



Mangrove-mudflat connectivity shapes benthic communities in a tropical intertidal system

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ABSTRACT

Understanding the connectivity among seascape habitats is an important emerging topic in marine ecology and coastal management. Mangroves are known to provide many ecosystem services such as coastal protection and carbon cycling, but their functional relationships with adjacent benthic intertidal communities are less clear. We examined how spatial adjacency to mangroves affects macrobenthic communities of intertidal mudflats in a tropical estuarine ecosystem. In the Bijagós Archipelago, Guinea-Bissau, benthic macrofauna assemblages were compared among sampling locations with different connectivities between intertidal mudflats and mangrove stands. We explored how a single mangrove connectivity index (MCI), combining mangrove tidal basin size and the distance to the mangrove edge, affected macrobenthic composition, and compared this effect to sediment properties. In addition, we used structural equation modelling (SEM) and ordination to determine how different environmental predictors directly and indirectly affected macrobenthic communities. MCI strongly affected macrobenthic composition and species abundance, and SEM revealed that this effect contained both a direct component and an indirect component through mudflat NDVI (normalized difference vegetation index, an indicator for microphytobenthos). Sediment properties (grain size, organic matter) affected macrobenthos independently from MCI, nevertheless sediment properties were also affected by MCI. We show the importance of accounting for the seascape structure of tidal basins when investigating the connectivity between mangroves and macrobenthic communities of intertidal mudflats. As benthic macrofauna is a key food source for endangered fish and waders in these systems, our findings provide strong arguments for the integrative conservation of intertidal mudflats and mangroves at the seascape scale.

1. Introduction

Nutrients and organic matter are transported from terrestrial to marine environments, and vice versa, in different (dissolved and particulate) forms via runoff, wind, tides, river flow, and through movement of organisms (Moore et al., 2004; Nagelkerken, 2009; Olson et al., 2019). This can affect both the productivity and biodiversity of the recipient systems (Gorman et al., 2019; Montagano et al., 2018; Thom et al., 2018). The connectivity between terrestrial and marine ecosystems is therefore important for both the productivity and resilience of marine and estuarine habitats, as movement of animals and nutrients

from other systems can help the recovery of disturbed habitats (Heck et al., 2008; Loreau et al., 2003; van de Koppel et al., 2015). State of the art, ecosystem-based, spatial planning should consider the networks of ecological connections, both within and between distinct habitats.

In coastal systems, habitats may be connected through different physical and biological linkages. Physical connections include the exchange of organic matter and nutrients via tidal and wind-driven currents and rainfall runoff (Bouillon and Connolly, 2009a; Davis et al., 2009; Hyndes et al., 2014). Tidal currents involve a bi-directional exchange of large quantities of energy and nutrients between tidal and subtidal habitats in coastal landscapes (Bouillon and Connolly, 2009a;

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Davis et al., 2009; Hyndes et al., 2014). Runoffs represent a unidirectional mode of transport of large amounts of nutrients and organic matter from terrestrial to estuarine habitats (Fabricius, 2005; Zheng and Tang, 2007). Biological connectivity involves the transport of nutrients and energy via animals that often move between habitats during different stages of the tidal cycle and/or their life cycles (Nagelkerken, 2009). Fish play an especially important role here because not only do they transport large quantities of energy between systems, but their temporary foraging bouts between different habitats can also maintain micro- and macroalgae-sensitive biogenic habitats, such as seagrass beds and coral reefs (Kohler et al., 2012; McMahon et al., 2012; Mumby and Hastings, 2007; Olds, Pitt, et al., 2012). Other motile organisms, such as birds, are also known to move nutrients across habitat boundaries, which affects the productivity and residence of the recipient habitats (Anderson and Polis, 1999; Polis et al., 1997; Post et al., 1998). Thus, the spatio-temporal exchange of nutrients and energy, and the role of motile organisms in this system, should be included for a comprehensive understanding of the stability and resilience of coastal and estuarine habitats.

Tropical marine habitats, such as mangroves, seagrass, and corals, are under tremendous pressure from overfishing and habitat degradation, threatening their ecological integrity (Jackson et al., 2001; Orth et al., 2006; Pandolfi et al., 2003; Polidoro et al., 2010). Mangrove forests are among the most productive systems worldwide and provide indispensable biological functions and economic services (Lee et al., 2014; Nagelkerken et al., 2008). The complex root structures of mangroves provide major nursery and refuge grounds for many commercially important fish species (Laegdsgaard and Johnson, 2001; Nagelkerken et al., 2008). Mangrove forests are also known to provide valuable coastal defence against the destructive forces of tides and waves (Horstman et al., 2014), as well as against extreme weather events such as tropical storms and cyclones (Dahdouh-Guebas et al., 2005). In addition, the tangled root systems of mangroves, combined with high sedimentation rates and waterlogged anoxic soil, store large quantities of carbon, and play a role in the mitigation of global warming (Atwood et al., 2017; Mcleod et al., 2011).

More recently, attention has been given to preserving important seascape functions that support high-biodiversity tropical habitats, such as coral reefs and mangroves. Mangroves grow in the upper intertidal zone but have been suggested to play a crucial role in the functioning and resilience of adjacent systems occurring at lower tidal gradients, such as corals and seagrasses, through wave attenuation and nutrient exchange, calling for an analysis of coastal systems at the scale of 'seascapes' (McMahon et al., 2012; Mumby and Hastings, 2007; Olds et al., 2012; Pittman, 2017).

While the relationship between mangrove and habitats such as seagrasses and corals has been well-established, less is known about the role that mangroves play in supporting their neighbouring soft-bottom intertidal flats. Intertidal mudflats provide important ecosystem services (Gillis et al., 2014; Levin et al., 2001; Martínez et al., 2007; Snelgrove et al., 1997). These areas often host rich benthic communities and numerous shorebirds that feed on them. Intertidal mudflats generally have high abundances of benthic organisms such as worms and bivalves, and typically support high microphytobenthic primary productivity (e.g., Christianen et al., 2017).

Intertidal benthic infauna also plays a critical role in the transfer of energy between trophic levels (Brey, 2012) in coastal food webs (Levin et al., 2001). During high tide, fish and larger crustaceans feed on sediment-dwelling biota (Sardá et al., 1998; Thrush et al., 1994), while, during low tide, birds, terrestrial mammals and reptiles can access this intertidal environment and prey on the same food items (Levin et al., 2001; Mathot et al., 2018). Intertidal mudflats therefore connect terrestrial and marine biomes; these are in constant exchange through tidal currents as well as the movement of animals. However, the remote and inaccessible nature of mangrove systems, makes it challenging to quantify the connectedness of mangrove systems with their adjacent

intertidal mudflats.

Mangrove forests can influence the benthic communities of adjacent intertidal mudflats as a source of nutrients and energy through outwelling with tidal currents, in addition to marine inputs (Lee, 1995). However, the quantitative importance of this outwelling is under much debate (Kruitwagen et al., 2010). So far, most studies have only analysed the effect of distance to mangrove edges, but did not include the landscape hydrological setting (tidal basin drainage structure) nor the total mangrove area within basins that are functionally connected to specific intertidal mudflats (Bouillon et al., 2000; Bouillon et al., 2004; Kruitwagen et al., 2010; Lee, 1995; Lourenço et al., 2018; Shahraki et al., 2014). Mangroves are characterized by their high efficiency in retaining and recycling nutrients (Alongi et al., 1993; Lee, 2008; Reef et al., 2010). This is closely linked to the density of their complex roots systems (Gillis et al., 2016). Larger mangrove areas would then have a reduced contribution of mangrove litter to tidal flat productivity compared to smaller areas. This is exemplified by the strong biogeochemical gradients observed in habitats ranging from vegetated mangroves to bare mudflats in Australia (Tolhurst et al., 2010; Tolhurst and Chapman, 2005). Nonetheless, several studies have shown significant shifts in the community composition of benthic organisms for mangrove associated mudflats along a distance gradient from the mangrove forest (Alongi, 1987; Alongi and Christoffersen, 1992; Ellis et al., 2004; Leung, 2015). In addition, Alongi et al. (1989) found a clear decline in mangrove-derived organic carbon stored in mudflat sediments with increasing distance from the mangrove edge. An increased nutrient input closer to mangroves may result in a higher local secondary production of mudflat macrofauna. However, additional factors such as the width of the mangrove fringe and the drainage structure of the adjacent mangrove forest complicate this relationship (Alongi et al., 1989).

In this study, we examined the connectivity between mangroves and adjacent intertidal mudflats in the relatively pristine and little studied Bijagós Archipelago in Guinea-Bissau, West-Africa, a crucial destination for wintering migratory shorebirds in the East-Atlantic flyway (Lourenço et al., 2018; van Roomen et al., 2012; Zwarts, 1988). We not only studied the effect of distance to shore, but also analysed how mangrove extent at the scale of local drainage basins was associated with mudflat macrobenthic community structure (total abundance, species richness, and biomass of the entire community). For this, we conducted a 125-point benthic survey in the Bijagós Archipelago. To capture the joint effects of the position of that point in its drainage basin (hydrologic unit based on a digital elevation model), the total area of the mangroves within that basin, and its distance to the mangrove edge, we developed a mangrove connectivity index (MCI), which could be assigned to each sampling point. Higher MCI values belong to sampling points with a larger 'upstream' mangrove area and/or closer to the mangrove edge. If mangroves are enriching the intertidal mudflats one way or another, this would be associated with higher abundances or biomass of benthic organisms as well as differences in community structure.

2. Material and methods

2.1. Study area

We conducted our study in the Bijagós Archipelago, Guinea-Bissau (Fig. 1). This archipelago consists of extensive mangrove forests, intertidal mudflats, and subtidal gullies, situated at the mouth of the Geba river, a regional river with a high sediment load. The Bijagós Archipelago is among the least disturbed mangrove-mudflat coastal ecosystems in Africa due to its relatively remote, offshore location. It is characterized by a complex archipelago of sandy islands associated with 760 km² of intertidal mudflats and 350 km² of mangroves (UNEP, 2007). Geologically it is situated at the most southern end of the Senegalo-Mauritanian sedimentary basin. High surface erosion rates resulting from high annual rainfall (2200 mm) combined with the soft, sandstone-type sedimentary geology and post-glacial sea level rise have resulted in

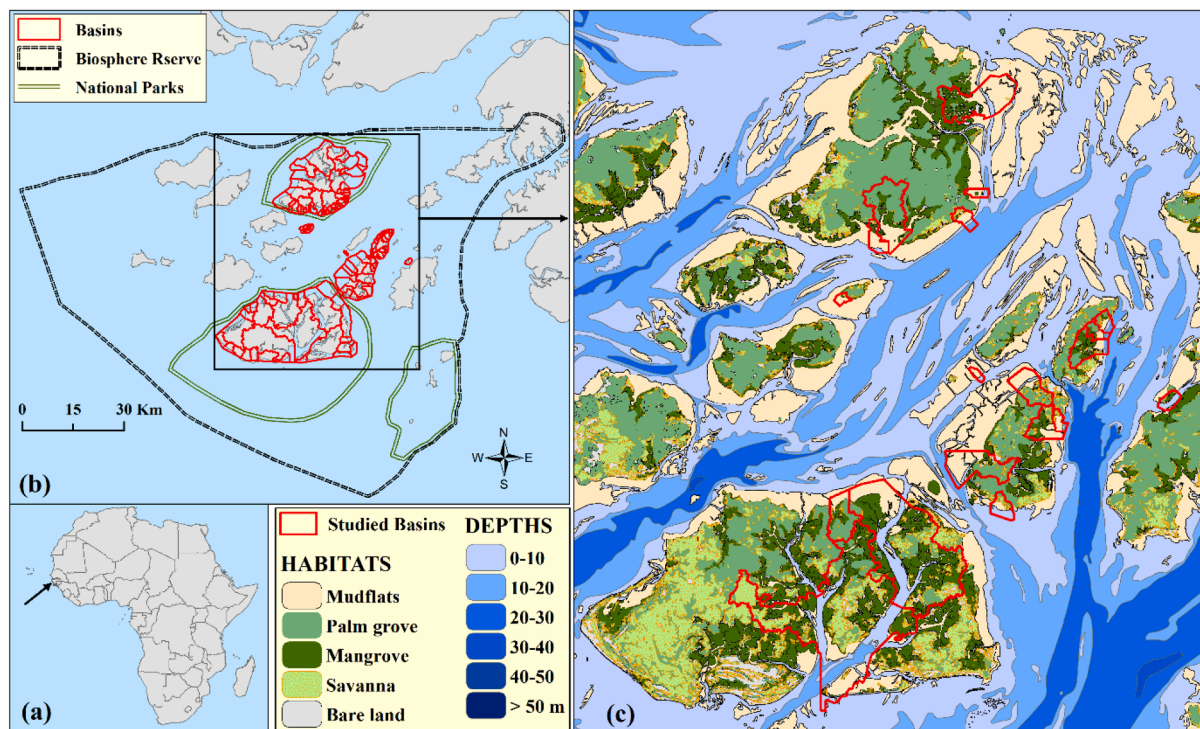


Fig. 1. (a) Map indicating the general location of the study region in West-Africa; (b) Map showing the Bolama-Bijagós Archipelago Biosphere Reserve in Guinea-Bissau and the core mangrove estuary and studied basins delineated using a digital elevation model (DEM) image (~10 m resolution; SRTM v3, U.S. Geological Survey) and modelled in ArcGIS (Spatial Analyst Tools); and (c) Detailed bathymetric and habitat map of the study area based on Spot imagery (source: Géomer, LETG UMR 6554-CNRS, published in [Campredon and Catry \(2018\)](#)). Studied mangrove basins are indicated in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

a strongly ragged ria-type coastal morphology ([Bird, 2008](#)), where the islands are the remaining peaks of the lowest parts of the eroded and flooded sedimentary basin.

The resulting small islands, with maximum elevations of up to 30 m above mean sea level, have become surrounded by a ring of mangroves and intertidal mudflats ([Fig. 1](#)). The mangrove systems in the archipelago are dominated by *Rhizophora* and *Avicennia* species ([Altenburg and van Spanje, 1989](#)). The extensive intertidal mudflats of the Bijagós Archipelago have been estimated to host around 700 000 wintering shorebirds ([Salvig et al., 1994; Zwarts, 1988](#)), which makes it the second most important wintering area in Africa for migratory shorebirds along the East Atlantic Flyway after the Banc d'Arguin ecosystem in Mauritania ([Delaney et al., 2009](#)).

2.2. Habitat classification, nutrient and salinity gradients, and mudflat productivity

A low-tide satellite RGB composite mosaic of the archipelago (Sentinel-2 satellite, ESA), using a mosaic of four scenes acquired on 16 December 2018, was digitized into polygons of upland (separated in palm groves and savannah), mangroves, intertidal mudflats and subtidal waters using supervised classification in QGIS version 3.4.1 ([QGIS Development Team, 2019](#)). Landform transitions as indicated by the image were checked on the ground. Small gullies originating from the mangrove forest and running over the mudflat were classified as drainage channels. The distances of each sampling point to the nearest drainage channel, subtidal habitat and mangrove forest edge were determined by calculating a proximity raster for each attribute. Furthermore, mudflat productivity was estimated from the Sentinel-2 image as Normalized Difference Vegetation Index (NDVI, using red and infrared bands), following well-established methods (e.g., [Benyoucef et al., 2014; Brito et al., 2013; Daggers et al., 2018; Echappé et al., 2018; van der Wal et al., 2008](#)).

2.3. Calculation of mangrove connectivity index (MCI)

To determine the potential area of mangroves that affects adjacent intertidal mudflats, 10 m resolution digital elevation data (SRTM v3, USGS) was used to compute watersheds using the Watershed tool in the Spatial Analyst Toolbox, ESRI ArcGIS 10.5.1. The mangrove area of the relevant watershed basin of each sampled mudflat was subsequently determined. To estimate the effect of mangroves on the mudflat community, we calculated the MCI for each sampling station, taking into account the total mangrove area within the basin as well as the nearest distance to the mangroves of each sampling point as follows:

$$\text{Mangrove connectivity index} = \frac{\sqrt{\text{Mangrove area within basin}}}{\text{Shortest distance to mangroves}}$$

The square root brings back the areas to their linear dimension and creates a unitless index after the division with distance to mangrove. This index then combines the declining outwelling effect with distance from the mangrove edge ([Alongi et al., 1989](#)) with the positive effect of a larger connected mangrove tidal basin. Next, the calculated MCIs were interpolated into a continuous map of the studied mudflats using the inversed distance weighted (IDW) tool in ArcGIS (Spatial Analyst Tools).

2.4. Macrobenthos sampling

Sampling took place in Jan–Feb 2019 on a total of 125 stations on 15 intertidal mudflats with high geomorphological variability within and across sites. At each site, 6 to 9 points aligned with a 250-meter grid were sampled. Sediment samples were taken with a PVC corer (15.3 cm in diameter) to a depth of 20 cm. The core was sieved with seawater through a 1 mm mesh directly in the field. In the lab, all organisms were stored in ethanol and brought to The Netherlands. Here, all organisms were identified to the lowest taxonomic level possible using a dissecting microscope and their length (longest dimension) was measured to the

nearest 0.1 mm. This typically resulted in identification to family level, as benthic species in this system have been the subject of few studies thus far, and no taxonomic reference material or identification guides were readily available. Additional species traits (habitat, feeding mode) were obtained via the databases “Polytraits” (Faulwetter et al., 2014) and “Encyclopedia of Life” (Parr et al., 2014).

After identification, individuals of different species were aggregated into groups based on main taxonomic groups (i.e., bivalves, polychaetes, gastropods & crustacea) and dried at 60 °C for a minimum of 48 h. After drying, samples were weighed to determine dry weight and then incinerated in a muffle furnace for 2 h at 560 °C and a heat up time of 4 h to determine the ash weight. Ash-free dry mass (AFDM) was then calculated as the difference between the total sample dry weight and the ash weight.

2.5. Sediment characteristics

To quantify sediment properties, we took a sediment sample of the upper 5 cm at each sampling location. All samples were dried at 40 °C for three days. Organic matter content in the sediment was determined for subsamples (10 g) taken from each station by measuring weight loss on ignition for 4 h at 450 °C.

The particle size distribution of four random samples per site (total of 60 samples) were determined on freeze-dried and sieved (1 mm mesh) subsamples by laser diffraction using a Malvern particle size analyzer (Master 2000). The particle size distribution of the remaining points were estimated using multivariate imputation by chained equations (MICE) (Azur et al., 2011) based on measured organic matter content and distance to the mangrove, which together were highly correlative with the median grain size. Estimated imputations were averaged for an accurate imputation of the missing data.

2.6. Statistical analyses

The relationships between MCI and macrofauna community structure (abundance, richness, AFDM, and evenness) were first analysed with linear regression models. The distribution of MCI and total abundance values were $\log(x + 1)$ transformed to fit normality assumptions. The predictive power of these relationships in comparison to using the individual mangrove distance measure was compared using Akaike's information criterion (AIC). To then assess whether the composition of benthic species assemble predictably along multiple environmental gradients at the landscape scale, constrained correspondence analysis (CCA) was performed at the station level (125) (Ter Braak, 1986) (see Appendix S1). Abundance data were Hellinger transformed (Legendre et al., 2011) to reduce the influence of the most abundant species. The environmental predictors tested were MCI, mudflat productivity (NDVI), organic matter content (%OM), sediment particle size distribution (D50, the median diameter of the particles in the sample), distance to drainage and distance to the subtidal. Variables were selected using backward elimination and permutation tests (Legendre et al., 2011), and only significant variables (Table S1) were plotted in the ordination.

As the next step we used multi-level piecewise structural equation modelling (piecewise SEM; Lefcheck (2016)) to study the direct and indirect effects of a suite of environmental variables, including MCI, on benthic community structure across the study area and to further explore the relationships between the environmental indicators that affect the community composition. The same environmental predictors as for the CCA were considered in the SEM models. Prior to SEM modelling, all variables were checked for normality and collinearity between variables (Grewal et al., 2004) (for details see Appendix S2, Fig. S1). Benthic total abundance and %OM were $\log(x + 1)$ transformed and NDVI and distance to drainage were square root transformed. The Piecewise SEM approach can account for hierarchical structure, spatial autocorrelation, and different combinations of non-normal distributions

of the residuals, which is well-suited for our grid sampling design. We included linear generalized least squares *gls* models (nlme; (Pinheiro et al., 2018)) for benthic total abundance, species richness, benthic AFDM, sediment % OM, NDVI, and D50. In addition, we tested for spatial autocorrelation in these models and selected the best covariance structure for each relationship before running the SEMs (Fletcher and Fortin, 2019). We first constructed an initial full model of hypothesized paths between all variables based on prior knowledge on directions of causality in intertidal systems (Appendix S2, Fig. S2). From the initial saturated model, seven reduced models were constructed by eliminating the non-significant paths and by evaluation the goodness-of-fit with the Fisher's C statistic (Grace, 2006; Grace et al., 2010; Lefcheck, 2016). The Shipley's test of directional separation (D-separation) was used to reveal significant missing relationships between variables to improve the model fit (Shipley, 2009). Models were compared using AIC scores (Edgar et al., 2017; Lefcheck et al., 2018; Lefcheck and Duffy, 2015; Rosseel, 2012). The model with the lowest AIC score was selected as the best fit to our data (see Appendix S2) and was validated by plotting residuals against fitted values for each relationship (Fig. S3). Finally, the MCI variable in the model with the lowest AIC score was substituted by the individual distance measure and compared for predictive power using AIC scores.

All statistical analyses were performed using R environment version 3.6.1 (R Core Team, 2019) using packages piecewiseSEM (Lefcheck et al., 2019) for structural equation modelling, nlme (Pinheiro et al., 2018) for analysis of variance, and vegan (Oksanen et al., 2019) for ordinations.

3. Results

3.1. Species abundance, richness, biomass, and MCI

Across all study sites, we found a total of 48 taxa of macrobenthic species, including 20 polychaetes, 11 bivalves, 7 crustaceans, 5 gastropods, and 5 others (Table 1). The number of taxa observed per site varied between 6 and 27 (mean = 19). Variation in abundance (number of individuals) per sampling station was high, ranging from 0 to 3736 individuals m^{-2} (742 ± 60 ; mean \pm SE). The relative importance (% of total abundance) of different taxonomic groups varied between sampling sites but the overall most abundant taxonomic groups were polychaetes (32% of all individuals) followed by bivalves (24%), crustaceans (11%), gastropods (9%), and enteropneusta (8%). The most abundant macrobenthic species in terms of abundance was the giant African bloody cockle *Senilia senilis* (Linnaeus, 1758) (14.6% of all individuals) and *Dosinia isocardia* (Dunker, 1845) (14.6%). These were followed by different polychaetes belonging to the families Orbiniidae (10.6%), Maldanidae (Malmgren, 1867) (8.8%), Lumbrineridae (Schmarda, 1861) (4.7%), and Glyceridae (Grube, 1850) (4.6%), and Enteropneusts (4.5%). This was also reflected in the contribution of each taxon to the observed macroinvertebrate biomass. The overall mean macroinvertebrate biomass was 7.8 ± 1.0 g AFDM m^{-2} . The groups that contributed to this the most were the bivalves (73%), followed by the crustaceans (17%), polychaetes (7%), and lastly gastropods (3%). *Senilia senilis* alone contributed to over half of the total biomass on average (4.2 ± 0.9 g AFDM m^{-2}).

Highest MCI values could be found around the northern island Formosa as well as the southern island Orango (Fig. 2). MCI values were notably higher close to the mangrove system. However, clear variation could be seen due to large differences in the size of mangrove stands within a drainage basin. MCI near-significantly correlated with the total abundance of benthic organisms, although the explained variation was low (Fig. 3a, Linear Regression, $R^2 = 0.02$, $P = 0.095$). In addition, benthic species evenness significantly declined with increasing MCI (Fig. 3b, Linear Regression, $R^2 = 0.04$, $P = 0.044$). However, MCI did not significantly explain variation in benthic total AFDM or species richness ($P = 0.41$ and $P = 0.55$ respectively). AIC comparison of models with

Table 1
Mean ± SE density (individuals m⁻²) of macroinvertebrate taxa sampled on intertidal mudflats of the Bijagós archipelago (n = 125 sampling stations).

Species	Class	Family	Density (individuals m ⁻²)
<i>Senilia senilis</i> (Linnaeus, 1758)	Bivalvia	Arcidae	85.5 ± 16.2
<i>Dosinia isocardia</i> (Dunker, 1845)	Bivalvia	Veneridae	85.1 ± 23.2
Orbiniidae (indet.)	Polychaeta	Orbiniidae	69.5 ± 9.7
Maldanidae (indet.)	Polychaeta	Maldanidae	56.1 ± 8.6
Lucinoma sp.	Bivalvia	Lucinidae	28.1 ± 6.8
Lumbrineridae (indet.)	Polychaeta	Lumbrineridae	27.6 ± 3.7
Glyceridae (indet.)	Polychaeta	Glyceridae	26.7 ± 3.8
Enteropneusta (indet.)	Enteropneusta	-	26.3 ± 6.4
Paraonidae (indet.)	Polychaeta	Paraonidae	24.5 ± 4.5
Enteropneusta (indet.)	Polychaeta	Nereididae	23.2 ± 5.9
Paraonidae (indet.)	Bivalvia	Lucinidae	23.2 ± 5.2
Nereididae (indet.)	-	-	12.5 ± 3.9
Ctena sp.	Bivalvia	Solecurtidae	10.2 ± 2.6
Amphipoda (indet.)	Malacostraca	Ocypodidae	10.2 ± 2.8
Tagelus adansonii (Bosc, 1801)	Malacostraca	Callinassidae	9.8 ± 3.8
Afruca tangeri (Eydoux, 1835)	Polychaeta	Onuphidae	8.9 ± 2.0
Calianassa sp.	Polychaeta	Syllidae	7.1 ± 3.2
Onuphidae (indet.)	Bivalvia	Thraciidae	6.2 ± 3.4
Syllidae (indet.)	Polychaeta	Capitellidae	5.8 ± 2.3
Thraciidae (indet.)	Polychaeta	Terebellidae	4.9 ± 1.7
Capitellidae (indet.)	Bivalvia	Tellinidae	4.0 ± 2.0
Terebellidae (indet.)	Bivalvia	Corbulidae	3.6 ± 1.8
Austromacoma nymphaelis (Lamarck, 1818)	Gastropoda	Retusidae	3.6 ± 1.9
Corbula sulcata (Lamarck, 1801)	Gastropoda	Cyrtulidae	3.1 ± 1.3
Retusa sp.	Gastropoda	Haminoeidae	3.1 ± 1.5
Cirratulidae (indet.)	Gastropoda	Cystiscidae	2.7 ± 1.4
Haminoea sp.	-	-	2.2 ± 1.0
Gibberula sp.	Malacostraca	Anthuridae	1.8 ± 1.1
Nemertea (indet.)	Polychaeta	Magelonidae	1.8 ± 0.9
Cyathura sp.	Polychaeta	Eunicidae	1.3 ± 0.8
Magelonidae (indet.)	Bivalvia	Lucinidae	1.3 ± 0.8
Eunice sp.	Polychaeta	Amphinomidae	0.9 ± 0.6
Lucinidae (indet.)	-	-	0.9 ± 0.6
Amphinomidae (indet.)	Gastropoda	Terebridae	0.9 ± 0.6
Caridea (indet.)	Bivalvia	Donacidae	0.4 ± 0.4
Marphysa sp.	-	-	0.4 ± 0.4
Pisionidae (indet.)	-	-	-
Sipuncula (indet.)	-	-	-
Terebridae (indet.)	-	-	-
Iphigenia laevis (Gmelin, 1791)	-	-	-
Platyhelminthes (indet.)	-	-	-

Taxa are sorted by decreasing average density found in samples

distance to mangrove instead of MCI revealed higher AIC scores (346.3 for total abundance and -211.3 for evenness), and thus less predictive power, compared to models with MCI (343.7 and -215.4 respectively).

3.2. Benthic community assemblages along environmental gradients

The constrained correspondence analysis (CCA) with stepwise backward selection revealed that the variance in species abundances significantly correlated with median grain size, OM content, as well as MCI (Fig. 4). The most important gradient (CCA1) represents %OM and D50 (Fig. 4). The second gradient (CCA2) mostly reflects %OM and MCI (Fig. 4). The most common macrobenthic species tended to group in few clusters in ordination space following different environmental gradients. High abundances of the most common deposit feeder, the fiddler crab *Afruca tangeri* (Eydoux, 1835), coincided with fine and organic sediments and low MCI (Fig. 4). The abundant *S. senilis* was associated with coarser sediment types with low contents of organic matter, as well as relatively higher MCI, whereas bivalves like *Tagelus adansonii* (Bosc, 1801) and *Dosinia isocardia* (Dunker, 1845) were associated with finer

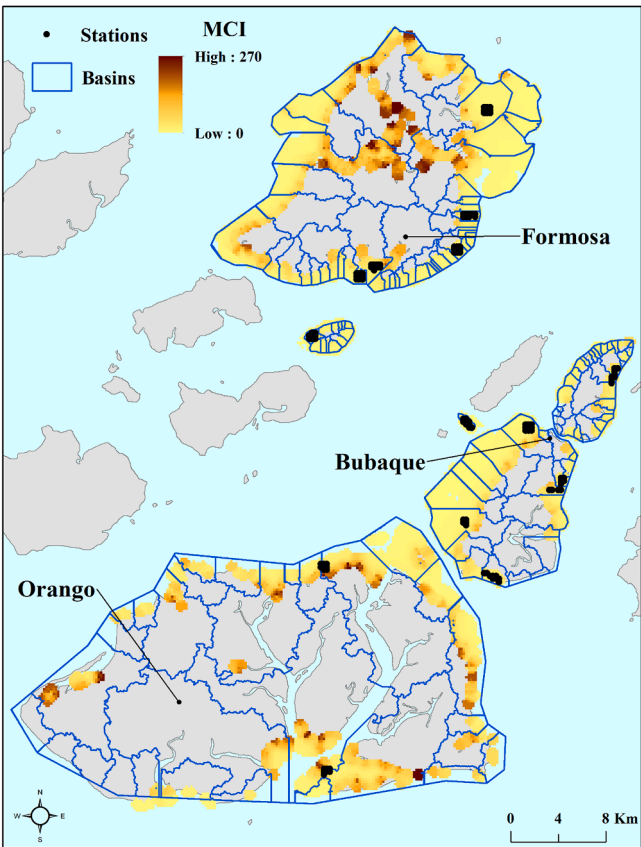


Fig. 2. Interpolated mangrove connectivity index (MCI) map of the mudflats using inverse distance weighing tool in ArcGIS (Spatial Analyst Tools) with sampling stations (black dots) and studied basins (blue outlines) delineated using a digital elevation model (DEM) image (~10 m resolution; SRTM v3, U.S. Geological Survey) and modelled in ArcGIS (Spatial Analyst Tools). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sediment types with higher organic matter content (Fig. 4). Polychaetes of the family Orbiniidae were associated mostly with coarse and organic-poor soils. Finally, the polychaetes of Pisionidae and Magelonidae preferred locations with lower MCI (i.e., further from mangroves and/or smaller mangrove forest, Fig. 4).

3.3. Macroinvertebrate community structure and mangrove connectivity index

The final SEM, which accounted for spatial autocorrelation, explained a moderate degree of variation in benthic total abundance (15%) and species richness (10%), whereas no significant statistical effect on AFDM was revealed (Fig. 5, Table S2). The Fisher's C = 15.65, P = 0.99). The results indicated that MCI had a direct positive effect on macrobenthic species abundance while distance to drainage had a direct positive effect on species richness (Fig. 5, Table S2). Both MCI and distance to drainage had a direct negative effect on OM (Fig. 5, Table S2). In addition, mudflat NDVI had a negative effect on both benthic species abundance and species richness (Fig. 5, Table S2). Furthermore, the model showed a strong positive correlation between benthic abundance and both richness and AFDM (Fig. 5, Table S2). Mean values of D50, NDVI, and OM are summarized in Table 2. Replacing MCI with individual measures of the distance to mangroves and mangrove area resulted in a higher AIC score (85.3 for MCI, 90.2 for distance to mangrove and 98.4 for mangrove area) and thus a worse predictive power.

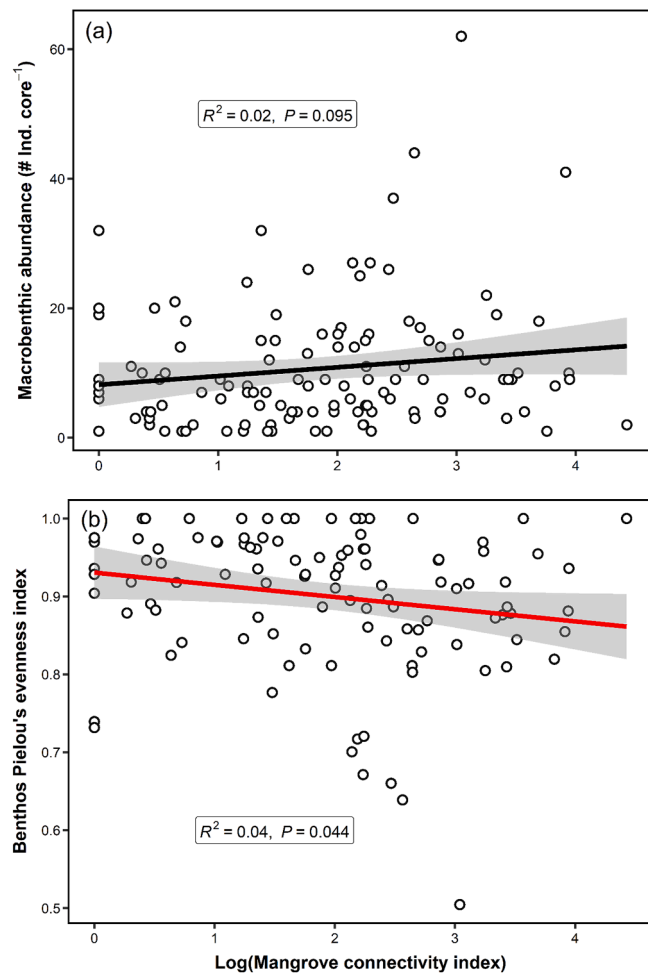


Fig. 3. Relationships between mangrove connectivity index and benthic community structure: (a) benthic total abundance, (b) benthic community evenness. The black line denotes a positive trend while the red line depicts a negative trend. 95% Confidence intervals are depicted in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

By taking landscape-scale connectivity indicators (MCI and mangrove drainage gullies) into account, this study revealed that mangrove-mudflat connectivity shapes the macrofaunal community structure of a tropical intertidal system. MCI, which varied greatly along and within intertidal mudflats, appeared to be an important variable in explaining variation in macrobenthic community composition. The structural equation model suggested strong mechanistic links between MCI and other well-known community structuring environmental factors such as OM and grain size (Compton et al., 2013; Gray and Elliott, 2009; Soto et al., 2017), indicating both a direct and indirect influence of mangrove connectivity on macrobenthic communities. Consideration of this connectivity is essential for many species, including migratory shorebirds and endangered fish (e.g., rays such as the Blackchin guitarfish (*Rhinobatus cemiculus*)) that depend on intertidal benthic productivity for prey. We hope that the use of this novel landscape-scale indicator can aid in assessing cross-habitat connectivity in coastal areas.

We found the intertidal macrobenthic community to be dominated by the bivalves *Senilia senilis* and *Dosinia isocardia* in combination with the polychaete families Orbiniidae and Maldanidae. Previously, Lourenço et al. (2018) found high abundances of Maldanidae but also reported high abundances of Spionidae (Grube, 1850) and Capitellidae

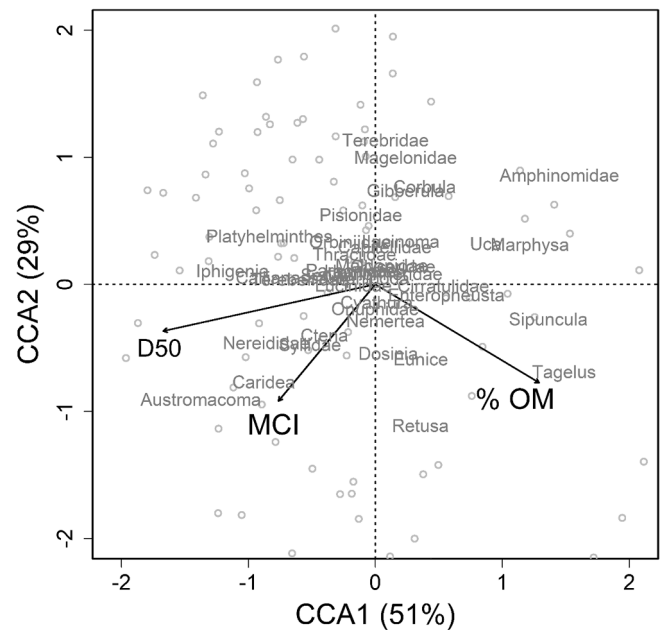


Fig. 4. Constrained correspondence analysis (CCA) of the abundance of 95% most common benthic species found in a largescale survey at Bijagós Archipelago and the environmental variables that have statistically ($P < 0.05$) affected the community assemblages. MCI = mangrove connectivity index, D50 = sediment median grain size, % OM = sediment organic matter content.

(Grube, 1862), which differs from our findings. The most likely explanation for this difference is in the scale of sampling. Whereas Lourenço et al. (2018) sampled three mudflats along a single island, we surveyed 15 different mudflats spread along different islands with different environmental gradients (i.e., salinity, grain size, and MCI). An over-representation of certain conditions within the sampling effort can quickly shift dominating species. In fact, the three mudflats examined by Lourenço et al. (2018) also showed between-site differences in macrobenthic dominance: two sites, Bijante and Bruce, were dominated by polychaetes, while the third one, Escadinhas, was bivalve-dominated (Lourenço et al., 2018). In terms of total macrobenthic biomass (e.g., important for waders), we found an overall average of 7.8 ± 0.98 g AFDM m^{-2} , a little higher than what Lourenço et al. (2018) reported in their study (5.22 ± 0.80 g). More generally, these biomass values are in agreement with previous research showing relatively low macrobenthic stocks in the tropics compared with temperate to high-latitude zones (reviewed by Piersma et al., 1993; Purwoko and Wolff, 2008). Macrobenthos is considered as an essential food source for higher trophic levels, especially migratory birds, but also benthic feeding fish (Mathot et al., 2018; Piersma, 2012). The Bijagós archipelago is considered among the most important sites for shorebirds along the East Atlantic Flyway (EAF) (Campredon and Catry, 2018; Salvig et al., 1994; Zwarts, 1988). Nonetheless, more than half of the observed biomass in the area is not available for shorebirds as it is locked inside the larger individuals of the thick-shelled African bloody cockle (*S. senilis*). Consequently, shorebirds have to rely on only about 3.6 ± 0.5 g AFDM m^{-2} . This could explain why Bijagós is mostly used by shorebirds that specialize on crustaceans (especially fiddler crabs) and polychaete worms such as sacred ibis (*Threskiornis aethiopicus*), whimbrel (*Numenius phaeopus*), grey plover (*Pluvialis squatarola*), redshank (*Tringa tetanus*), bar-tailed godwit (*Limosa lapponica*), curlew sandpiper (*Calidris ferruginea*), sand-erling (*Calidris alba*), and ringed plover (*Charadrius hiaticula*) (Altenburg and van Spanje, 1989; Lourenço et al., 2017; Zwarts, 1985). Fiddler crabs, likely sustained by the associated bacterial production on mangrove litter (Koch and Wolff, 2002; Wolff et al., 2000), are very abundant in the archipelago (Zwarts, 1985) and may be a valuable food source for bird and fish alike while molluscivorous shorebirds are

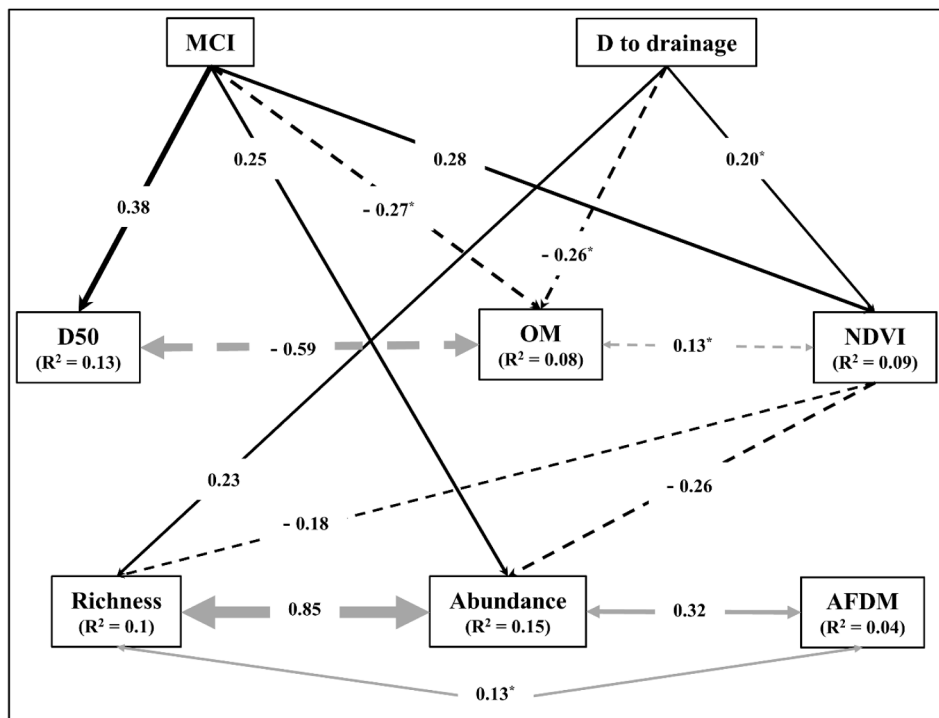


Fig. 5. The final piecewise structural equation model (Fisher's C statistic = 15.65, $P = 0.99$), depicting the effects of environmental variables (Mangrove connectivity index (MCI), distance to drainage, sediment median grain size (D50), and NDVI) on macrobenthic richness, abundance, and total biomass (AFDM). The width of arrows is proportional to the path coefficient, with solid lines represent positive causal links, dashed lines negative links, and grey arrows non-causal correlations. The R^2 value indicates the amount of variance explained by the model. The final model included only significant and almost significant pathways ($0.05 > p < 0.1$; indicated by * pathways). Distance to subtidal was removed as this was not included in any significant pathway.

Table 2

Mean \pm SD and min–max range of the environmental parameters measured.

Environmental parameter	Mean \pm SD	Min	Max
D50 (μm)	139.1 \pm 36.8	24.9	273.2
NDVI	0.079 \pm 0.050	0.0016	0.31
OM (%)	2.17 \pm 1.91	0.57	14.28

relatively low in abundance in the Bijagós (van de Kam et al., 2004). A similar food web structure has been described for the intertidal mudflats in Oman, where the molluscan community is largely unavailable and well-defended against shorebird predation (Bom et al., 2018).

The constrained correspondence analysis of macrobenthic assemblages showed a clear species clustering along four environmental gradients: grain size (D50), OM, and MCI. Although D50 and OM did not significantly affect benthic structure (abundance, richness, and AFDM), they appear to be an important environmental filter determining spatial heterogeneity in community composition: which species dominate where. For example, the two largest and most common bivalve species in the area, *Senilia senilis* and *Tagelus adansonii*, showed opposite habitat preferences. While *S. senilis* occurred in sandy and low OM areas, *T. adansonii* occurred mostly in areas with relatively high organic matter content and muddier sediment. Similarly, the most common species of polychaete (Onuphidae) and crustacean (*Afruca tangeri*) occurred in two opposite sides of D50 and OM gradients, the former in sandy and low OM zones, whereas the latter preferred muddier with high OM content zones. Sediment grain size, organic matter content, and nutrient loads are all known variables to influence distribution of macrobenthic species (Compton et al., 2013; Gray and Elliott, 2009; Soto et al., 2017). Sediment grain size is an especially important variable for tube-building species which require relatively coarse sediments to build their tubes (Compton et al., 2013). Correspondingly, tube-building taxa like Maldanidae, Onuphidae (Kinberg, 1865), and Terebellidae (Johnston, 1846) were all found at higher median grain size levels. The form and availability of organic matter can also strongly structure macrobenthic communities (Lee, 2008). Areas with large organic sources (i.e., mangrove leaves) are dominated by shredders that help to break down

this matter and make it available to a larger extent of taxa. As expected, the main shredder in the Bijagós Archipelago, the fiddler crab *A. tangeri*, was predominantly observed in environments with high organic matter content. High organic matter contents had distinctive communities often composed of Enteropneusts, which are deposit feeders that ingest organic matter-coated sediment particles, as well as few suspension feeding bivalves such as *T. adansonii* and *Dosinia isocardia*. Additionally, high organic matter contents are strongly associated with anoxia due to high oxygen demand of heterotrophic bacteria (Bolam et al., 2004), which is a strong environmental filter for benthic species composition (Nilsson and Rosenberg, 1994; Vaquer-Sunyer and Duarte, 2010). Furthermore, organic matter derived from mangrove litter may contain high concentrations of tannins and polyphenolics that act as feeding deterrents for many benthic species (Gillis et al., 2015; Schories et al., 2003). This, in combination with the low nutrient quality of mangrove leaves, makes mangrove-derived organic matter a highly unsuitable nutritional source for all but a few species (Alongi, 1987; Alongi and Christoffersen, 1992; Lee, 2008).

The structural equation model shows that MCI is both directly and indirectly associated with macrobenthic community structure. Our findings suggest that the effect of MCI on macrobenthic structure is (partly) independent of the organic matter content of the sediment. This result is in agreement with earlier research in the area suggesting little contribution of mangrove litter to the intertidal macrobenthic communities of the Bijagós intertidal mudflats (Catry et al., 2016). Catry et al. (2016) show low dependence of the intertidal macrobenthic communities on mangrove litter through stable isotope analysis. Nonetheless, the structural equation model does show a negative effect of MCI on OM, which in turn explains a large part of the variation in macrobenthic community composition. However, the extent to which mangrove-derived litter has contributed to the carbon pool of the area versus other sources known to deliver important contributions as well, is not certain. Potentially, organic matter in mangrove systems can be delivered in large quantities from other terrestrial (Bouillon et al., 2008; Bouillon and Connolly, 2009a; Ellis et al., 2004) as well as marine sources (Bouillon et al., 2000; Bouillon et al., 2003; Duarte and Cebrián, 1996). Nevertheless, mangroves may still affect the retention and

remineralization of the matter from such allochthonous sources (Sasmith et al., 2020).

In view of the profound effect that sediment and nutrient dynamics have on macrobenthic communities, it is likely that the larger mangrove areas (larger MCI) have significant effect on benthic community structures and stability (Bernardino et al., 2018; Bissoli and Bernardino, 2018). Mangrove forests are generally nutrient-limited despite being highly productive (Alongi et al., 1993). Efficient nutrient retention and recycling capabilities are the foundation that sustains these high productivity rates (Alongi et al., 1993; Reef et al., 2010). This is facilitated by the ecosystem-engineering properties of mangrove forests, such as the aeration of otherwise anaerobic sediments through their root structures (Alongi et al., 1993; Reef et al., 2010). Mangroves have a close plant-microbe association which results in enhanced decomposition and remineralization rates through high microbial activity (Alongi et al., 1993; Rodriguez and Stoner, 1990). The released minerals and nutrients (especially nitrate and phosphate) may be transported to adjacent intertidal mudflats with the outgoing tide and utilized by mudflat associated organisms. This may promote microphytobenthos and sequentially secondary productivity of the mudflat macrobenthic community. The extensive and complex root structures of larger mangrove areas will then more easily retain particulate organic matter and larger suspended material (Gillis et al., 2016; Gillis et al., 2014; Nagelkerken et al., 2008), which in combination with the close plant microbe association will result in enhanced decomposition and remineralization rates and thus export more nutrients. As such, higher MCI zones (larger mangrove areas) are expected to retain more organic matter and suspended material compared to small MCI zones, and as a consequence will contain richer and more abundant macrobenthic communities. Meanwhile, released nutrients from trapped organic matter flow out onto the mudflat with receding tide promoting microphytobenthos and secondary productivity. Organic matter, then, indirectly influences mudflat fauna through its retention and remineralization in the mangrove stands. Conversely, smaller mangroves stands will be less efficient in trapping organic matter, both from terrestrial inputs as well as mangrove litter. This would result in a higher outflow of mangrove-derived organic matter to the mudflat compared to a lower outflow of nutrients that this organic matter would have released through microbial activity if it had been retained in the mangrove forest. Indeed, the structural equation model shows a negative effect of MCI on OM, and a positive effect on intertidal productivity (NDVI). In addition, OM is negatively related to the distance from a drainage channel as mangrove litter is often more concentrated in these gullies (Alongi and Christoffersen, 1992). Conversely, NDVI increases with greater distance to drainage channels. As the system appears to be rich in organic matter compared to other sub- and tropical systems in the region (Dan et al., 2020; El Asri et al., 2019; El-Hacen et al., 2019; Nzoussi-Mbassani et al., 2005; Sakho et al., 2015), the limiting factor for macrobenthic growth might not be organic matter. Instead, it might be a combination of low nutritional quality of mangrove derived organic matter (Alongi, 1987; Alongi and Christoffersen, 1992; Lee, 2008) and insufficient microphytobenthic growth. NDVI is mainly driven by the photosynthetic activity of microphytobenthos (Kromkamp et al., 2006), yet was negatively correlated with macrobenthic richness and abundance in the present study. Worldwide, microphytobenthos is the main contributor to the total primary production of many estuarine systems, especially for unvegetated intertidal mudflats (Christianen et al., 2017; Macintyre et al., 1996; Underwood and Kromkamp, 1999). It is also an important food source for higher trophic levels (Christianen et al., 2017; Macintyre et al., 1996; Ubertaini et al., 2012; van Oevelen et al., 2006), especially macrobenthic surface grazers and deposit feeders (Blanchard et al., 2001; Galván et al., 2008; Weerman et al., 2011). High macrobenthic feeding rates can prevent the buildup of microphytobenthos (e.g., Weerman et al., 2011), resulting in a negative correlation between richness and abundance of macrobenthic communities and NDVI.

Previous studies that studied the effect of mangroves on

macrobenthos often used distance to mangroves and looked mostly at contributions by way of stable isotope analyses (Alongi, 1987; Alongi and Christoffersen, 1992; Ellis et al., 2004; Lee, 2008; Leung, 2015). These studies found conflicting results, with some reporting little to no effect of carbon or nitrogen outwelling through mangrove litter (Bouillon and Connolly, 2009b), and with others reporting a major carbon and/or nitrogen source contributing significantly to the support of the benthic food web (Bouillon et al., 2008). Leaf litter and organic matter flowing from the mangrove forests with receding tide may provide a source of nutrients to the adjacent mudflat (Lee, 1995). The quantity of this effect is dependent on the distance to the mangrove (Alongi et al., 1989; Granek et al., 2009) as well as the effective size of mangrove forest flowing out on the mudflat. By incorporating both into one spatial indicator we have shown a clear effect of mangrove connectivity on macrobenthic communities. This highlights the importance of incorporating landscape morphology in the study of cross-habitat landscape-scale interactions.

5. Conclusion

The question of if and how mangroves affect adjacent intertidal systems represents a long-standing debate in estuarine ecology. We show a clear influence of both mangrove extent and mangrove configuration on the community structure and composition of endobenthic organisms, by considering the landscape configuration (basins), the total area of the mangrove forest in a basin, and the distance to the mangrove forest. In addition, landscape-scale mangrove connectivity is revealed to affect other habitat characteristics, such as organic matter and sediment median grain size, well-known for structuring macrobenthic communities. This landscape-scale perspective on cross-habitat connectivity between mangroves and intertidal mudflats paves the way for integrative conservation planning of these biodiverse habitats that provide essential foraging grounds for species such as migratory shorebirds and endangered elasmobranchs.

6. Data accessibility

Data supporting the findings of this study are available from the authors and will be made archived and publicly available in the University of Groningen Research Data Repository: <https://doi.org/10.34894/TJASME>.

Authors contributions

HO, EME, LG, KM and TP conceived the ideas and designed methodology; KM and EME conducted the field work with help from HO; KM, EME, and ML identified species and processed the samples with support from TP; KM, EME and HO analyzed the data; KM and EME led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.108030>.

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