

# Seagrass Biodiversity and its Drivers in the Kepulauan Banyak Marine Nature Park, Indonesia

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## Abstract

Seagrasses are important marine plants that provide a variety of ecosystem services, including food and shelter for marine life, and protection from coastal erosion. This study investigated the biodiversity (alpha and beta diversity) of seagrass in the Kepulauan Banyak Marine Nature Park, Indonesia, with a specific focus on eight sites. Alpha diversity was calculated using Shannon's index, Simpson's index, and Pielou evenness. Beta diversity was determined using Bray-Curtis dissimilarity and Jaccard dissimilarity allowing us to examine the variations in species composition among different sites. Principal coordinate analysis and Partial distance-based redundancy analysis was used to visualize and investigate the impact of constraint variables to the structure of the seagrass communities. Alpha diversity varied among the sites, with the highest alpha diversity found at the Orongan and Matahari site and the lowest at the Ujung Lolok and Balai sites. The dominant substrate type (mud or sand) was found to be a significant ( $P \leq 0.01$ ) determinant of seagrass alpha diversity, with mud substrates supporting higher diversity than sand substrates. The relationship between alpha diversity and constrain variables was only significant with closest distance to forest lost and longitude variables. The analysis found that water pH, closest distance to forest lost, mean distance to tourism spots, and closest distance to settlement collectively explained a significant ( $P \leq 0.001$ ) portion (88.48%) of the variation in beta diversity of seagrass across the sites. The results of this study can be used to develop management strategies for the conservation of seagrass meadows in the park.

**Keywords:** Seagrass, Alpha diversity, Beta diversity, Constraint variables, Biodiversity.

## Introduction

Seagrass ecosystems are recognized as some of the most productive and biologically diverse habitats. They play a pivotal role in maintaining ecological balance and supporting human well-being by providing a plethora of ecosystem services, such as carbon sequestration, nutrient cycling, habitat provision for a myriad of marine species, coastal protection, sediment stabilization, water quality improvement, and climate change mitigation (Orth *et al.*, 2006; Fourqurean *et al.*, 2012; Unsworth *et al.*, 2018).

However, these vital ecosystems are under siege worldwide. Anthropogenic pressures, such as coastal development, pollution, overfishing, eutrophication, invasive species, and climate change have caused a precipitous decline in their extent and

condition over the last century (Waycott *et al.*, 2009; Short *et al.*, 2011; Unsworth *et al.*, 2018; Irawan *et al.*, 2019). This decline threatens not only the rich biodiversity they harbor but also the essential ecosystem services they provide for millions of people who depend on them for food, livelihood, and well-being (Duarte *et al.*, 2013; Irawan *et al.*, 2018; Unsworth *et al.*, 2018).

In this study, focused on the seagrass ecosystems of the Kepulauan Banyak Marine Nature Park, which is a unique marine environment in Indonesia that hosts a diverse array of seagrass species. Indonesia is home to about 30,000 km<sup>2</sup> of seagrass meadows (Kuriandewa *et al.*, 2003), which form a significant coastal habitat throughout the archipelago, extending from intertidal to subtidal zones, along mangrove coastlines, estuaries, and shallow embayments, as well as coral-reef

platforms, inter-reef seabeds, and island locations (Sala *et al.*, 2021). Seagrass meadows in Indonesia play a vital role in supporting coastal marine communities and maintaining diverse flora and fauna (Hernawan *et al.*, 2021). They are an important component of coastal fisheries productivity and are also an important food source for marine green turtles and dugongs (Unsworth *et al.*, 2014).

Despite its ecological importance and conservation potential, the status and drivers of seagrass biodiversity in the Kepulauan Banyak Marine Nature Park remain unclear. This knowledge gap impedes the formulation of effective conservation and management strategies, leaving these vital ecosystems vulnerable to various threats and challenges, such as coastal development, pollution, overfishing, and climate change (Unsworth *et al.*, 2018). While seagrass ecosystems have been the subject of numerous studies globally, research focusing on the Kepulauan Banyak Marine Nature Park is scant. To the best of our knowledge, no study has yet undertaken a comprehensive examination of the alpha and beta diversity of seagrass across multiple sites within the park, even the latest national-scale seagrass studies (Unsworth *et al.*, 2018; Hernawan *et al.*, 2021), seagrass meadows in the park were not detected.

To fill this gap, the study aimed to investigate the biodiversity of seagrass in the park with a specific focus on eight sites: Matahari, Orongan, Balai, Asok, Pabisi, Rago-rago, Lamun, and Ujung Lolok. We sought to unravel the factors that shape seagrass diversity at these sites, taking into account a range of physical, spatial, and geographical distance variables. Specifically, this study addressed the following research questions: What is the level of seagrass diversity (alpha and beta) at the eight study sites? How do physical (salinity, depth, water pH, water temperature, and dominant substrate type), spatial (latitude and longitude), and geographical (including closest distance to forest loss, mean distance to forest loss, closest distance to a tourism spot, mean distance to a tourism spot, closest distance to a settlement, and mean distance to a settlement) distances influence seagrass diversity patterns?

The findings of this research are expected to shed new light on the ecological dynamics of seagrass ecosystems and offer valuable insights for conservation and management efforts in parks. In doing so, this study aligns with the global trend towards achieving sustainability and well-being through the conservation of marine biodiversity (Fan *et al.*, 2022).

## Materials and Methods

### Study area

A multi-scale sampling design implemented to study seagrass meadows in the Kepulauan Banyak Marine Nature Park at eight sites (Figure 1.). Sites were selected based on the geographic representation of the park areas, a variety of land uses across the archipelago, and accessibility for conducting fieldwork. Each site exhibited a combination of different land uses ranging from minimal human impact (Matahari and Orongan Island) to highly impacted islands from tourism and settlement activities (Balai, Asok, Pabisi, Rago-rago, Lamun island and Ujung Lolok).

### Seagrass survey

Data seagrass ecological collection was conducted using three transects of 50 m length and 25 m spacing, covering a total area of 50 x 50 m<sup>2</sup>. Quadrats with 0.252 were positioned on the right side of each transect, with a 5 m interval between adjacent quadrats, resulting in 11 quadrats per transect (Figure 2.) (Rahmawati *et al.*, 2014). The starting point of each transect was placed at a distance of 5-10 m from the first occurrence of seagrass (from the shoreward direction), at each quadrat measured seagrass species richness, shoot density using standardized Seagrass Watch (McKenzie, 2008).

The coordinates of the 1st and 11th quadrats on each transect at each site were recorded and documented using an underwater digital camera. Seagrass cover was estimated in two stages: first, by comparison with the standard photo percentage of seagrass cover (McKenzie, 2008), and second, by validation with the ImageJ application (comparison of pixel area covered by seagrass and area not covered by seagrass) (Jurjen, 2015).

### Constrain variables

This study gathered data on several physical, spatial, and geographical distance variables. Physical variables included salinity, depth, water pH, water temperature, and dominant substrate type (categorical data: sand and mud), as suggested by De Battisti *et al.*, (2021). The spatial variables included Latitude and Longitude (Friess *et al.*, 2019). The geographical distance variables encompassed the distance area of settlement, tourism spots (Certel *et al.*, 2021; Lukman *et al.*, 2022), and the distance area of deforestation as per Carugati *et al.* (2018).

The mean values of each variable per site were used as independent replicates. The depth variable

was divided into minimum, mean, and mean values. Similarly, geographical distance variables were categorized into closest and mean distances, including closest distance to forest loss (CDFL), mean distance to forest loss (MDFL), closest distance to a tourism spot (CTS), mean distance to a tourism spot (MTS), closest distance to a settlement (CTS), and mean distance to a settlement (MDS).

Anthropogenic (tourism and settlement) and forest dieback (forest lost) were identified through NDVI analysis using Planet NICFI Satellite Images (specification: area: tropical Asia, spatial resolution:

4.77 m per pixel, spectral resolution: R, G, B, NIR, temporal resolution: June 2021-October 2021; Planet Team, 2021). These images were processed using Google Earth Engine (GEE; Gorelick *et al.*, 2017). The coordinates of each site were determined using the inspector feature of the GEE.

The geographical distance to the surveyed seagrass sites (*i.e.*, linear distance) was calculated using the "geosphere" package in R 4.2.2 (R Core Team, 2023). This package calculates a distance matrix between sets of points (*i.e.*, latitude and longitude) based on the "law of cosines" and assumes that the earth is spherical (Hijmans, 2022).

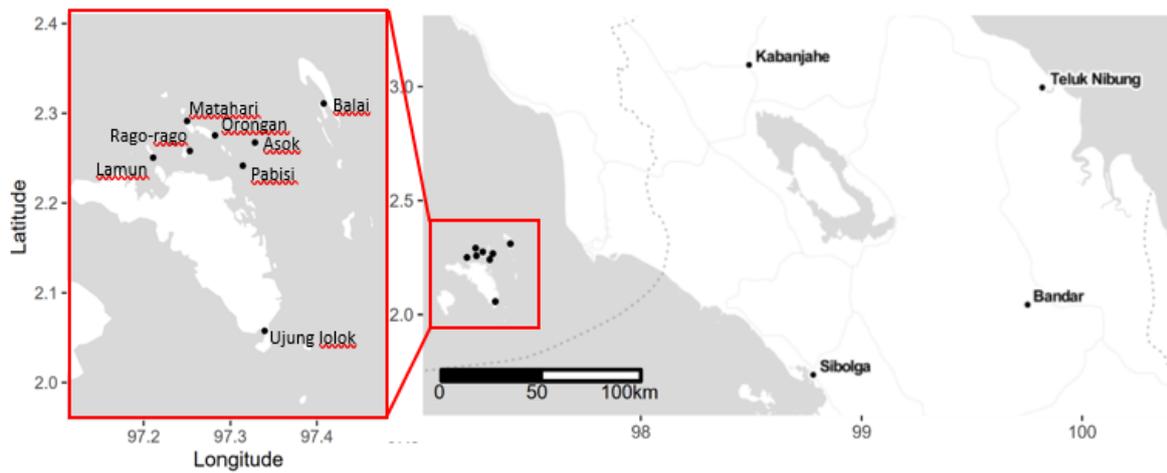


Figure 1. Eight sites were collected from seagrass bed locations used for this study, with white representing terrestrial and gray representing ocean.

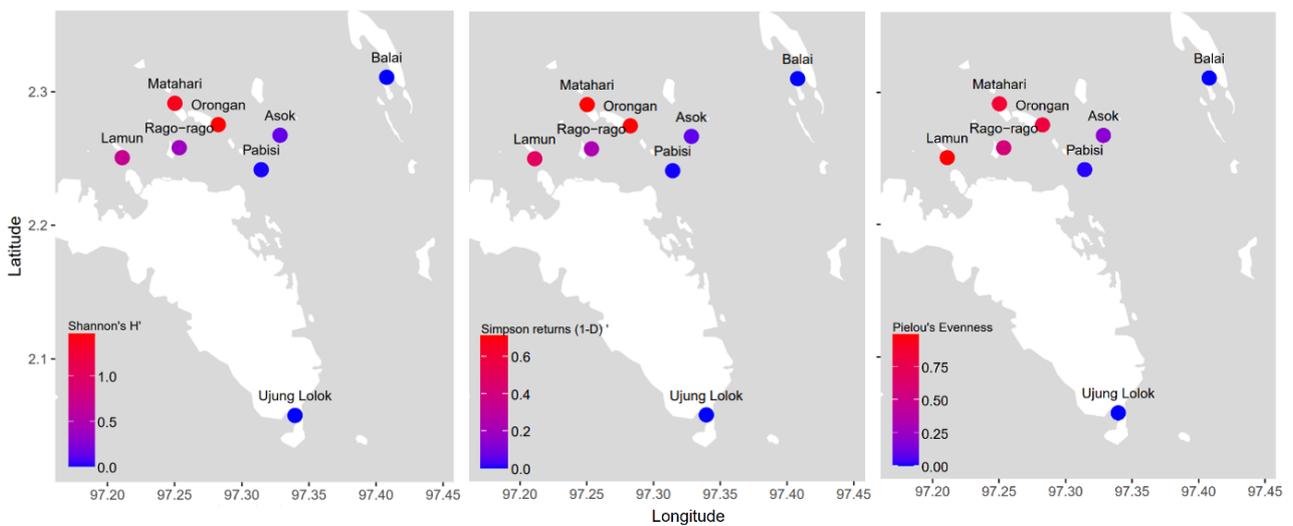


Figure 2. Values of alpha diversity metrics (Shannon index ( $H'$ ), Simpson returns ( $1-D'$ ), and Pielou evenness ( $J'$ )) gradients at each site.

## Data analysis

All data analyses were conducted using R version 4.2.2 (R Core Team, 2023). Initially, alpha diversity was calculated using shoot density data to derive Shannon's index ( $H'$ ), Simpson returns (1-D), and Pielou evenness ( $J'$ ). The calculations were performed using the vegan package (Oksanen et al., 2022).

Linear models were used to examine the relationship between alpha diversity and constraint variables (excluding the dominant substrate type) across the eight sites. Robust standard errors were employed to test the significance of the coefficients. Owing to the limited sample size of seagrass abundance data, the Akaike information criterion (AIC) was used to select the most appropriate relationship. The relationship with the lowest AIC value was considered the best fit (Burnham and Anderson, 2002).

The association between alpha diversity and dominant substrate type was assessed using one-way analysis of variance (ANOVA). The ANOVA results included a p-value that indicated statistical significance. Statistical than 0.05 was considered at significant (Girden, 1992).

Beta diversity was determined by calculating Bray-Curtis dissimilarity (Bray and Curtis, 1957) and Jaccard dissimilarity (Jaccard, 1912) across all eight sites. The vegan package (Oksanen et al., 2022) was used for calculations. According to Baselga and Leprieur (2015); Baselga (2012), Jaccard dissimilarity measures the overlap/turnover in species presence/absence between pairs of communities, resulting in a Jaccard score of 0 when communities share identical species regardless of their relative abundance. Conversely, Bray-Curtis dissimilarity considers species abundance and allows differentiation between communities based on composition (Legendre and De Cáceres, 2013; Ricotta and Podani, 2017). Comparing the outputs of both dissimilarity metrics provided deeper insights into the structure of seagrass communities across the eight sites.

Principal coordinate analysis (PCoA) was employed to visualize the structure of the seagrass communities. Bray-Curtis and Jaccard dissimilarity matrices were calculated, and the resulting data were plotted using the PCoA technique. PCoA is a variant of multidimensional scaling that employs the Euclidean distance measure of compositional dissimilarity based on the relative abundance of taxa. The vegan, viridis, ggplot2 and cowplot package in R (Oksanen et al., 2022) facilitated the execution and visualization of the principal coordinates analysis.

To investigate the impact of physical variables, spatial variables, and geographical distance variables on dissimilarity among the eight sites, the partial distance-based redundancy analysis (partial db-RDA) method was applied (Legendre and Anderson, 1999; Anderson and Willis, 2003), to calculate using capscale {vegan}. The db-RDA method is suitable when the dissimilarity matrix follows non-Euclidean characteristics (Sofer et al., 2021).

Before conducting partial db-RDA, variables exhibiting significant ordination ( $P < 0.05$ ) were selected using the ordistep function from the vegan package in R. Additionally, it was crucial to normalize the physical, spatial, and geographical distance variables to facilitate concurrent comparisons. This was accomplished by applying z-score transformation. Multicollinearity, which refers to high correlations between environmental variables, was assessed using variance inflation factors (VIFs). Environmental variables were iteratively removed from the model until all VIF scores were below 10, following Kutner et al., (2005) and Chatterjee et al., (2000).

## Result and Discussion

### Alpha diversity of seagrass

Six seagrass species were sampled (*Enhalus acoroides*, *Thalassia hemprichii*, *Cymodocea serrulata*, *Cymodocea rotundata*, *Halodule universis*, and *Halodule pinifolia*) from eight sites in the study area. *Enhalus acoroides* and *Thalassia hemprichii* were the most abundant and widely distributed seagrass species, consistent with previous studies in Indonesia (Hernawan et al., 2021). *Halodule universis* was the least common species, with low occupancy and abundance. Orongan site had the highest seagrass richness (six species), followed by Matahari site (five species). These results were similar to those reported by Saswito (2015) for the Matahari site, except for the presence of *Syringodium isoetifolium* and absence of *Halodule universis* and *Halodule pinifolia*. Compared with the seagrass communities in the Aceh Besar region (Maulida et al., 2018; Octavina et al., 2020), our study area had one more species.

The percentage cover of seagrass varied significantly among the sites ( $P < 0.05$ ), ranging from a mean of 2.5% to 87%, with an overall average of  $37 \pm 9\%$ . The highest percent cover was recorded at the Orongan site ( $87 \pm 5\%$ ), followed by the Matahari site ( $62 \pm 6\%$ ), whereas the lowest was recorded at the Balai site ( $2.5 \pm 1\%$ ). These values were within the range of seagrass percentage cover reported by Hernawan et al. (2021) for 17 locations in Indonesia, which ranged from 19% to 65%, with an overall

average of 39±4%. They also found that the seagrass cover was higher in eastern Indonesia than in western Indonesia.

the alpha diversity of the seagrass community was measured using the Shannon index (H'), Simpson returns (1-D), and Pielou evenness (J') at each site. Figure 2 shows that alpha diversity differed among the sites, ranging from 0 to 1.46 for H', and from 0 to 0.71 for Simpson returns (1-D). The highest alpha diversity was found at the Orongan site, followed by that at the Matahari site. According to Duffy (2006), higher seagrass diversity can enhance the productivity, stability, and resilience of seagrass ecosystems by increasing resource-use efficiency, functional redundancy, and resistance to disturbances. Higher seagrass diversity can also support higher biodiversity of associated organisms by providing more niches and food resources.

The lowest alpha diversity was found at the Ujung Lolok and Balai sites, each of which contained only one seagrass species. Lower seagrass diversity can reduce ecosystem functions and services and increase vulnerability to environmental changes and human pressure (Nordlund et al., 2017). Low diversity makes it easy to lose seagrass ecosystems, which impacts not only natural resources but also the lives of people who directly or indirectly depend on these systems. Seagrass ecosystems play a multifunctional role in human well-being, for example, food through fisheries (Giakoumi et al., 2015), control of erosion, and protection against floods (Christianen et al., 2014).

Based on the Pielou evenness (J') calculated range 0–0.99, The highest value of J' was found at Lamun, followed by Matahari and Orongan (0.99, 0.85 and 0.81 respectively), while the lowest was recorded in Ujung lolok and Balai (Figure 2.). A high value of J' indicates that the species are evenly distributed, whereas a low value of J' indicates that

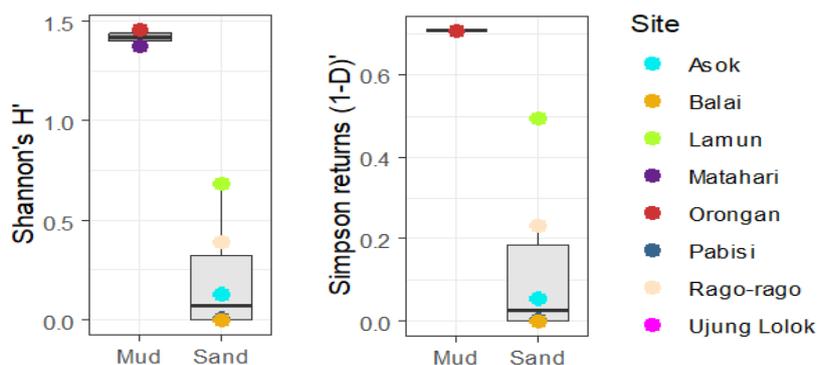
one or a few species are dominant. The Lamun site showed that *Enhalus acoroides* and *Thalassia hemprichii* were evenly distributed by abundance.

**Correlation dominant substrate type with alpha diversity**

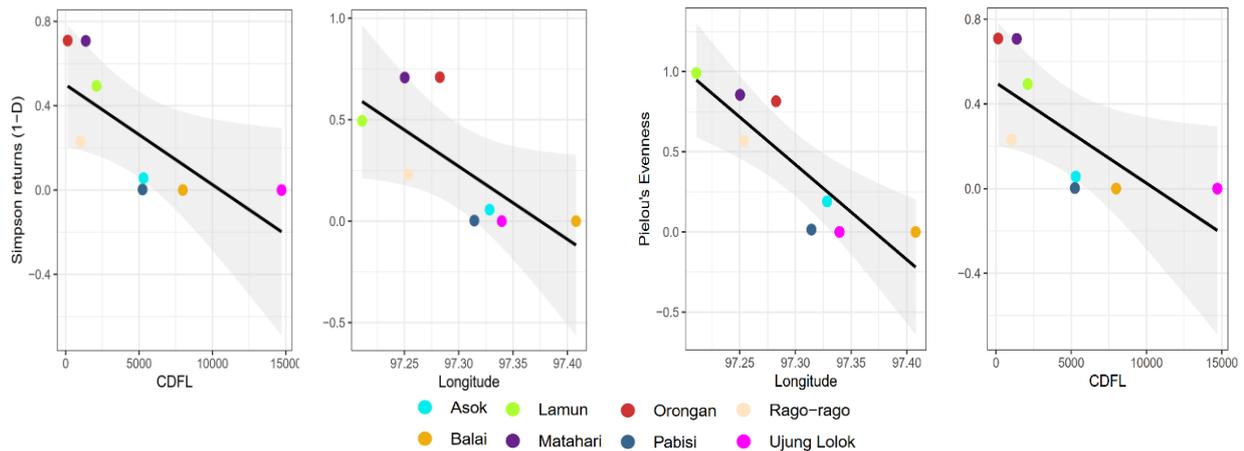
This study revealed a significant ( $P < 0.05$ ) association between the dominant substrate type (sand and mud as categorical variables) and the indices of Shannon's H' and Simpson returns (1-D), as shown in Figure 3. This suggests that seagrass diversity (H' and 1-D') was influenced by the predominant substrate type. We observed greater seagrass diversity in areas where the substrate was primarily mud compared to areas with a sand-dominant substrate. Specifically, the organic content found within the mud substrate at the Orongan and Matahari sites appeared to be beneficial for seagrass diversity. This finding aligns with previous research that has identified substrate type as a key determinant of seagrass diversity across various spatial scales and bioregions (Carter et al. 2021; Short et al., 2007).

However, it is important to note that not all mud substrates are equally beneficial for the survival and growth of seagrass. For instance, mud with high organic content can lead to adverse physico-chemical effects on seagrass (Zabarte-Maeztu et al., 2021).

In contrast, we did not find a significant relationship between the dominant substrate type and Pielou evenness (J'). Communities with high evenness indices, such as Matahari and Orongan, typically exhibit high Shannon's H' and Simpson returns (1-D) indices, as shown in figure 2. This observation suggests that evenness may not be as sensitive to changes in environmental factors, including substrate type, as it is primarily related to the dominance of certain opportunistic species (Simboura et al., 2014; Kilminster et al., 2015).



**Figure 3.** Relationship between dominant substrate type (mud and sand) and alpha diversity (Shannon's H' and Simpson return s (1-D)) (one-way ANOVA,  $P \leq 0.01$ ) at each sites.



**Figure 4.** Linear model relationships were fitted between response variables (Simpson index and Pielou's evenness) and predictor closest distance forest lost (CDFL) and longitude, which were significant ( $p \leq 0.05$ ) at each site.

One possible explanation for this insignificant relationship between dominant substrate type and Pielou evenness ( $J'$ ) could be that substrate type does not significantly influence the abundance or density of individuals across different species. Instead, it may affect other aspects of the ecosystem, such as percent cover or composition. Moreover, the relationship between species richness and evenness tends to disappear at larger scales (Zhang *et al.*, 2012), which further complicates our understanding of these dynamics.

**Alpha diversity relationship with constrain variables**

The results showed that the relative influence of physical, spatial, and geographical distance variables tends to be uniform among the seagrass alpha biodiversity indices. However, none of these variables had a significant impact on Shannon's H diversity index, which measures species abundance and evenness. The only exception was the CDFL driver, which almost reached statistical significance ( $P= 0.052$ ), explaining 40% of the variation ( $R^2 = 0.4$ ) in Shannon's H' index, indicating that seagrass species coexist and share similar ecological niches and tolerances in the study area (Carter *et al.*, 2021).

Interestingly, the results reveal a significant and negative relationship between longitude and the Simpson returns (1-D) index as well as the Pielou evenness index ( $p= 0.049$ ,  $R^2= 0.41$  and  $p=0.0052$ ,  $R^2= 0.71$ , respectively). This implies that lower longitudinal coordinates are associated with higher alpha diversity indices (Figure 4.). Moreover, the distance to CDFL also showed a significant and negative impact on these two alpha diversity indices ( $p=0.04$ ,  $R^2= 0.45$  and  $p= 0.02$ ,  $R^2= 0.54$ , respectively), indicating that closer proximity to CDFL leads to higher alpha diversity indices (Figure 4.).

These findings align with the influence of geographical factors on seagrass diversity discussed in the Great Barrier Reef study (Carter *et al.*, 2021). This study highlighted the strong effect of latitude on the probability of seagrass presence (Short *et al.*, 2007), with seagrass being more likely to occur at latitudes  $>18^\circ$  S (Carter *et al.*, 2021). The negative relationship between longitude and alpha diversity indices observed in our results suggests a potential role for longitudinal variation in shaping seagrass diversity (Daru *et al.*, 2023).

On the other hand, the lack of significant influence of environmental drivers on seagrass alpha diversity indices (Carter *et al.*, 2021), apart from dominant substrate type (Nordlund *et al.*, 2017), contrasts with the findings of previous studies (Nordlund *et al.*, 2017). The Great Barrier Reef study identified various environmental conditions (Carter *et al.*, 2021), including depth (Short *et al.*, 2007), water temperature (Shields *et al.*, 2019; Marbà *et al.*, 2022 and Daru *et al.*, 2023), and salinity (Bell *et al.*, 2019; Misson *et al.*, 2021), which are important factors in predicting seagrass presence and influencing the extent of seagrass communities. Similarly, a study on seagrass-associated fauna emphasized the influence of physical structure and environmental factors such as nutrient enrichment (Heck *et al.*, 2000; Qin *et al.*, 2021), exposure to waves and tides, and large-scale disturbances (Hirst *et al.*, 2017; Uhrin and Turner, 2018).

These discrepancies may arise because of variations in seagrass species composition (Daru *et al.*, 2023), specific environmental conditions of the study sites, or methodological differences in assessing alpha diversity and environmental variables.

### **Variability in seagrass beta diversity among the survey sites**

We performed principal coordinate analysis (PCoA) for both Bray-Curtis and Jaccard dissimilarity matrices to visualize the dissimilarities among the sites based on richness. The PCoA graph shows the results of this analysis and reveals some interesting patterns of seagrass variation across sites. PCoA 1 explained 56% of the variation, PCoA 2 explained 22% of the variation in beta diversity Bray-Curtis dissimilarity, PCoA 1 explained 59% of the variation, and PCoA 2 explained 25% of the variation in beta diversity Jaccard dissimilarity (figure 5).

Figure 5 of the PCoA Bray-Curtis dissimilarity matrix shows the sites as points in a low-dimensional space, where the distance between the points reflects the dissimilarity in seagrass community structure. Balai and Ujung Lolok exhibited positive values for both PCoA 1 and PCoA 2, indicating their similarity to each other and distinction from other sites. Furthermore, they were positioned farthest from the origin (0,0), signifying a high dissimilarity compared to the average site. Matahari and Orongan, on the other hand, display negative values for PCoA 1 and positive values for PCoA 2, indicating their similarity to each other while differing from Balai and Ujung Lolok. Additionally, they were in close proximity to the origin, indicating low dissimilarity from the average site. Asok and Rago-rago share negative values for both PCoA 1 and PCoA 2, indicating their similarity to each other and distinction from Matahari and Orongan. Similarly, they were positioned close to the origin, indicating low dissimilarity from the average site. Finally, Lamun and Pabisi demonstrated positive values for PCoA 1 and negative values for PCoA 2, signifying their similarity and distinguishing them from Asok and Rago-rago. Moreover, they were positioned farthest from the origin along PCoA 1, indicating a high dissimilarity from the average site along this axis.

The graph depicting the variation in Jaccard dissimilarity in the PCoA visualization is limited in its ability to demonstrate excessive variation. Low-dimensional data representations that remove noise while retaining the signal of interest can be instrumental in understanding hidden structures and patterns (Nguyen and Holmes, 2019). The presence of overlapping points, specifically Ujung Lolok and Lamun, hinders an accurate analysis. Because of the overlap between Pabisi and Lamun as well as the overlap between Balai and Ujung Lolok, these points are lost in the graph. Consequently, to ensure reliable results for further analysis, we relied solely on Bray-Curtis dissimilarity.

### **Constrain variables influence the variation beta diversity**

The graph of dbRDA shows how beta diversity based on seagrass abundance across different sites is influenced by four constraint variables: water pH, closest distance of forest loss to sites (CDFL), mean distance of tourism spot to sites (MTS), and closest distance of settlement to sites (CS). The graph has four axes that represent the linear combinations of constraint variables that explain the greatest variation in seagrass beta diversity (Figure 6).

The partial dbRDA analysis indicated that the combination of the constraint variables (water pH, CDFL, MTS, and CS) collectively explained a significant portion (88.48%) of the variation in the Bray-Curtis dissimilarity of seagrass composition across the sites. The first two axes (RDA1 and RDA2) explained 74.25% of the variation in seagrass dissimilarity among the sites, which is also quite high. This means that these two axes capture most of the variation in data and are suitable for visualization. The points on the graph represent the site response and their distances reflect their similarities or dissimilarities in terms of seagrass beta diversity. The vectors on the graph represent the constraint variables and their directions and lengths reflect their correlations and contributions to the variation in seagrass beta diversity.

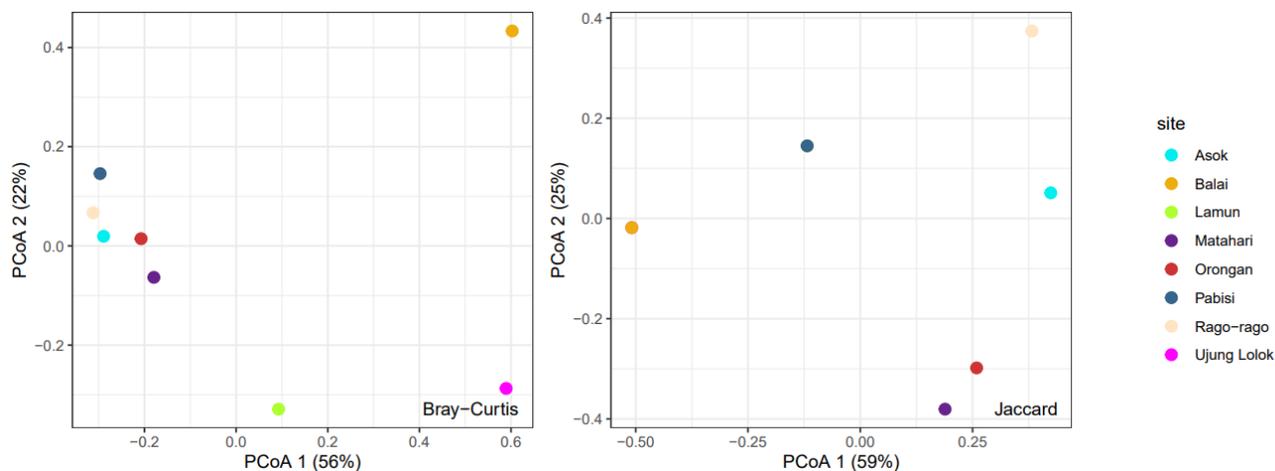
The overall correlation between the response variable and constraint variables was significant, with a p-value of 0.001. This means that there was a statistically significant relationship between the constraint variables and seagrass beta diversity across different sites. The individual constraint variables were also significant, with p-values of 0.006, 0.002, 0.033, and 0.016. This means that each of the constraint variables (water pH, CDFL, MTS, and CS) was significantly associated with seagrass beta diversity.

The partial dbRDA plot shows that Balai and Ujung Lolok. These sites had the highest values on RDA1, indicating that they had higher MTS and CDFL than the other sites. This indicates that these sites are far from tourism spots and forest loss; thus, Balai and Ujung Lolok have no unit in common with other sites (Alsaffar *et al.*, 2020; Collier *et al.*, 2021). These sites also had low RDA2 values, indicating that they had lower CS and Water pH than other sites. This indicates that these sites are close to settlements and have acidic water, which may negatively affect seagrass growth and survival (Sotelo-Casas *et al.*, 2022; Jiménez-Casero *et al.*, 2023). These sites are separated from the other sites along RDA1, indicating that they have different seagrass composition than the other sites. The plot shows that these sites were

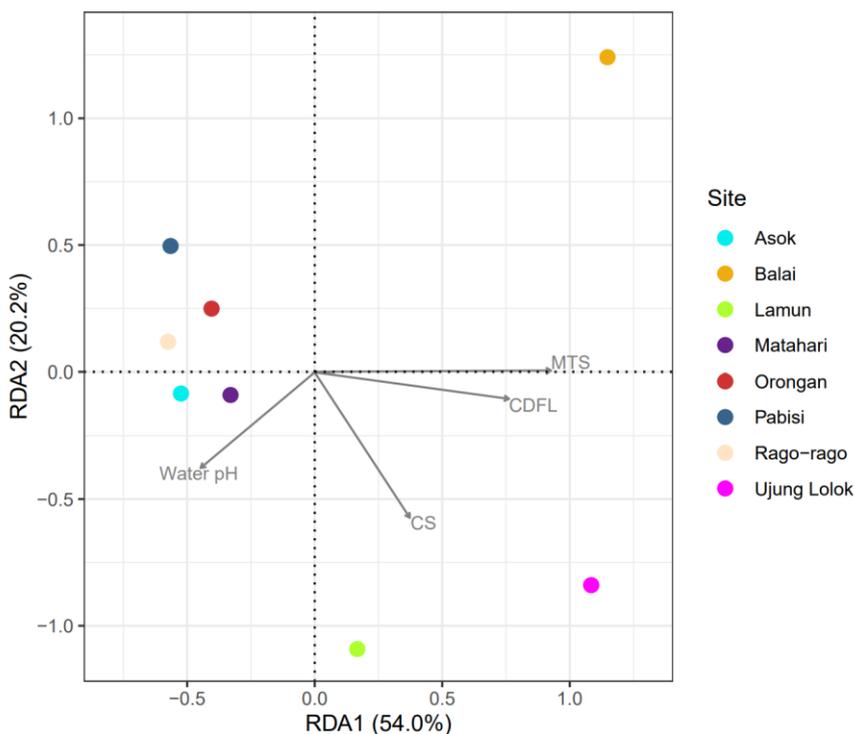
mainly influenced by MTS and CDFL, as their vectors were parallel to RDA1.

Balai and Ujung lolok have one seagrass species (*Enhalus acoroides*); balai and Ujung lolok also have the lowest values on the Shannon index ( $H'$ ), Simpson returns ( $1-D$ ), and Pielou evenness ( $J'$ ) (figure 2); they may have lower resilience to pressure

than other sites. Resilience is the capacity of an ecosystem to absorb disturbances and adapt to change without fundamentally switching to an alternative state (Holling, 1973). Resilience depends on several key traits, such as genetic and species diversity, good water quality, connected and continuous habitats, energy reserves, seed banks, and balanced trophic interactions (Unsworth et al., 2014; Connolly et al.,



**Figure 5.** Principal coordinates analysis (PCoA) for both Bray-Curtis and Jaccard dissimilarity matrices was used to visualize the seagrass community structure across the sites.



**Figure 6.** Distance-Based Redundancy Analysis (dbRDA) for the best model (Bray-Curtis dissimilarity ~ Water pH +CS +CDFL +MTS), significant ( $P \leq 0.05$ ) to detect linear relationships between constraint variables and dissimilarity of seagrass composition (beta diversity) across sites.

2018; Dierick *et al.*, 2021; Li *et al.*, 2021). The low diversity and evenness of seagrass species indicate that balai and ujung lolok sites have low genetic diversity, habitat complexity, resource availability, and adaptation potential (Duarte, 2002). These factors may make them more vulnerable to pressures such as eutrophication, sedimentation, herbivory, disease, and human activity (Waycott *et al.*, 2009).

Lamun had the lowest value on RDA2, meaning that it had a lower CS than the other sites. This indicates that this site is far from the settlements, which may have positive effects on seagrass health and quality (Sotelo-Casas *et al.*, 2022). This site also has low RDA1 values, indicating that it has lower MTS and CDFL values than other sites. This indicates that the site is close to tourism spots and forest loss, which may have negative effects on seagrass distribution and density (Unsworth *et al.*, 2018; Alsaffar *et al.*, 2020; Collier *et al.*, 2021). This site is separated from the other sites along RDA2, indicating that it has a different seagrass composition. The plot shows that this site was mainly influenced by CS and Water pH, as their vectors were parallel to RDA2.

Matahari, Orongan, Pabisi, Asok, and Rago-rago. These sites have intermediate values on both axes, indicating that they have moderate values for all constraint variables. This indicates that these sites are not strongly affected by any of the constraint variables, or that they are affected by a combination of them (O'Brien *et al.*, 2018; Collier *et al.*, 2021a; Pearman *et al.*, 2020). These sites were clustered together in the middle of the plot, indicating that they have similar seagrass compositions. The plot shows that these sites are not strongly influenced by any of the constraint variables because their vectors are not parallel or perpendicular to any of the axes.

However, there were some slight differences between the Orongan and Matahari sites. Orongan had a higher value of abundance and richness, followed by Matahari (figure 2), indicating that it had lower MTS and CDFL than Matahari. Orongans are closer to tourism spots and forest loss than Matahari, which may have negative effects (closer to tourism spots) and positive effects (close to forest loss) on seagrass diversity and abundance (Holmer *et al.*, 2016). CDFL alters sedimentation, nutrient, and light regimes in coastal waters (Zabarte-Maetzou *et al.*, 2020). Forest loss may increase erosion and runoff of terrestrial sediments and nutrients, which can smother seagrass plants and reduce their light availability (Rodil *et al.*, 2021). Closer to tourism spots, it does not seem to really affect the abundance and richness of seagrass because, based on observations of the closest tourist spot to Orongan and the Sun, it has a small scale.

Orongan also has a higher value of RDA2 than Matahari, meaning that it has higher CS and Water pH than Matahari. This indicates that Orongan are farther from settlements and have less acidic water than Matahari, which may have positive effects on seagrass growth and survival (Lin *et al.*, 2021).

## Conclusion

Seagrass alpha diversity varied significantly among sites and was influenced by the dominant substrate type, longitude, and distance to forest loss. The highest alpha diversity was observed at the Orongan site, which had the highest seagrass richness and evenness. The lowest alpha diversity was found at the Balai and Ujung Lolok sites, which each had only one seagrass species. The study also revealed that seagrass beta diversity was influenced by a combination of constraints such as water pH, distance to forest loss, distance to tourism spots, and distance to settlements. The sites were grouped into four clusters based on their similarity or dissimilarity in seagrass beta diversity: Balai and Ujung Lolok, Lamun, Matahari and Orongan, and Asok, Pabisi, and Rago-rago. This study highlighted the importance of seagrass diversity in ecosystem functions and services, as well as human well-being. The study suggests that seagrass conservation and management should consider the spatial variation and multiple drivers of seagrass diversity in the study area.

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