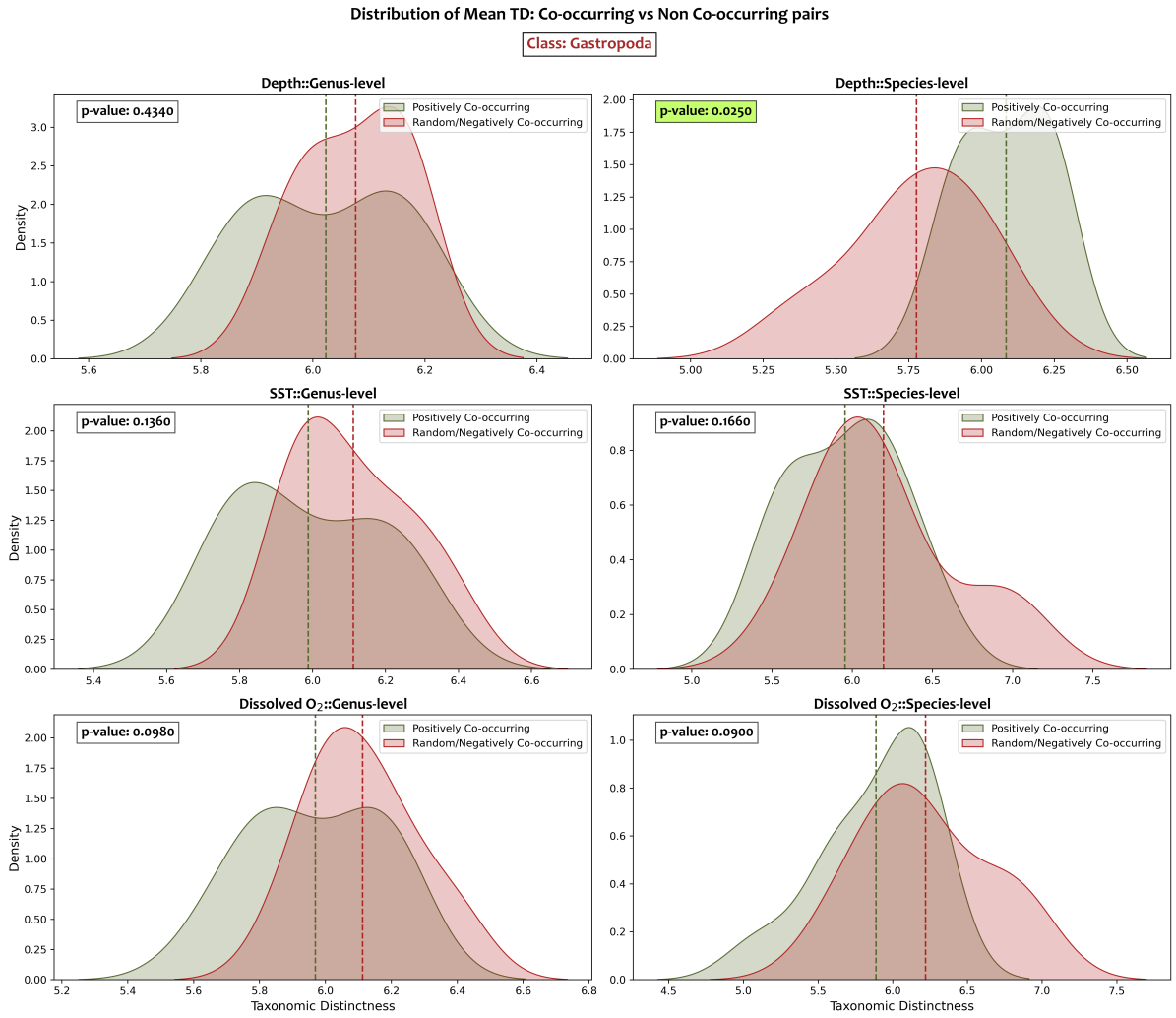


Figure 4.5: **Co-occurring vs. Non Co-occurring Pairs (Gastropods)**

4.4 Temperature-dependent Interactions

In line with our goal of assessing the influence of sea surface temperature on inter-specific/generic competition (or coexistence), we plotted the mean taxonomic distinctness of co-occurring species in each temperature bin. Bin 1 represents the coldest 10% of sites, Bin 10 represents the hottest 10% of sites, while the intermediate bins correspond to the temperatures between these two extremes.

4.4.1 Gastropods

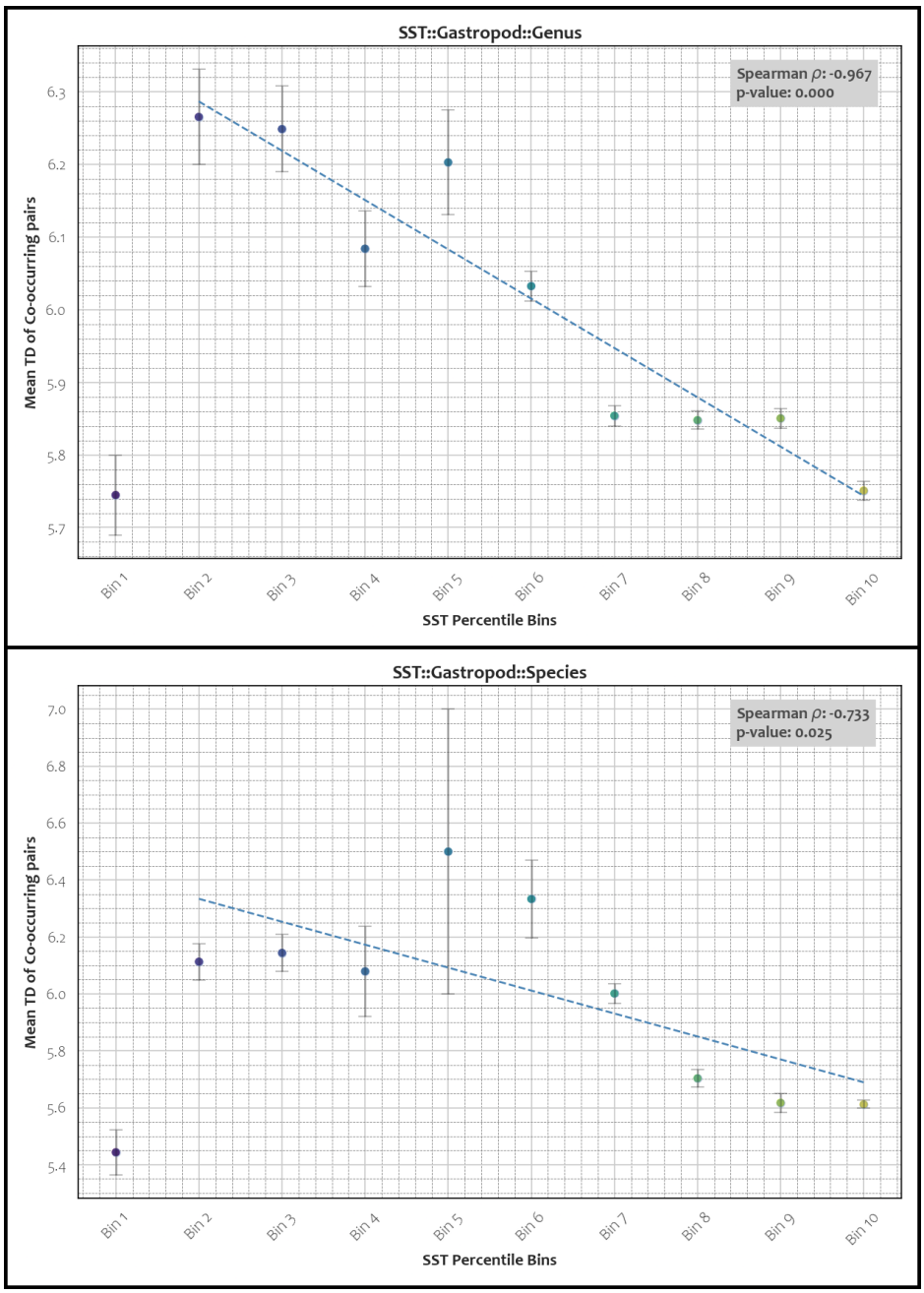


Figure 4.6: **Effect of Temperature on Competition: Gastropods**

4.4.2 Bivalves

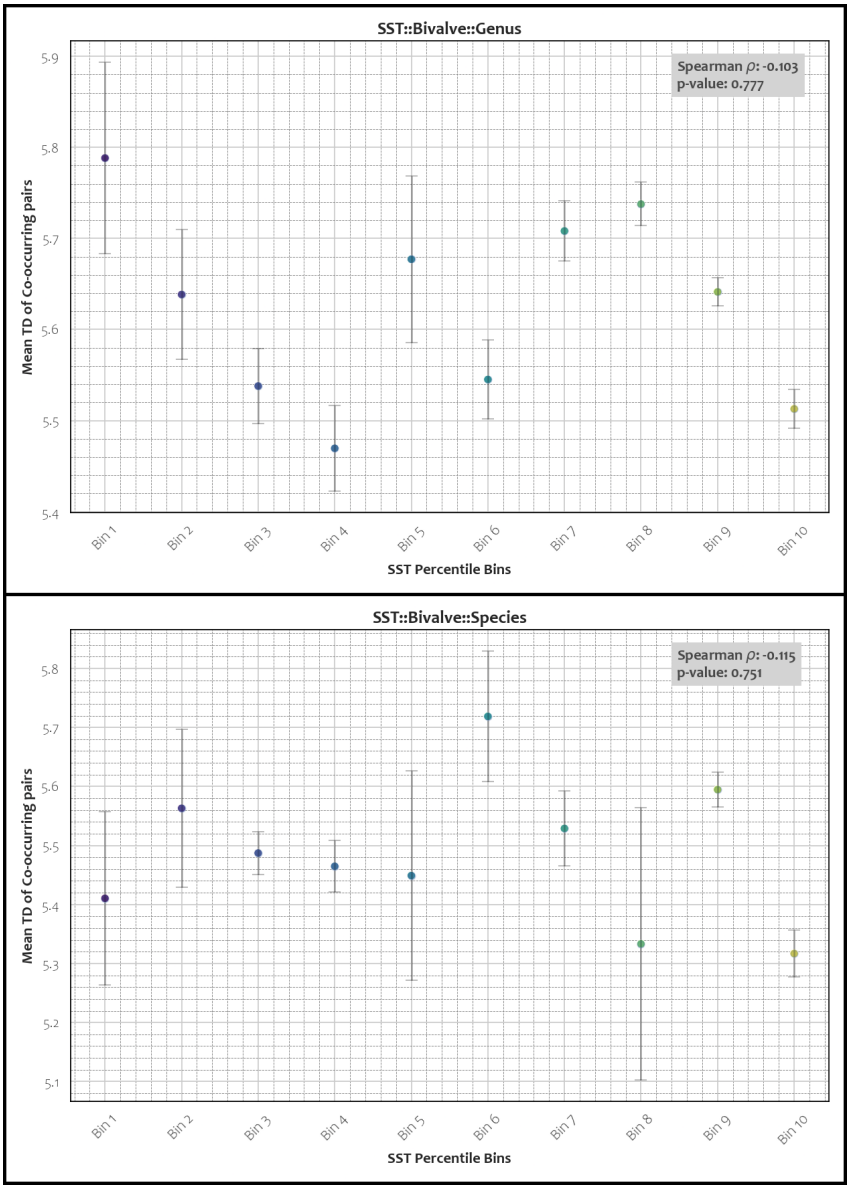


Figure 4.7: **Effect of Temperature on Competition: Bivalves**

4.5 Depth-dependent Interactions

Similarly, to gauge the influence of depth on inter-specific/generic competition (or coexistence), we plotted the mean taxonomic distinctness of co-occurring species in each depth bin. The bins progressively correspond to deeper depths: starting from shallow depths of 0-10m and eventually going beyond 200 meters.

4.5.1 Gastropods

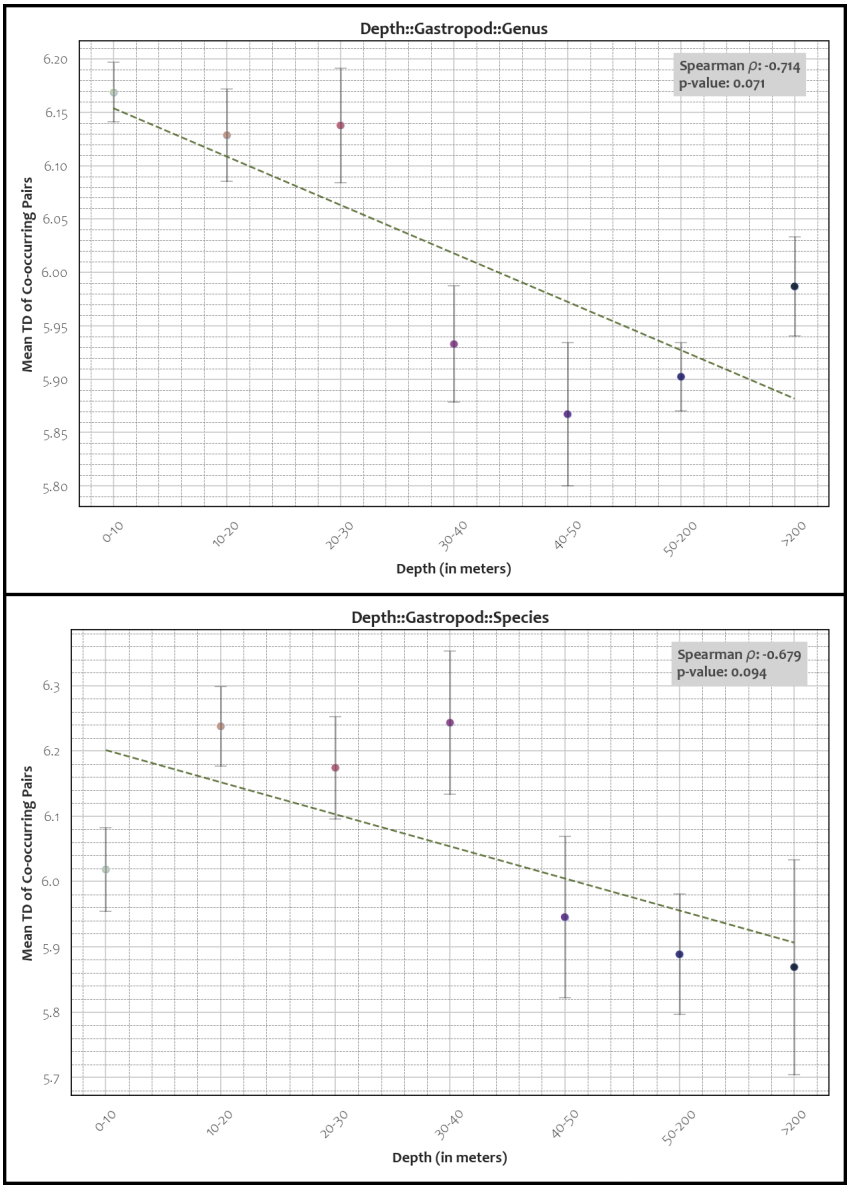


Figure 4.8: Effect of Depth on Competition: Gastropods

4.5.2 Bivalves

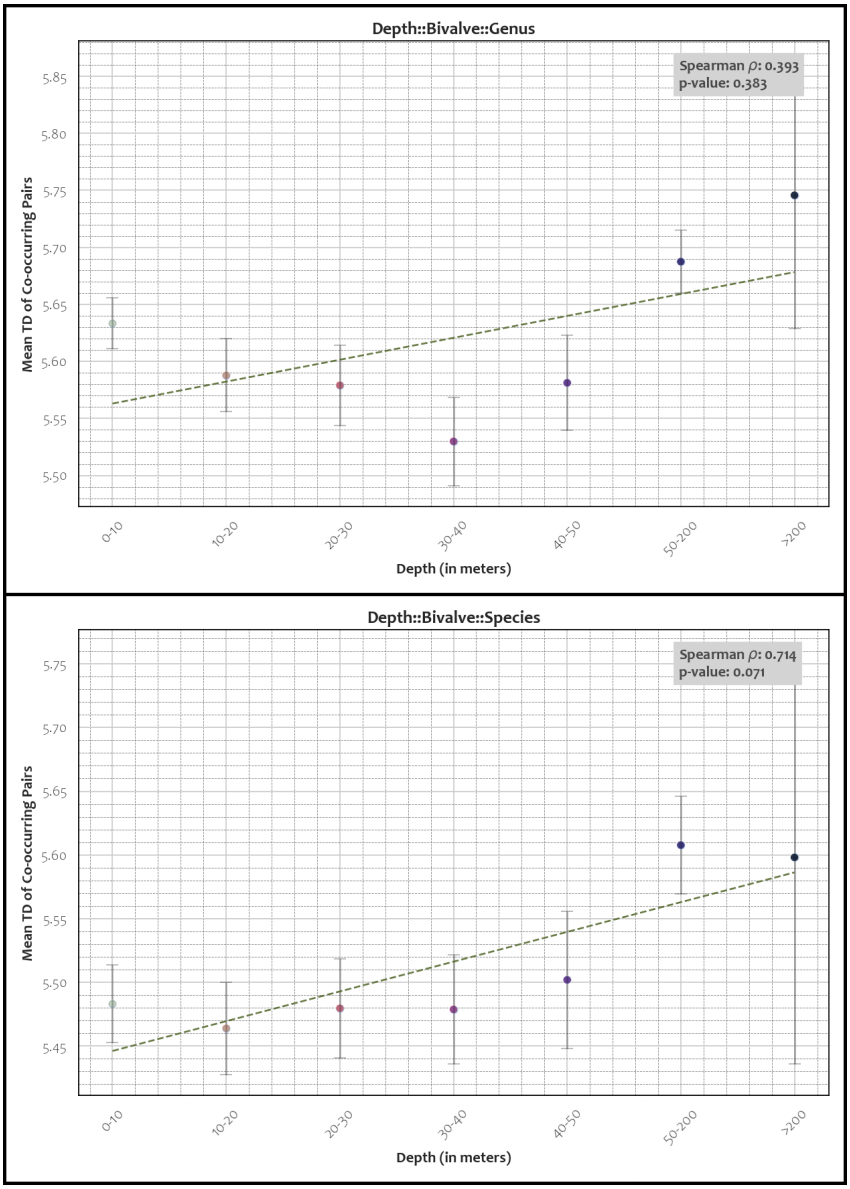


Figure 4.9: Effect of Temperature on Competition: Bivalves

4.6 Interactions for Dissolved O_2

To assess the role of Dissolved Oxygen in shaping mechanisms of coexistence or competition in marine molluscs, we calculated the mean TD of co-occurring species/genus pairs in communities differing in the dissolved oxygen available to them. Bin 1 clubs together all the sites which corresponding to the 10% of sites with lowest oxygen availability, Bin 10 clubs together the sites with the highest 10% of oxygen availability with the other bins corresponding to the communities with intermediate oxygen availability.

4.6.1 Gastropods

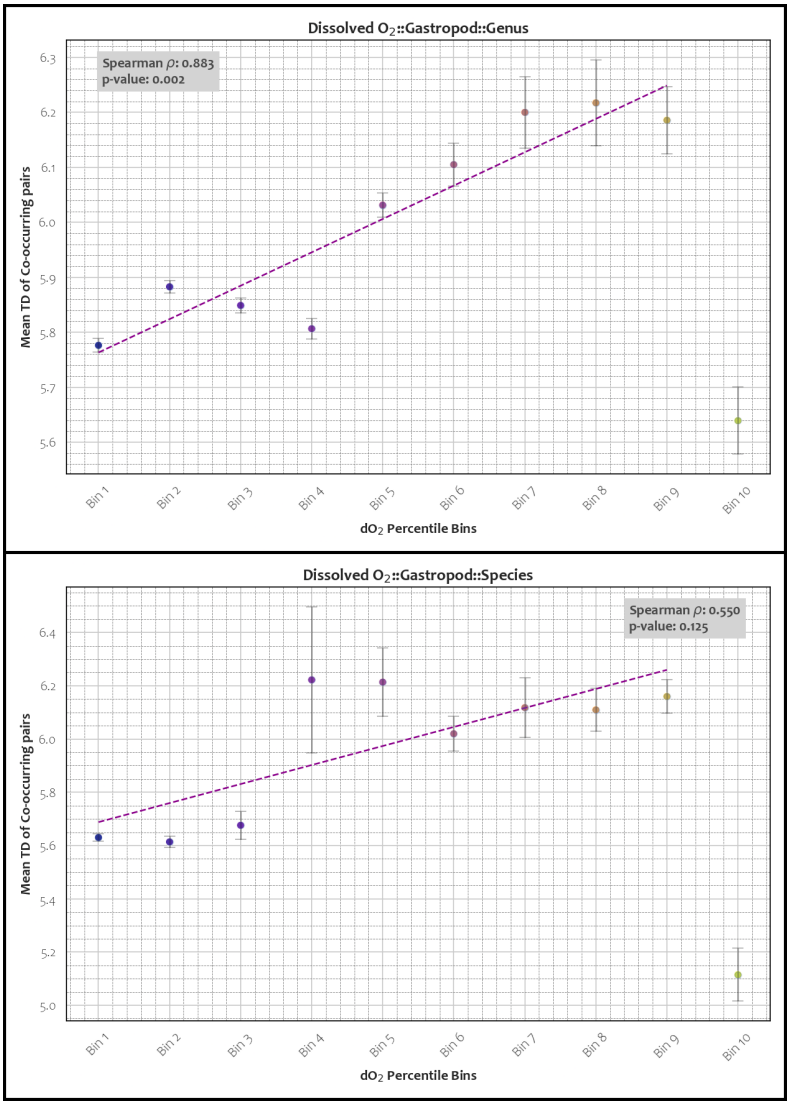


Figure 4.10: Effect of Dissolved O_2 on Competition: Gastropods

4.6.2 Bivalves

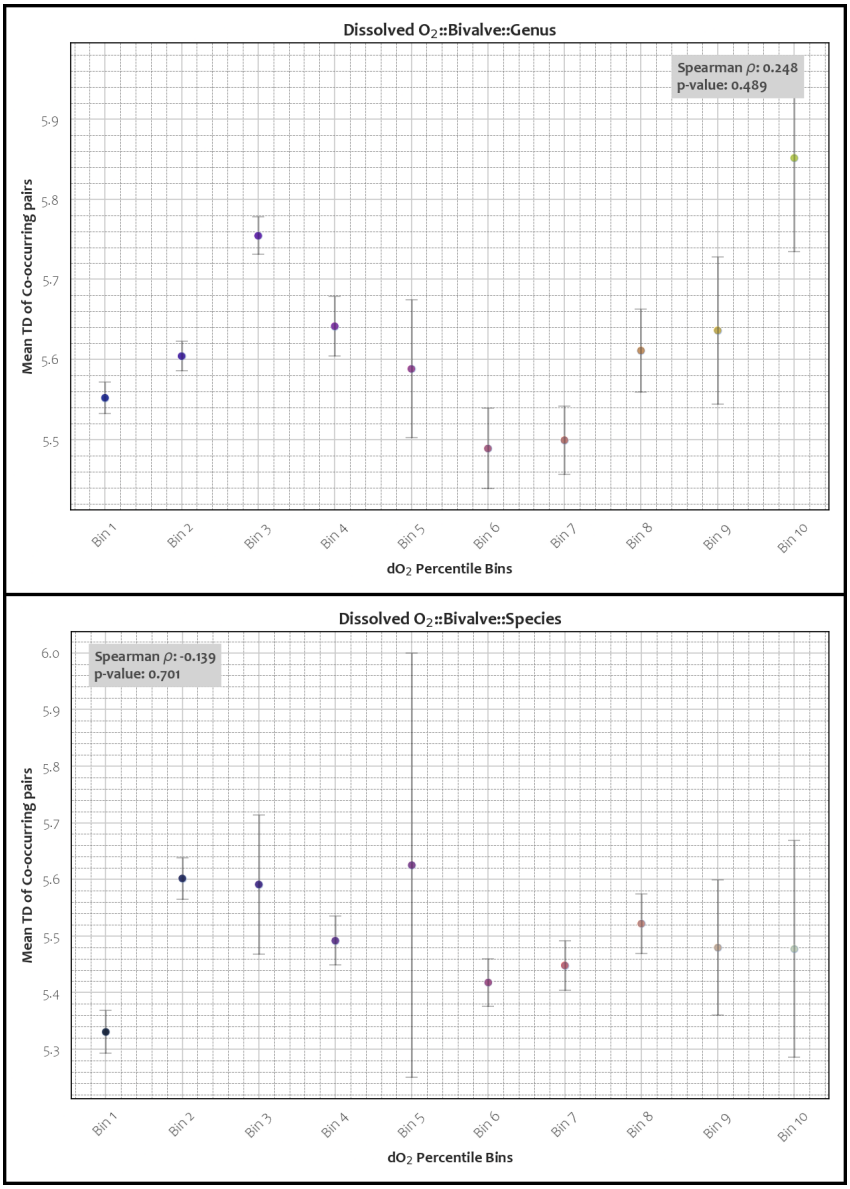


Figure 4.11: Effect of Dissolved O_2 on Competition: Bivalves

4.7 Interactions along Latitudinal Gradients

Latitude plays an important role in determining the ambient temperature, insolation, species richness, etc. and can hence shape interactions of coexistence or competition in an ecological community. Hence, to study its influence, we plotted the mean TD of co-occurring species/genera across different latitudinal bands - going from the equator to the poles.

4.7.1 Gastropods

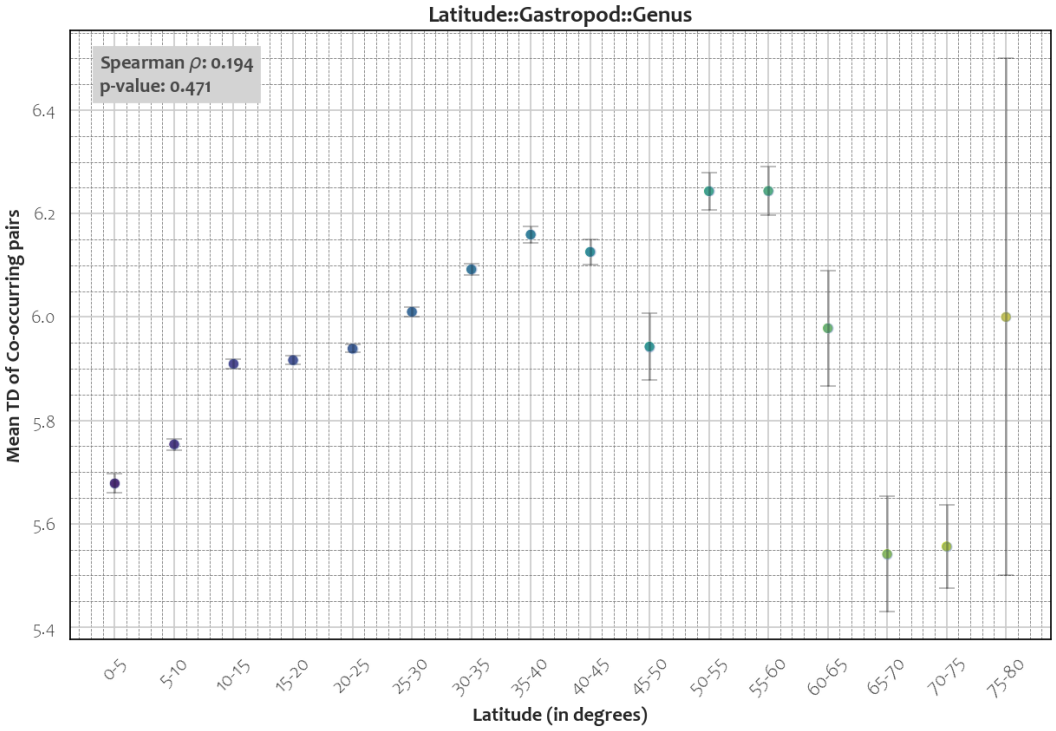


Figure 4.12: Effect of Latitude on Competition: Gastropods

4.7.2 Bivalves

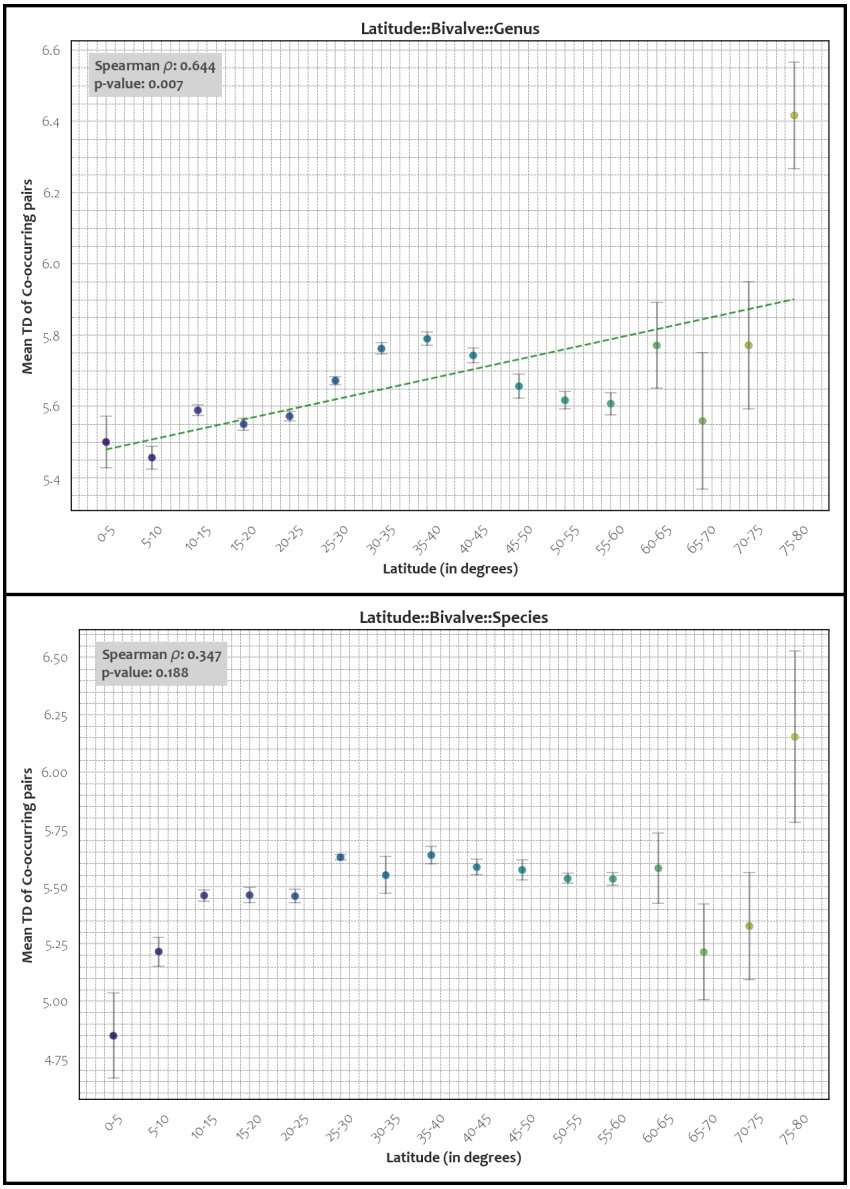


Figure 4.13: Effect of Latitude on Competition: Bivalves

Chapter 5

Discussion

5.1 Sample Size and Mean TD

From figure 4.1, it can be observed that there is no systematic dependence between the number of individuals in a community and the mean taxonomic distinctness among species pairs. While there is a fluctuation in the observed mean TD at lower sample sizes (<5000 individuals), it is of the order of 10^{-2} and can be deemed inconsequential under the resolution of our study.

This is indeed a reassuring result since the dependence of mean TD on sample size could have significantly biased our analyses conducted on communities with a low population size. The stability of this metric at lesser populations makes it an effective tool to gauge the extent of competition/coexistence, even in smaller communities.

5.2 Species Richness

From figure 4.2 and 4.3, we notice the absence of any clearly discernible trend between the species/genus richness in a community and the mean taxonomic distinctness among species/genus pairs. This again reaffirms the reliability of using the metric 'mean TD of co-occurring pairs' as it is not affected by the species richness of the community being studied. It suggests that the outcomes of competition do not necessarily impact the species/genus richness.

5.2.1 In Bivalves

An interesting trend can be observed in the dependence of species/genus richness on a) Sea Surface Temperature and b) Dissolved Oxygen. From 4.2, we can clearly see that the communities in higher sea surface temperature bins (reddish dots) have

markedly higher values of species and genus richness. On the other hand, it can be seen that the communities having higher dissolved O_2 at their disposal exhibit a lower species/genus richness compared to their counterparts which have lesser dissolved O_2 at their disposal.

5.2.2 In Gastropods

An interesting result can also be observed from figure 4.3 that corroborates our findings in section 5.2.1. Similar to what was observed in Bivalves, the species (or genus) richness in Gastropods is markedly higher at higher sea surface temperatures. On the other hand, similar to the trend observed in Bivalves, the species/genus richness is lower in communities which have a higher dissolved O_2 at their disposal.

5.2.3 Consistent Trends

In the two preceding sections, we saw a common trend in both Bivalves and Gastropods which indicated a link between species (genus) richness and SST/Dissolved O_2. We propose the following explanations for the observed trends:

- Areas with lower availability of dissolved oxygen can have complex physical and chemical conditions, giving rise to new forms of micro-habitats. These microhabitats might host a diverse array genera, giving rise to an increased genus richness in lower dissolved O_2 bins. Alternatively (or complementarily), this might also be a corollary of competitive exclusion. The highly competitive species that dominate well-oxygenated environments might be unfit to persist in low-oxygen environments. This would allow the less competitive species to thrive and coexist in low-oxygen environments
- Spatial bins with higher temperatures impose a greater environmental stress on the molluscan groups. To adapt to these conditions, they develop a range of adaptations, which is reflected in the form of higher species/genus richness.

5.3 Competition or Coexistence?

5.3.1 In Bivalves

From figure 4.4, we can observe that the distributions corresponding to mean taxonomic distinctness of co-occurring species pairs consistently have lower values compared to those of the distributions corresponding to non-cooccurring species. Since

we are operating under the assumption that a higher mean TD is a consequence of increased effects of competitive exclusion, this result serves as an opposition to the idea of competition operating at a community level.

Instead, our results suggest that Bivalves develop strategies to effectively partition the available resources and manage to co-exist in the shared habitats. This might be achieved by choice of microhabitats for settlement and growth, based on very subtle differences in preference for water depth, temperature etc.

5.3.2 In Gastropods

From figure 4.5, we can see that most pairs of distributions do not indicate any statistically significant difference between the taxonomic distinctness of co-occurring and non co-occurring gastropod species. However, when observed across different depth levels, positively co-occurring gastropod species pairs have a higher mean taxonomic distinctness compared to their non-cooccurring counterparts. This suggests the presence of species-level competitive interactions when observed at a fixed depth level.

This observation can be attributed to vertical niche partitioning in gastropods, in form of minor variations in temperature tolerance, feeding strategies, shell morphology or other behavioral adaptations depending on different depth range they inhabit. When we tried to look for signatures of competitive exclusion in gastropods at a specific temperature or oxygen level, we could not observe the same because the gastropods resorted to vertical niche separation to avoid competition for resources. However, when studied at the same depth level, these effects of competition were readily apparent - which reflected in form of higher mean TD in positively co-occurring species pairs. Species co-occurring at the same depth range can compete intensely for resources with limited availability such as prey, dissolved oxygen, etc. The constraints imposed by limited resources might be more evident at higher depths in the absence of disturbances and predatory pressure. Disturbances and predatory pressures in shallow marine environments keep the communities below their carrying capacity, thereby reducing the effects of competitive interactions.

While species-level competition was observed at a given depth range, there was no statistically significant trend observed for genus-level competition. This is probably because similarities at a genus level fall below the threshold of 'limiting similarity' and the niches do not overlap enough for competitive interactions to be significant at this relatively coarse taxonomic resolution.

Variable	Observed Taxon	Trend w/ Mean TD
Depth	Genus	Decreasing*
Depth	Species	Decreasing*
Dissolved O_2	Genus	Increasing
Dissolved O_2	Species	Not significant
SST	Genus	Decreasing
SST	Species	Decreasing
Latitude	Genus	Not significant

Table 5.1: **Environmental Factors vs. Mean TD - Gastropods**
Statistically significant relationships between environmental variable and mean TD of co-occurring species/genus pairs have been depicted in green (increasing) and red (decreasing). The trends which are not statistically significant, but slightly above the chosen significance level (0.05) have been depicted in pink.

Variable	Observed Taxon	Trend w/ Mean TD
Depth	Genus	Not significant
Depth	Species	Increasing*
Dissolved O_2	Genus	Not significant
Dissolved O_2	Species	Not significant
SST	Genus	Not Significant
SST	Species	Not significant
Latitude	Genus	Increasing
Latitude	Species	Not significant

Table 5.2: **Environmental Factors vs. Mean TD - Bivalves**
Statistically significant increasing trend in Green, trends slightly outside the chosen significance level (0.05) in yellow.

5.4 Effect of Environmental Factors on Competition

The results presented in sections 4.4-4.7 have been summarized in table 5.1 (for Gastropods) and table 5.2 (for Bivalves). We seek to understand the effect of a specific environmental factor on competition and observe its effect over evolutionary timescale.

5.4.1 Depth

Earlier, in section 5.3.2 we noted the presence of competition among gastropod species when observed at a specific depth level. The results from figure 4.8 allow us to quantify the effect of depth on these competitive interactions. We observe that the mean taxonomic distinctness of Gastropod species pairs has a decreasing linear trend as we go to deeper depth levels. This can be interpreted as a reduction in competitive interactions among gastropod species with increase in depth.

These results are contrary to the proposition of elevated competition at deeper depths [Klompmaker et al. 2018], expected due to the relative lack of predatory disturbances at depths [Stanley 2008] which keep the community below carrying capacity. Hence, our results warrant an alternative explanation.

Predation pressure at shallower depths (due to a variety of predators like shorebirds, crabs, fishes) is still not high enough [Chang et al. 2023] to keep the gastropod communities below the carrying capacity. Instead, in response to the predation pressure, gastropod species with considerable overlap in their niches may face an increased competition for access to refuges or hiding spots. Furthermore, shallower waters are home to greater temperature fluctuations and desiccation stress during low tides - resulting in a lower number of optimum microhabitats. Hence the species with the most efficient strategies for predator avoidance and habitat selection prevail over the others. On the other hand, in deeper waters where predation pressure is even lower and conditions are more stable in terms of temperature stress, competition for the optimum refuges might be reduced. This allows species with considerable niche overlap to coexist, thereby reflecting in a lower mean taxonomic distinctness.

However, our results from bivalves are in agreement with the proposition of elevated competition at deeper depths (or increased coexistence at shallow depths). Previously, from figure 4.4 and in section 5.3.1 we observed that co-occurring bivalve species prefer to coexist rather than compete for resources, within a specific depth bin. The trends of increasing mean TD with depth now suggest that bivalve species are more likely to coexist at shallower depths, as compared to deeper depths.

This observation is can be attributed to the lack of disturbances and predation pressure at deeper depths [Klompmaker et al. 2018, Stanley 2008]. In shallower depths, unlike Gastropods, Bivalves are presumably more affected by the predation pressure which keeps their population below the carrying capacity and mitigates competitive interactions. As these stresses are removed from the Bivalve population, the effects of competition are more apparent as the population nears the carrying capacity and species start competing among themselves.

5.4.2 Sea Surface Temperature

In section 5.3.2 and from figure 4.5, we could not concretely establish (i.e. results were not statistically significant) whether co-occurring gastropod species/genera compete for resources or if they develop strategies for coexistence at a specific temperature bin.

However, as a general observation, we saw that co-occurring species/genus pairs had a lower mean TD compared to non-cooccurring pairs which points towards coexistence. This trend of coexistence within specific temperature bins turned out to be statistically significant for bivalves (see 4.4), where the mean TD of co-occurring species within temperature bins was consistently lower than that of non co-occurring species.

We infer from fig 4.7 that temperature does not play a consequential role in influencing the competitive interactions among bivalves.

On the other hand, the ambient temperature conditions do exert a significant influence on the competition among gastropods. A decrease in mean TD of co-occuring gastropod species/genus pairs with increase in sea surface temperature (see 4.6) indicates that coexistence in gastropods is promoted at higher temperatures.

Higher temperatures can be linked to higher insolation, which translates to increased primary productivity due to the availability of more sunlight. This would result in an increased availability of resources, thereby reducing competition and supporting the coexistence of a greater number of species. In addition to this, it is also possible that at colder conditions which are generally suboptimal for the sustenance of gastropods, select species with higher tolerance to low temperatures dominate other species by outcompeting them for resources. This results in increased competition at lower temperatures, and thus reduced coexistence.

5.4.3 Dissolved Oxygen

From table 5.1, we see that dissolved oxygen does not play a noteworthy role in dictating competitive interactions in bivalves. On the other hand, the mean TD in co-occurring gastropod genera increases linearly with available dissolved oxygen (although such a trend is not seen at the species level). This is contrary to our expectations and previous results claiming higher competition at lower levels of dissolved oxygen.

We propose that this trend can be attributed to the increased energy/resource availability concurrent with the rise in oxygen levels. Improved oxygen levels can support larger and denser populations of gastropods. As population densities increase, competition for limited resources like food, shelter, and breeding sites becomes more intense. Furthermore, in well-oxygenated environments, there may be an increase in the number of predators. As predation pressure rises, gastropods from different genera may compete to avoid being preyed upon, which can lead to indirect competition among gastropod genera.

Chapter 6

Limitations

6.1 Issues associated with Taxonomic Nomenclature

Our approach of quantifying competitive interactions through measures of taxonomic distinctness is not without its shortcomings, a big part of which is due to the discepancies associated with taxonomy. Therefore, it is imperative to be aware of the associated pitfalls and exercise caution while interpreting the results to avoid erroneous conclusions.

Taxonomic efforts have historically exhibited biases, primarily favoring extensively studied and charismatic species while leaving less conspicuous groups underrepresented in the scientific/taxonomic literature. Moreover, there exists a persistent shortage of experts, particularly in specialized taxonomic groups, resulting in numerous species remaining undescribed or classified with outdated and potentially inaccurate information.

The advent of molecular techniques such as DNA sequencing has revolutionized taxonomy but has also introduced complexities. It has unveiled cryptic species—those visually alike but genetically distinct—altering traditional morphological-based identifications and contributing to ongoing taxonomic revisions. Additionally, subjectivity in species delimitation and disagreements among taxonomists further compound the challenges.

6.2 Problems with Species Co-occurrence Analysis

The method of species co-occurrence analysis used in this study is also not without deficiencies, and the flaws indeed carry the capability to seriously bias or distort our interpretations. We will touch upon a few of them below:

- **Choice of grid size** - The chosen grid size for our analyses was 0.1 x 0.1 degrees, which roughly corresponds to an area of 10km x 10km at equator. While we recognize that such a resolution might be too coarse and might obscure the patterns caused by competitive exclusion, it was the optimum trade-off between computational complexity and ecological relevance.

- **Imperfections in Occurrence records** - We conducted our analyses with the assumption that the occurrence records are fairly complete and representative of reality, and did not perform any range-through interpolations. However, flawed occurrence records can heavily bias the list of "positively" co-occurring species pairs. In many cases, the presence of a species at a location might not be recorded due to poor sampling effort, while being present there in reality. Similarly, if a species is present in grids adjacent to a location grid, it is also likely that the species is also present in that location.

- **Computational Resources** - While the R-based 'cooccur' package used for species cooccurrence analysis is touted to be much faster than the alternatives, it is still extremely time and resource-intensive. This poses many practical limitations on conducting reproducibility tests, especially while working with extremely large datasets such as ours.

- **Reliability of the calculations** - The mathematical formulation behind the species coocurrence analysis has been, in a way, treated as a black-box. While the formulation is definitely very useful as a tool for ecologists, it will be better to have more field-based studies which corroborate the accuracy of these results.

Chapter 7

Conclusion

In summary, this thesis challenges the belief that competition among marine molluscs leads to the separation of closely related species over evolutionary time scales. The study emphasizes the complexity and context-dependent nature of how abiotic factors (SST, Depth & Dissolved O_2) influence competition, revealing that there is no universal rule and the patterns vary across different classes. It was found that "mean taxonomic distinctness of co-occurring species pairs" can be a useful metric to gauge the impacts and mechanisms of competition, despite its reductionist approach and potential issues with taxonomic nomenclature. This research lays the groundwork for future studies aiming to deepen our understanding of competitive interactions in modern and past marine ecosystems and their dependence on environmental factors. The need for such inquiries must be underscored, as they can influence measures for biodiversity measures in the wake of climate change.

Bibliography

Abrams, P. (Nov. 1983). "The Theory of Limiting Similarity". In: *Annual Review of Ecology and Systematics* 14.1, pp. 359–376. ISSN: 0066-4162. DOI: 10.1146/annurev.es.14.110183.002043.

Allesina, S. et al. (Mar. 2008). "Network structure, predator–prey modules, and stability in large food webs". In: *Theoretical Ecology* 1.1, pp. 55–64. ISSN: 1874-1738, 1874-1746. DOI: 10.1007/s12080-007-0007-8.

Azaele, S. et al. (Jan. 2010). "Inferring plant ecosystem organization from species occurrences". In: *Journal of Theoretical Biology* 262.2, pp. 323–329. ISSN: 00225193. DOI: 10.1016/j.jtbi.2009.09.026.

Barnes, D. K. A. (Oct. 7, 2002). "Polarization of competition increases with latitude". In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269.1504, pp. 2061–2069. ISSN: 0962-8452, 1471-2954. DOI: 10.1098/rspb.2002.2105.

Begon et al. (Jan. 2006). *Ecology: From Individuals to Ecosystems*.

Berlow, E. L. et al. (May 2004). "Interaction strengths in food webs: issues and opportunities". In: *Journal of Animal Ecology* 73.3, pp. 585–598. ISSN: 0021-8790, 1365-2656. DOI: 10.1111/j.0021-8790.2004.00833.x.

Borthagaray, A. I. et al. (Oct. 7, 2014). "Inferring species roles in metacommunity structure from species co-occurrence networks". In: *Proceedings of the Royal Society B: Biological Sciences* 281.1792, p. 20141425. ISSN: 0962-8452, 1471-2954. DOI: 10.1098/rspb.2014.1425.

Breitburg, D. L. et al. (Nov. 1997). "VARYING EFFECTS OF LOW DISSOLVED OXYGEN ON TROPHIC INTERACTIONS IN AN ESTUARINE FOOD WEB". In: *Ecological Monographs* 67.4, pp. 489–507. ISSN: 0012-9615. DOI: 10.1890/0012-9615(1997)067[0489:VEOLDO]2.0.CO;2.

Cazelles, K. et al. (Feb. 2016). "A theory for species co-occurrence in interaction networks". In: *Theoretical Ecology* 9.1, pp. 39–48. ISSN: 1874-1738, 1874-1746. DOI: 10.1007/s12080-015-0281-9.

Chang, C.-c. et al. (Jan. 6, 2023). "Reduced predation pressure as a potential driver of prey diversity and abundance in complex habitats". In: *npj Biodiversity* 2.1, p. 1. ISSN: 2731-4243. DOI: 10.1038/s44185-022-00007-x.

Chase, J. M. (June 11, 2010). "Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments". In: *Science* 328.5984, pp. 1388–1391. ISSN: 0036-8075, 1095-9203. DOI: 10.1126/science.1187820.

Chesson, P. (Nov. 2000). "Mechanisms of Maintenance of Species Diversity". In: *Annual Review of Ecology and Systematics* 31.1, pp. 343–366. ISSN: 0066-4162. DOI: 10.1146/annurev.ecolsys.31.1.343.

Clarke, K. R. et al. (Aug. 1998). "A taxonomic distinctness index and its statistical properties". In: *Journal of Applied Ecology* 35.4, pp. 523–531. ISSN: 0021-8901, 1365-2664. DOI: 10.1046/j.1365-2664.1998.3540523.x.

Cloern, J. et al. (2005). "Phytoplankton community ecology: principles applied in San Francisco Bay". In: *Marine Ecology Progress Series* 285, pp. 11–28. ISSN: 0171-8630, 1616-1599. DOI: 10.3354/meps285011.

Connell, J. H. (Oct. 1961). "The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle Chthamalus Stellatus". In: *Ecology* 42.4, pp. 710–723. ISSN: 00129658. DOI: 10.2307/1933500.

Darwin, C. (Jan. 1, 1859). *The Origin of Species: By Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. 6th ed. Cambridge University Press. ISBN: 978-1-108-00548-7 978-0-511-69429-5. DOI: 10.1017/CBO9780511694295.

De Bello, F. et al. (Oct. 2012). "Functional species pool framework to test for biotic effects on community assembly". In: *Ecology* 93.10, pp. 2263–2273. ISSN: 0012-9658. DOI: 10.1890/11-1394.1.

Diez, J. M. et al. (July 2008). "Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions". In: *Ecology Letters* 11.7, pp. 674–681. ISSN: 1461023X, 14610248. DOI: 10.1111/j.1461-0248.2008.01178.x.

Faust, K., L. Lahti, et al. (June 2015). "Metagenomics meets time series analysis: unraveling microbial community dynamics". In: *Current Opinion in Microbiology* 25, pp. 56–66. ISSN: 13695274. DOI: 10.1016/j.mib.2015.04.004.

Faust, K. and J. Raes (Aug. 2012). "Microbial interactions: from networks to models". In: *Nature Reviews Microbiology* 10.8, pp. 538–550. ISSN: 1740-1526, 1740-1534. DOI: 10.1038/nrmicro2832.

Ferguson, N. et al. (Jan. 2013). "Competition in benthic marine invertebrates: the unrecognized role of exploitative competition for oxygen". In: *Ecology* 94.1, pp. 126–135. ISSN: 0012-9658. DOI: 10.1890/12-0795.1.

Fox, J. F. (June 22, 1979). "Intermediate-Disturbance Hypothesis". In: *Science* 204.4399, pp. 1344–1345. ISSN: 0036-8075, 1095-9203. DOI: 10.1126/science.204.4399.1344.

Fuhrman, J. A. et al. (Mar. 2015). "Marine microbial community dynamics and their ecological interpretation". In: *Nature Reviews Microbiology* 13.3, pp. 133–146. ISSN: 1740-1526, 1740-1534. DOI: 10.1038/nrmicro3417.

Hardin, G. (Apr. 29, 1960). "The Competitive Exclusion Principle: An idea that took a century to be born has implications in ecology, economics, and genetics." In: *Science* 131.3409, pp. 1292–1297. ISSN: 0036-8075, 1095-9203. DOI: 10.1126/science.131.3409.1292.

Harley, C. D. G. et al. (Aug. 2017). "Conceptualizing ecosystem tipping points within a physiological framework". In: *Ecology and Evolution* 7.15, pp. 6035–6045. ISSN: 2045-7758, 2045-7758. DOI: 10.1002/ece3.3164.

Harper, E. M. et al. (June 2016). "Latitudinal and depth gradients in marine predation pressure: Gradients in marine predation pressure". In: *Global Ecology and Biogeography* 25.6, pp. 670–678. ISSN: 1466822X. DOI: 10.1111/geb.12444.

Hillebrand, H. (May 2011). "Temperature mediates competitive exclusion and diversity in benthic microalgae under different N:P stoichiometry". In: *Ecological Research* 26.3, pp. 533–539. ISSN: 0912-3814, 1440-1703. DOI: 10.1007/s11284-011-0810-y.

Hixon, M. A. et al. (Nov. 2005). "COMPETITION, PREDATION, AND DENSITY-DEPENDENT MORTALITY IN DEMERSAL MARINE FISHES". In: *Ecology* 86.11, pp. 2847–2859. ISSN: 0012-9658. DOI: 10.1890/04-1455.

Hutchinson, G. E. (Jan. 1, 1957). "Concluding Remarks". In: *Cold Spring Harbor Symposia on Quantitative Biology* 22.0, pp. 415–427. ISSN: 0091-7451, 1943-4456. DOI: 10.1101/SQB.1957.022.01.039.

Kéfi, S. et al. (Aug. 3, 2016). "How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience". In: *PLOS Biology* 14.8. Ed. by D. Simberloff, e1002527. ISSN: 1545-7885. DOI: 10.1371/journal.pbio.1002527.

King, A. W. et al. (Aug. 1983). "Complexity, Diversity, and Stability: A Reconciliation of Theoretical and Empirical Results". In: *The American Naturalist* 122.2, pp. 229–239. ISSN: 0003-0147, 1537-5323. DOI: 10.1086/284132.

Klompmaker, A. A. et al. (Aug. 1, 2018). "Extreme rarity of competitive exclusion in modern and fossil marine benthic ecosystems". In: *Geology* 46.8, pp. 723–726. ISSN: 0091-7613. DOI: 10.1130/G45032.1.

Kneitel, J. M. (2019). "Gauses Competitive Exclusion Principle". In: *Encyclopedia of Ecology*. Elsevier, pp. 110–113. ISBN: 978-0-444-64130-4. DOI: 10.1016/B978-0-12-409548-9.00816-2.

Kozłowski, J. (Jan. 1992). "Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity". In: *Trends in Ecology & Evolution* 7.1, pp. 15–19. ISSN: 01695347. DOI: 10.1016/0169-5347(92)90192-E.

Lafferty, K. D. et al. (2016). "Revisiting Paine's 1966 Sea Star Removal Experiment, the Most-Cited Empirical Article in the American Naturalist". In: *The American Naturalist* 188.4. PMID: 27622872, pp. 365–378. DOI: 10.1086/688045. eprint: https://doi.org/10.1086/688045.

Lehman, C. L. et al. (Nov. 2000). "Biodiversity, Stability, and Productivity in Competitive Communities". In: *The American Naturalist* 156.5, pp. 534–552. ISSN: 0003-0147, 1537-5323. DOI: 10.1086/303402.

Link, J. S. et al. (Jan. 1, 2013). "The Challenges of Evaluating Competition Among Marine Fishes: Who Cares, When Does It Matter, and What Can One Do About It?" In: *Bulletin of Marine Science* 89.1, pp. 213–247. ISSN: 00074977. DOI: 10.5343/bms.2011.1121.

Liow, L. H., T. Reitan, et al. (May 2019). "Size, weapons, and armor as predictors of competitive outcomes in fossil and contemporary marine communities". In: *Ecological Monographs* 89.2, e01354. ISSN: 0012-9615, 1557-7015. DOI: 10.1002/ecm.1354.

Liow, L. H., E. Di Martino, et al. (Aug. 2017). "Relative size predicts competitive outcome through 2 million years". In: *Ecology Letters* 20.8. Ed. by E. Jeffers, pp. 981–988. ISSN: 1461-023X, 1461-0248. DOI: 10.1111/ele.12795.

Lotka, A. A. (Jan. 1932). "The growth of mixed populations: Two species competing for a common food supply". In.

Lubchenco, J. et al. (Dec. 1978). "Community Development and Persistence in a Low Rocky Intertidal Zone". In: *Ecological Monographs* 48.1, pp. 67–94. ISSN: 0012-9615, 1557-7015. DOI: 10.2307/2937360.

Menge, B. A. et al. (Dec. 1986). "A test of the Menge-Sutherland model of community organization in a tropical rocky intertidal food web". In: *Oecologia* 71.1, pp. 75–89. ISSN: 0029-8549, 1432-1939. DOI: 10.1007/BF00377324.

Morales-Castilla, I. et al. (June 2015). "Inferring biotic interactions from proxies". In: *Trends in Ecology & Evolution* 30.6, pp. 347–356. ISSN: 01695347. DOI: 10.1016/j.tree.2015.03.014.

Novak, M. et al. (Aug. 2008). "ESTIMATING NONLINEAR INTERACTION STRENGTHS: AN OBSERVATION-BASED METHOD FOR SPECIES-RICH FOOD WEBS". In: *Ecology* 89.8, pp. 2083–2089. ISSN: 0012-9658. DOI: 10.1890/08-0033.1.

— (Jan. 22, 2010). "Using experimental indices to quantify the strength of species interactions". In: *Oikos* 119.7, pp. 1057–1063. ISSN: 00301299, 16000706. DOI: 10.1111/j.1600-0706.2009.18147.x.

Palmer, M. W. (Dec. 1994). "Variation in species richness: Towards a unification of hypotheses". In: *Folia Geobotanica et Phytotaxonomica* 29.4, pp. 511–530. ISSN: 0015-5551, 1573-1170. DOI: 10.1007/BF02883148.

Peres-Neto, P. R. et al. (Apr. 2001). "Environmentally constrained null models: site suitability as occupancy criterion". In: *Oikos* 93.1, pp. 110–120. ISSN: 00301299. DOI: 10.1034/j.1600-0706.2001.930112.x.

Peterson, C. H. (1980). "APPROACHES TO THE STUDY OF COMPETITION IN BENTHIC COMMUNITIES IN SOFT SEDIMENTS". In: *Estuarine Perspectives*. Elsevier, pp. 291–302. ISBN: 978-0-12-404060-1. DOI: 10.1016/B978-0-12-404060-1.50032-0.

Ricciardi, A. et al. (Oct. 17, 2006). "Does Darwin's Naturalization Hypothesis Explain Fish Invasions?" In: *Biological Invasions* 8.6, pp. 1403–1407. ISSN: 1387-3547, 1573-1464. DOI: 10.1007/s10530-006-0005-6.

Sander, E. L. et al. (Aug. 2, 2017). "Ecological Network Inference From Long-Term Presence-Absence Data". In: *Scientific Reports* 7.1, p. 7154. ISSN: 2045-2322. DOI: 10.1038/s41598-017-07009-x.

Schemske, D. W. et al. (Dec. 1, 2009). "Is There a Latitudinal Gradient in the Importance of Biotic Interactions?" In: *Annual Review of Ecology, Evolution, and Systematics* 40.1, pp. 245–269. ISSN: 1543-592X, 1545-2069. DOI: 10.1146/annurev.ecolsys.39.110707.173430.

Schoener, T. W. (July 5, 1974). "Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity." In: *Science* 185.4145, pp. 27–39. ISSN: 0036-8075, 1095-9203. DOI: 10.1126/science.185.4145.27.

Stanley, S. M. (2008). "Predation defeats competition on the seafloor". In: *Paleobiology* 34.1, pp. 1–21. ISSN: 0094-8373, 1938-5331. DOI: 10.1666/07026.1.

Thomas, M. K. et al. (Aug. 2017). "Temperature–nutrient interactions exacerbate sensitivity to warming in phytoplankton". In: *Global Change Biology* 23.8, pp. 3269–3280. ISSN: 1354-1013, 1365-2486. DOI: 10.1111/gcb.13641.

Thompson, J. N. (2005). *The Geographic Mosaic of Coevolution*. University of Chicago Press. ISBN: 978-0-226-79762-5 978-0-226-79761-8 978-0-226-11869-7. DOI: 10.7208/chicago/9780226118697.001.0001.

Tilman, D. et al. (Nov. 1982). "Phytoplankton Community Ecology: The Role of Limiting Nutrients". In: *Annual Review of Ecology and Systematics* 13.1, pp. 349–372. ISSN: 0066-4162. DOI: 10.1146/annurev.es.13.110182.002025.

Tilman, D. (June 1985). "The Resource-Ratio Hypothesis of Plant Succession". In: *The American Naturalist* 125.6, pp. 827–852. ISSN: 0003-0147, 1537-5323. DOI: 10.1086/284382.

Tilman, D. (May 1987). "The Importance of the Mechanisms of Interspecific Competition". In: *The American Naturalist* 129.5, pp. 769–774. ISSN: 0003-0147, 1537-5323. DOI: 10.1086/284672.

— (Sept. 2011). "Diversification, Biotic Interchange, and the Universal Trade-Off Hypothesis". In: *The American Naturalist* 178.3, pp. 355–371. ISSN: 0003-0147, 1537-5323. DOI: 10.1086/661245.

Ulrich, W. et al. (Jan. 2013). "Pattern detection in null model analysis". In: *Oikos* 122.1, pp. 2–18. ISSN: 00301299. DOI: 10.1111/j.1600-0706.2012.20325.x.

Volterra, V. (Oct. 1926). "Fluctuations in the Abundance of a Species considered Mathematically1". In: *Nature* 118.2972, pp. 558–560. ISSN: 0028-0836, 1476-4687. DOI: 10.1038/118558a0.

Warwick, R. M. et al. (Aug. 1998). "Taxonomic distinctness and environmental assessment". In: *Journal of Applied Ecology* 35.4, pp. 532–543. ISSN: 0021-8901, 1365-2664. DOI: 10.1046/j.1365-2664.1998.3540532.x.

Wilkinson, D. M. (Jan. 1999). "The Disturbing History of Intermediate Disturbance". In: *Oikos* 84.1, p. 145. ISSN: 00301299. DOI: 10.2307/3546874.

Yang, T. et al. (Aug. 2017). "Resource availability modulates biodiversity-invasion relationships by altering competitive interactions". In: *Environmental Microbiology* 19.8, pp. 2984–2991. ISSN: 1462-2912, 1462-2920. DOI: 10.1111/1462-2920.13708.