

Use of Generalized Dissimilarity Model for Analyzing Environmental Drivers of Marine Beta Diversity and Bioregionalization in Lesser Sunda Island

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Abstract

The diversity and density of marine organisms have gradually declined due to prolonged human influences on the ocean and climate change pressures. Complex marine organism diversity distribution is linked with beta diversity. The environmental factors influence the pattern of marine beta diversity in the aquatic system. In this study, we aim to analyze the environmental drivers of beta diversity pattern of Lesser Sunda Island by using generalized dissimilarity model (GDM) approach. This technique employs nonlinear basis (I-spline) functions, which recognized to be a good fit for common compositional and environmental patterns than linear models. Lesser Sunda Island is located in coral triangle area that prioritized for global marine conservation. The observed beta diversity was computed from species occurrence data retrieved from Ocean Biodiversity Information System (OBIS) database, while environmental variables derived from MARSPEC and Bio-Oracle database. The result showed deviance explained percentage of GDM was 44.284%. It also revealed that nitrate, pH, salinity, and SST as the main driver of beta diversity in Lesser Sunda Island. Furthermore, we used the predicted beta diversity resulted from GDM to create bioregion as well as evaluate the representativeness of current marine protected area (MPA), which were indicate a gap in marine conservation area in study region.

Keywords: biodiversity, conservation, ecosystem change, generalized linear model, pair-wise dissimilarity

1. INTRODUCTION

The diversity and density of marine organisms gradually decline as a result of prolonged human influences on the ocean. Reduced species richness can adversely impact ecosystem functions like fishery resources and nitrogen cycling, as well as impair ecosystem health and resilience. Most of these alterations are caused by anthropogenic activities such as climate warming, overexploitation, and marine litter [1]. In specific, climate warming is usually accompanied by other conditions such as rising sea levels, acidification, changes in ocean circulation and stratification, as well as other aspects of global change [2]. Therefore, the degradation of marine biodiversity due to climate change is unavoidable. Hence, effective conservation effort of the biodiversity and the critical ecosystem services which it facilitates is

already a priority as people become more aware of the healthy ecosystems' benefits for human wellbeing [3].

Coral triangle (CT) is referred to triangular marine tropical waters area around Indonesia, Philippines, Malaysia, East Timor, Papua New Guinea, and the Solomon Islands [4]. Due to its high species richness and endemism, it is regarded as the worldwide center of marine biodiversity. Therefore, over the last decade, the area has been a primary priority of biodiversity conservation acts by both government and non-government institutions. Several ecoregions were recognized within the CT, including one that corresponds to the Lesser Sunda region of Bali, West, and East Nusa Tenggara [5]. The Lesser Sunda Islands are located at the "cross position" of major global climate forces, giving them the harshest tropical environment on the Indonesian maritime region [6]. Furthermore, the area is becoming increasingly vulnerable to human activities on the environment such as seismic oil exploration and production, development of tourism, and urban and industrial waste, all of which have resulted in environmental destruction [7]. These factors are unavoidably affecting the marine biodiversity loss.

In recent decades, ecosystem-based management (EBM) strategy has been considered as a sufficient tool for marine conservation efforts [8]. It is widely recognized that this approach

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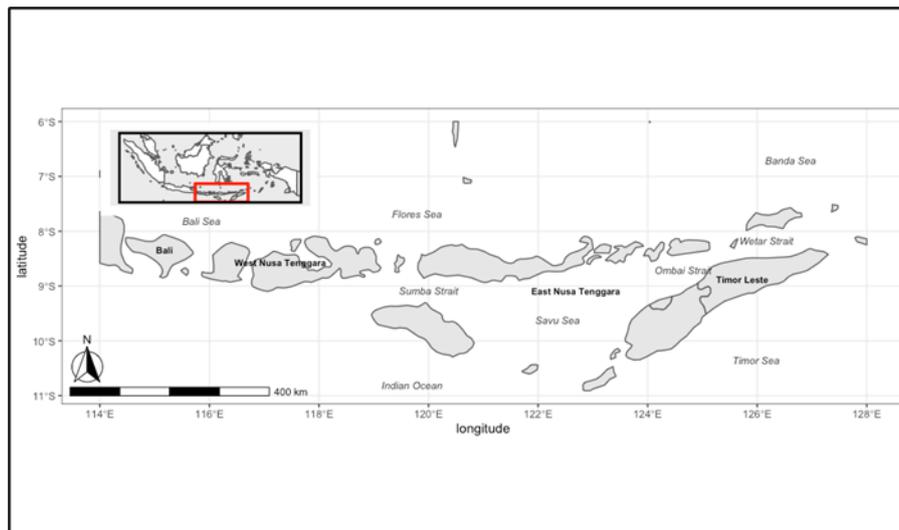


Figure 1. Geographical location of study area in Lesser Sunda Island.

governs human activities that have an impact on ecosystems, rather than the ecosystems themselves, and puts these effects into consideration when making decisions [9]. Some key principles of EBM involving biodiversity and ecosystem connection in space and time scale by using a cutting-edge scientific knowledge integration for ecological relationship [10]. Therefore, EBM's implementation requires extensive spatial data, such as the distribution of species community or composition data as well as relevant statistical model and data analysis [11].

Beta diversity, which evaluates the difference in species composition between ecosystems, is critical for EBM since it emphasizes the distinct ecological aspects of different places as well as their connection. This is especially crucial in island ecosystems, where high beta diversity can result from habitat fragmentation and varying environmental conditions. Understanding beta diversity can guide focused conservation efforts and help address regional policy gaps relating to habitat management, invasive species, and climate change impacts. The existing policy on Lesser Sunda Island frequently ignores the necessity of climate adaptation in marine conservation initiatives. Local maritime management plans do not adequately incorporate climate change predictions, which leads to conservation efforts that are insufficiently resilient to the long-term impacts of climate change on fisheries, coral reefs, and coastal habitats [7]. By incorporating beta diversity into EBM strategies can

better conserve its unique biodiversity, enhance ecosystem resilience, and promote sustainable development. Several research studies highlight the importance of beta diversity in understanding and managing complex ecosystems, particularly in the face of ongoing environmental changes

Generalized dissimilarity model (GDM) is one of the prominent distance-based statistical approaches for analyzing and mapping geographical patterns of community composition change which supports EBM [11,12]. The model architecture constrains the fitted functions to be monotonic, with the assumption that increasing separation of sites along an environmental gradient can only result in increasing compositional dissimilarity. It has a wide range of applications like survey gap analysis, bioregionalization, and climate change effects evaluation [12]. GDM has been applied for various studies such as insect diversity [13], spatial taxonomic diversity of British breeding bird [14], invertebrate [15], and marine species [11].

Using distance-based linear models, the most recent study investigates environmental factors that are connected with species distributions within the Lesser Sunda scale and reveals alternative ecoregions to improve the effectiveness of conservation efforts in the Lesser Sunda Islands [16]. However, the linear model approach tends to be less realistic in ecological problems, due to the non-linear nature of the relationship between environmental factors and species diversity [8]. Therefore, GDM modeling would be more

appropriate because it accommodates the non-linearity of the relationships between variables. In this paper, we aim to analyze the environmental drivers of beta diversity pattern of Lesser Sunda Island by using GDM approach. This technique employs nonlinear basis (I-spline) functions, which recognized to be a good fit for common compositional and environmental patterns than linear models [17]. Furthermore, we also seek to evaluate the representativeness of current marine conservation area based on the modelling result. This is significant in supporting effective marine conservation efforts in Lesser Sunda Island.

2. MATERIALS AND METHODS

2.1. Materials

2.1.1. Study Area

Lesser Sunda Island spans 44.5 million hectares, specifically located at [11.000°S 114.000°E; 11.000°S 128.000°E; 7.000°S 128.000°E; 7.000°S 114.000°E]. The region is administratively

classified into four Indonesian provinces: Bali, West Nusa Tenggara, East Nusa Tenggara, and Maluku, as well as territory within Timor Leste (Figure 1). This is also a limitation to data collection for this research. The Lesser Sunda region encompasses 1,056 islands, the majority of which are small. Majority of them are divided by oceanic trenches.

2.1.2. Species Data

We obtained occurrence records for marine species in Lesser Sunda Island waters from the Ocean Biodiversity Information System (OBIS) database (<https://www.obis.org/>) version 2.0 which accessed at 19 January 2024 [18]. The information in the data is provided with point georeferenced positions and the corresponding presence/absence information. Access to this database was performed by using package ‘robis’ and ‘obistools’ in R software. Species occurrence data in the research location were available from 2000 to 2014. Data recorded in OBIS has been synchronized and

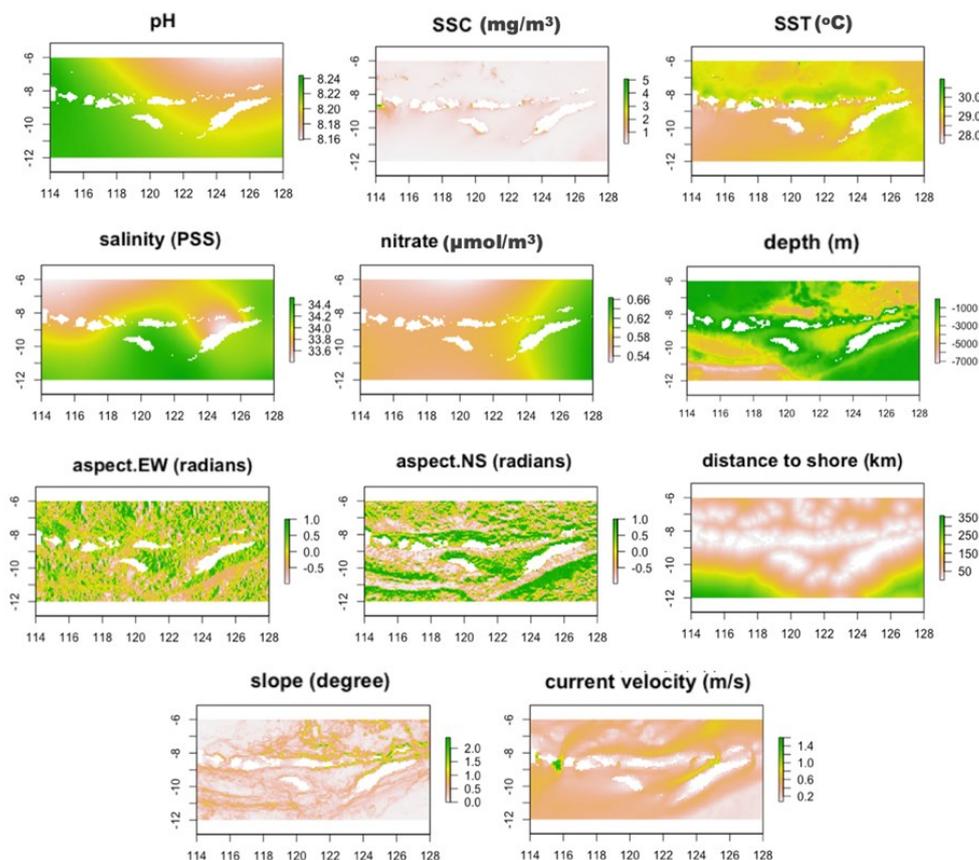


Figure 2. Spatial pattern of environmental predictor inputs.

checked for quality from numerous sources [19]. Previous studies have estimated species distributions in other areas using occurrence records from the OBIS database [11]. We then performed a data quality check, verifying species identification and looking for synonym using the WoRMS database, as well as removing any duplicate records.

2.1.3. Environmental Data

Candidate environmental predictors were selected according to their relevance to marine species distribution and based on knowledge from previous study. These are included sea surface chlorophyll or SSC (mg/m^3), sea surface temperature or SST ($^{\circ}\text{C}$), nitrate ($\mu\text{mol}/\text{m}^3$), phosphate ($\mu\text{mol}/\text{m}^3$), salinity (PSS), pH, depth (m), and slope of the seabed (degree), distance to shore (km), current velocity (m/s), the eastness (aspect EW) and the northness (aspect NS) of the slope. These data were obtained from the MARSPEC and Bio-Oracle database (<http://www.bio-oracle.org>, date accessed 19 January 2024) (Figure 2). This global database provides in situ current and satellite-based oceanic information of the surface and seabed in a 30 arc seconds resolution ($\sim 1 \text{ km}^2$) [20].

2.2. Methods

2.2.1. Beta Diversity Measure: Bray-Curtis Index

Beta diversity is essential in ecological systems and biogeography since it denotes variations in species composition that emerge across an environment. It is considered as the ratio of regional gamma diversity to local alpha diversity [21]. There are many beta diversity metrics, but the Bray-Curtis index is by far the most popular in the ecological studies. This index measures the dissimilarity of species between points, for instance point m and n, which can be expressed in the following Equation 1 [22];

$$\beta_{mn} = \frac{\sum_{j=1}^S |x_{mj} - x_{nj}|}{\sum_{j=1}^S (x_{mj} + x_{nj})} \quad (1)$$

where, β_{mn} is Bray-Curtis index between point m and n, x_{mj} is the abundance of species j at point

m, x_{nj} is the abundance of species j at point n, and S is total number of species found at point m and n. The Bray-Curtis index value ranges between 0 and 1, where a value of 0 indicates that the two location points have the same species and a value of 1 means that the two location points do not shared any species at all [22].

2.2.2. Generalized Dissimilarity Model (GDM)

GDM aims to evaluate the relationship of the corresponding distance matrices. In this case, the distance matrix as the response variable used is the species composition inequality between all possible pairs of sampling points in a survey area. The assumption of linearity in matrix regression models is often violated in ecological data for several reasons. First, as the distance between two points increases, chance of the same species are found in both locations is smaller, or even no similar species is found at all. Second, the relationship between environmental gradient and species dissimilarity is curvilinear/nonlinear. Linear relationships generally occur for low levels of inequality. Thus, modelling of the dissimilarity between location points was reformulated with the generalized linear model (GLMs) approach [8]. As any other GLMs models, link function (μ) of the GDM can be expressed as follows Equation 2;

$$\mu = 1 - e^{-\eta} \quad (2)$$

where μ is the expected dissimilarity between points and η is linier function of the environmental dissimilarity across points. The function of η can be written as Equation 3.

$$\eta = \beta_0 + \sum_{j=1}^p |f(x_{jm}) - f(x_{jn})| \quad (3)$$

To provide the best fit for biological dissimilarity at each point, the predictor is used in the form of k_j nonlinear functions from each predictor, x_j . In addition, it is assumed that the biological dissimilarity between locations will be greater as the distance between locations increases. Therefore, to ensure the monotony and flexibility of the curve shape, the function $f(x_j)$ denoted as basis I-spline function as follows Equation 4;

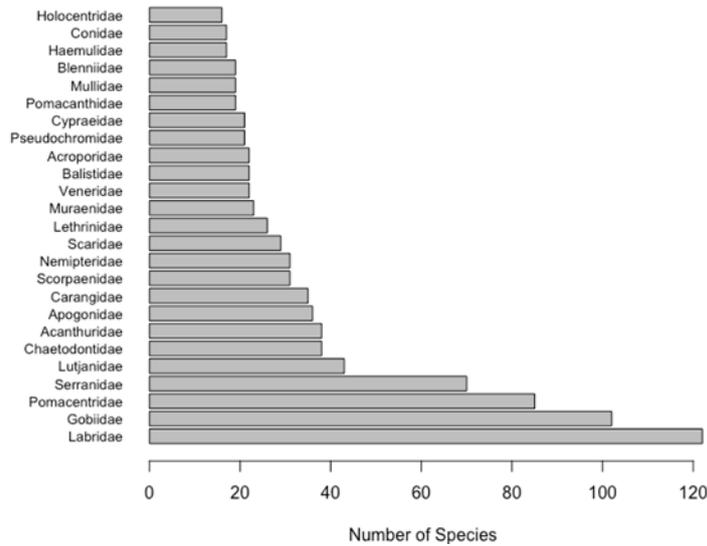


Figure 3. Number of species at each family of marine species occurrence.

$$f(x_j) = \sum_{l=1}^{k_j} \beta_{jl} I_{jl}(x_j) \quad (4)$$

where, $I_{jl}(x_j)$ denoted the l -th basis I-spline function of x_j and β_{jl} is coefficient of the l -th basis I-spline function of x_j . Therefore, the GDM can be described as follows Equation 5.

$$\eta = \beta_0 + \sum_{j=1}^p \sum_{l=1}^{k_j} \beta_{jl} |I_{jl}(x_{jm}) - I_{jl}(x_{jn})| \beta_{jl} \geq 0 \quad (5)$$

The estimation of GDM parameters is carried out like other GLMs models by using maximum likelihood estimation (MLE) method and iteratively re-weighted least square (IRLS) algorithm. However, to ensure that the regression coefficient is positive ($\beta_{jl} \geq 0$), modifications were made by replacing least-square regression in IRLS with non-negative least squares (NNLS). Analysis of GDM in this study was carried out by using package ‘gdm’ that available in R software. As default, the number of knot was set to 3 [11]. To diagnose the environmental factors affecting changes in community structure, GDM was calculated by removing one environmental explanatory variable. Since the GDM technique is susceptible to predictor correlations, strongly correlated predictors ($r > 0.70$) were excluded from the analysis [23].

2.2.3. Beta Diversity Projection and Clustering

Method

Output of GDM was predicted dissimilarity matrix across sampling sites. Since the predicted dissimilarity matrix is hard to picture, then a principal component analysis (PCA) was utilised to capture the variation of the dissimilarity [24]. Furthermore, the result of PCA was then projected into RGB color map. In addition, we also classify the predicted dissimilarity of Lesser Sunda Island by using fuzzy C means (FCM) clustering technique to identify bioregion of studied area.

3. RESULTS AND DISCUSSIONS

3.1. Marine Species Composition of Lesser Sunda Island

Understanding the spatial pattern of species diversity is a critical requirement for conservation planning purposes. As one of the biodiversity measures, beta diversity can capture more complex mechanisms of biodiversity, giving details on connectivity patterns and processes of geographical biodiversity preservation, which is important for conservation scale-appropriate action. Since Indonesian institutions, both government and non-government, are currently using an EBM approach to achieve the sustainability of marine ecosystems [25], there is a need to rely on an ecologically relevant geographical arrangement.

Our dataset included information on a total of 747 sites and 2028 species from 77 families. The most represented families in this dataset were

Table 1. Importance of environmental variables in GDM.

Variable	Importance	p-value
pH	2.956	0.020
SSC (mg/m ³)	1.009	0.440
SST (°C)	3.783	0.080
Salinity (PSU)	2.209	0.100
Nitrate (µmol/m ³)	14.264	0.000
Depth (m)	1.495	0.320
aspect.EW (radians)	1.952	0.280
aspect.NS (radians)	1.287	0.040
Distance to shore (km)	1.231	0.280
Slope (degree)	2.231	0.120
Current velocity (m/s)	1.207	0.280
Model deviance	1412.188	
Percent deviance explained	44.284	
Model p-value	0.000	
Intercept	0.737	

Labridae (122 species), Gobiidae (102 species) and Pomacentridae (85 species) as depicted in Figure 3. It means that marine species found at Lesser Sunda Island was dominated by reef fish family. It is understandable since the Lesser Sunda Island is a key region of marine biodiversity which is situated in the center of the Coral Triangle [5]. Reef fish species has been globally accepted as flagship indicators for building conservation strategy. They are greatly rich in species and possess a broad range of geographical distribution, ranging from world widely distributed species to constrained local endemics. Moreover, reef fish species are conveniently to be observed and their diversity has strong association with other organisms like corals and mollusks. In addition, tropical reef fishes are typically adapted to a relatively narrow suite of environmental conditions. Thus, reef fishes may also be vulnerable to the direct effects of climate change [26]. As a result, the geographical reef fish community can be used to assess both habitat and general biodiversity. A common types coral reef is home to a large number of fishes, which rely on a complex food chain involving numerous plants and invertebrates.

The use of online databases (OBIS and Bio-Oracle) in this study has a number of limitations. There was a significant disparity in how various

taxa were represented in OBIS, with some taxa predominating the database. This taxonomic bias is also changing as a result of emerging technologies, which have led to a relative increase in the sampling of some taxa [19]. However, Bio-Oracle's environmental layer limitation, which includes nearshore and shallow coastal regions, might be poorly resolved or averaged with nearby land or deep-sea cells. Layers may not capture fine-grained spatial heterogeneity, such as upwelling zones, because they are based on interpolated observations or model outputs [20].

3.2. Modelling the Drivers of Spatial Beta-Diversity

Prior to GDM, our correlation analysis results suggested that phosphate and salinity has strong association ($r = 0.75$). Therefore, we decided to omit phosphate and retained salinity as one of the environmental predictors in GDM. According to Table 1, the GDM explained 44.28% of the variation in community composition. Predictor importance is quantified as the percent change in deviance explained between a model fit with and without that predictor permuted. Following a comparison of the different GDM results, it was clear that nitrate was the most important explanatory variable for changes in marine species variation. This was followed by pH, salinity, and

SST. In addition, the overall produced model is significant to explain the beta diversity distribution in the study area.

Nitrate is a fixed nitrogen and generally known as nutrient in aquatic ecosystem, along with phosphate and silicate. Nitrogen supply is a main determinant of primary production in marine environments. However, a nutrient enrichment may result from anthropogenic activities and at any level will lead to eutrophication [27]. The phenomenon is one of the most serious harms to the health of coastal, estuarine, and marine ecosystems around the world [28]. Eutrophication contributes to the growth of phytoplankton known as algal bloom. These blooms can deplete oxygen levels in the water column as they decompose, resulting in hypoxia, which can be harmful to fish and other aquatic species [29]. Eutrophication-induced changes in phytoplankton communities can upset the food chain, influencing fish food supplies and possibly favoring some species over others (species turnover). Thus, recent study revealed that the total fish biomass was significantly affected by concentration of nitrates [30].

The ocean carbon sink helps to slow down climate change by lowering the CO₂ in the atmosphere. Nonetheless, the massive amounts of dissolved CO₂ results to a change in the ocean's chemical balance, inevitably reducing its pH or known as ocean acidification. It reduces the concentration of calcium carbonate, which has a particularly negative impact on calcareous species [31]. They create their shells and skeletal structures from calcium carbonate minerals using carbonate ions. Calcium and hydrogen ions fight for the

carbonate ions, which lowers the rates of calcification. Most importantly, it has an impact on the growth levels and reproduction rate of calcareous species. Finally, the impacts on calcareous species have the potential to damage the food chain and change the species diversity of marine system [32]. A recent study projected differing indirect consequences of ocean acidification in biogenic habitats: Reduced structural complexity may lead to a decline in biodiversity in coral reefs, mussel beds, and some macroalgal ecosystems [33].

On the other hand, unfavorable salinity may affect zooplankton in some ways, such as disruption in development, growth, and reproduction. The organisms serve an important role in the pelagic trophic chain by connecting primary producers to heterotrophs (such as fish) [34]. As a result, their density and community composition have a significant influence on the development of fisheries resources and also higher trophic level biodiversity. Changes in zooplankton community structure as a result of salinity alteration are likely to have a detrimental impact on food capacity and planktivorous fish growth. This could then have an impact on organisms at higher trophic levels, like fish, seabirds, and mammals [35].

SST is an important driver of marine species distribution and behavior. Worldwide phenomena like Indian Ocean Dipole (IOD) and El Niño-Southern Oscillation (ENSO) have an indirect impact on the dynamics of SST [36]. Since there are less microclimates in marine ecosystems than in terrestrial ecosystems, marine animals, especially ectotherms, are more susceptible to rising

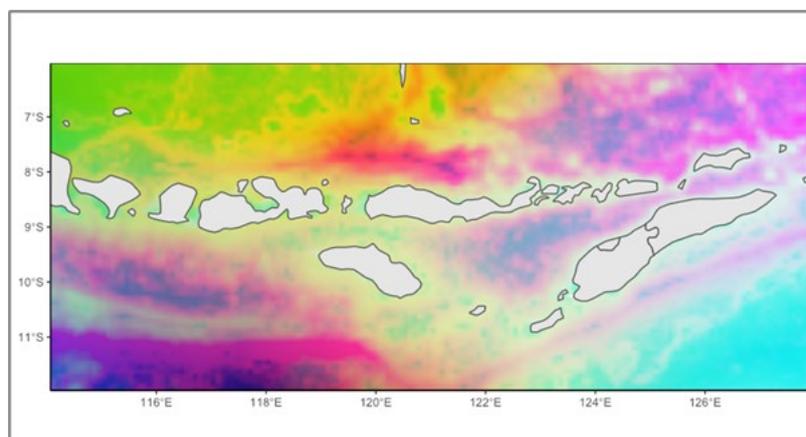


Figure 4. RGB plot projection of predicted beta diversity calculated from GDM in Lesser Sunda Island.

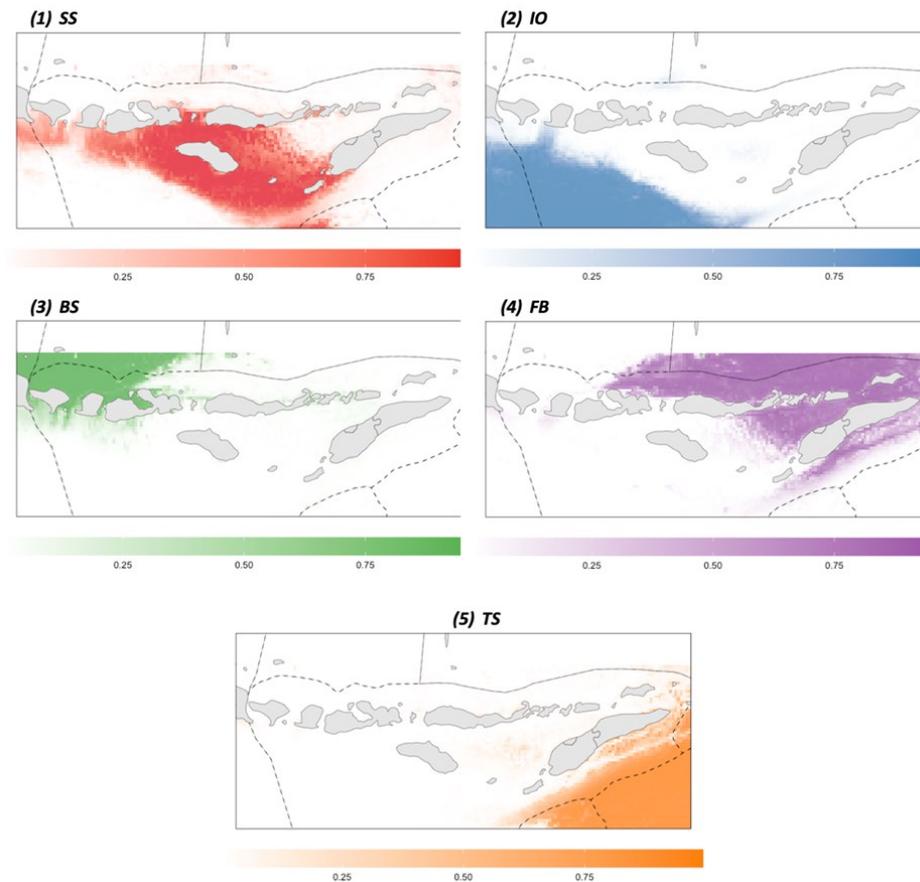


Figure 5. Bioregion classification from FCM clustering of predicted beta diversity. The dashed line indicating the boundary of MEOW bioregions.

temperatures. This environmental factor is highly correlated to climate change and global warming. It is widely acknowledged that these phenomena are great threats to marine biodiversity. In addition, recent studies have found that climate change has caused a more intense decline in marine species diversity and abundance close to the equator or tropics region. This implies that the temperature is already too high for several organisms to live [37]. Therefore, SST is a one of major consideration for conservation planning in Lesser Sunda Island.

3.3. Spatial Analysis Results of Predicted Beta Diversity

The resulted model of GDM then used to classify the biogeographical region and evaluate the representativeness of the current applied MPAs in the study area. Bioregionalization allows for the classification of marine environments into relevant and controllable regions. This process is often the first step in prioritizing marine nature reserves and supporting resource management and spatial

planning. Firstly, we produce PCA projection of predicted biological dissimilarity as depicted in Figure 4 by using the first three principal components explained 88.36% of its total variation. The predicted beta diversity were visualized using RGB color maps, with similarly colored area predicted to have similar species community structure. It can be seen that Bali and West Nusa Tenggara have similar species assemblage than those at East Nusa Tenggara regions. This projection then clustered into biogeographical region using FCM. Based on Silhouette index, the optimum number of clusters for this research is 5 with fuzzy eoefficient equals to 1.20.

The five fuzzy biogeographical regions identified using the FCM were each assigned a membership value, as shown in Figure 5, i.e. (1) Savu Sea, Lombok Strait, Sumba Strait, and Ombai Strait (SS), (2) : Indian Ocean (IO), (3) Bali Sea (BS), (4) Flores Sea and Banda Sea (FB), and (5) Southern Timor Sea (TS). The coverage representativeness of cluster SS is the widest among

others. The groups defined in this study portray the extent of variation in marine species structure throughout the Lesser Sunda Island. The bioregions produced in our study may serve as a supplement for existing global marine management scheme such as MEOW [38].

Our analysis reveals that Cluster SS occupies 27.76% of the study area but only 12.53% of the MPA coverage. In comparison, Cluster IO covers 20.40% of the study area, yet its MPA coverage accounts for just 11.50%. Cluster BS, while covering 10.87% of the study area, holds 12.03% of the MPA coverage. Similarly, Cluster Fb spans 24.21% of the study area, but only 12.38% of the MPA coverage. Cluster TS, covering 16.75% of the study area, contributes 11.82% to the MPA coverage. In contrast, the Lesser Sunda seascape, as delineated in the existing MEOW bioregion, has an MPA coverage of 12.32%. The study results show that conservation in smaller areas could ensure that coverage of the important characteristics of the study area are taken into account more than in larger areas.

Evaluation the representativeness of current MPAs in studied location based on our predicted beta diversity is shown in Figure 6. Areas with higher values are better represented by the protected areas (shown as polygons) than areas with lower values. It is showed that the MPAs that have been in Lesser Sunda Island able to cover most of the

predicted beta diversity in this region. The largest MPA, Savu Sea, has the most wider coverage in this regard.

Almost all of the current MPAs in Lesser Sunda are situated in the area of SS cluster, such as Savu Sea Marine National Park (SSMNP), Pantar Strait Marine Conservation Area, Gili Banta Marine Conservation Area, and Nusa Penida Marine Conservation Area. They are lied within Lesser Sunda seascape. Cluster FB alignes with Banda Sea seascape which is regarded a part of Sunda Banda seascape along with Lesser Sunda [39]. Compared to cluster SS, cluster FB has lower nitrate concentration, higher pH and salinity. Meanwhile, cluster IO and TS which represents Indian Ocean which borders many countries. Hence marine protected areas in this region are managed separately by each country. The research results indicate that cooperation between countries is needed to achieve effective conservation of ecological systems and organisms across the islands and continental countries of the Indian Ocean region [40]. Some efforts that can be made by these countries to preserve marine ecosystems through regional organizations, such as the United Nations Convention on the Law of the Sea (UNCLOS) or the Convention on Biological Diversity (CBD), to establish common conservation goals and coordinate conservation efforts [41].

On the other hand, cluster BS located in northern

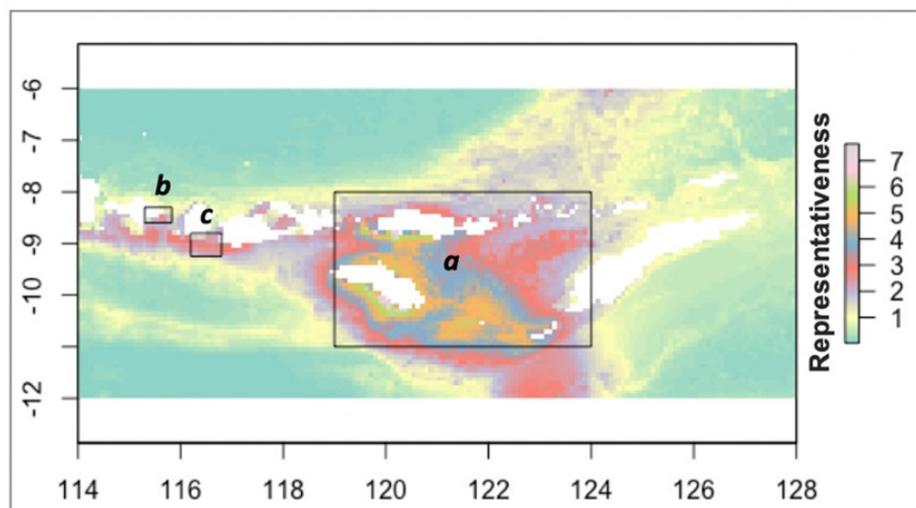


Figure 6. Representativeness pattern of current MPA in Lesser Sunda Island to predicted beta diversity; (a) Savu Sea Marine National Park (SSMNP); (b) Nusa Penida Marine Conservation Area; (c) Gili Meno, Gili Ayer, Gili Trawangan Marine Conservation Area.

Bali is also not well represented by current MPA which focused more on southern and west Bali [42]. However, there exist a local initiative MPA in Pemuteran, Buleleng at north Bali. Some studies have been conducted such as identification reef fish species, coral reef index, environmental characteristics as well as social community [43]. Hence, this area should be taken into consideration for a higher level of conservation ecoregion to induce the representativeness of Lesser Sunda Island marine reserve. Low promoting of marine conservation area in Bali region may cause by competing human interest and it has been protecting its coastal ecosystem for centuries through customary and formalized conservation [44]. This study provided an underpinning for more strategic planning for marine development analysis in Lesser Sunda Island by grouping the island into separate bioregional categories. With growing investments in conservation efforts on the Lesser Sunda Island [45], a better grasp of the environment and biodiversity will contribute to improvement management planning, such as identifying priority areas where ecosystems are more likely to cope to natural and human disruptions.

4. CONCLUSIONS

The Lesser Sunda Islands, which are at the center of the internationally important Coral Triangle, are crucial to Indonesia's marine biodiversity and ecological integrity. By identifying spatial patterns of beta diversity and the environmental factors that affect them, this work provides useful insights that extend beyond regional conservation. The identification of underrepresented clusters highlights significant gaps in the current coverage of MPAs, particularly in areas such as the Bali Sea and Indian Ocean. These findings demonstrate the importance of incorporating beta diversity indicators into marine spatial planning frameworks to ensure that species richness, habitat distinctiveness, and ecological turnover are all taken into consideration in conservation efforts. Implementing these strategies can help create more resilient, linked, and representative MPA networks that meet national and international biodiversity targets.

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Conceptualization, and Methodology, E. D. L. and S. A.; Software, Formal Analysis, Visualization, Funding Acquisition, Writing – Original Draft Preparation, Writing – Review & Editing, E. D. L. and S. S. ; Validation, and Data Curation, M. M.; Investigation, Resources, Supervision, and Project Administration, S. A.

Conflicts of Interest

The authors declare no conflict of interest.

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