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Habitat complexity drives food web structure along a dynamic mangrove coast

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ABSTRACT

Structurally complex habitats, such as mangrove forests, allow for rich assemblages of species that benefit from the provided space, volume and substrate. Changes in habitat complexity can affect species abundance, diversity and resilience. In this study, we explored the effects of habitat complexity on food web networks in four developmental stages of mangrove forests with differing structural complexities: climax > degrading > colonizing > bare, by analyzing food web structure, stable isotopes and habitat complexity. We found that food webs became gradually more biodiverse (species richness: +119 %), complex (link density: +39 %), and robust (connectance: -35 %) in climax versus bare stages with increasing complexity of the mangrove forest (i.e., number of trees, leaf cover, and pneumatophore densities). This study shows that habitat complexity drives food web network structure in dynamic mangrove forests. We recommend restoration practitioners to use this food web network approach to quantify habitat restoration successes complementary to traditional biodiversity metrics.

1. Introduction

Habitat complexity is a key-driver of biodiversity in a range of different ecosystems such as upland streams, temperate lakes, and deciduous forests (Dean and Connell, 1987; Downes et al., 1998; Kostylev et al., 2005; Lawton, 1983; MacArthur and MacArthur, 1961). For example, branching trees support fish biodiversity in temperate lakes (Newbrey et al., 2005), and the height profile of foliage density can predict bird species diversity in deciduous forests (MacArthur and MacArthur, 1961). In many of these ecosystems, structural habitat complexity is provided by foundation species (Dayton, 1972), also

referred to as ecosystem engineers (Jones et al., 1994). These species dominate in abundance and/or biomass and modify the physical environment by increasing interstitial space, providing settlement substrate and attenuating physical forces (Bruno et al., 2003; Callaway, 2018). These habitat modifications enhance the diversity of microhabitats and niches, provide shelter against predation and competition and consequently allow species to co-exist (Aguilera et al., 2014). However, the magnitude of species diversity facilitation highly relates to the shape, quality and quantity of habitat structure (e.g., surface area, volume, interstitial space, space size frequency, refuge space, fractal dimensions; Warfe et al., 2008). Although habitat complexity is often

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interchangeably used with habitat heterogeneity, differences can be explained. While habitat heterogeneity has been described as the diversity of structural elements (diversity of microhabitats), habitat complexity implies the existence of different structural elements that constitute a habitat which also includes the complexity within elements (e.g., interstitial space and fractal dimensions) (Kovalenko et al., 2012; Tokeshi and Arakaki, 2012). The concept - increased biodiversity by habitat complexity - is also well documented for marine and coastal ecosystems such as seagrass meadows (Henderson et al., 2017), biogenic reefs (e.g., coral reefs and shellfish reefs (Messmer et al., 2011)), and mangroves (Leung, 2015).

Mangroves form the foundation of a complex, biodiverse and heterogeneous ecosystem and are found world-wide, fringing tropical and subtropical coasts (Alongi, 2002; Kruitwagen et al., 2010; Medina Contreras et al., 2018). Mangrove trees add unique structural complexity in bare soft-sediment ecosystems through their root structures and consequently enhance biodiversity. They create predator free space between their roots and provide substrate for species like algae, barnacles, bivalve mollusks, sponges, corals and ascidians to colonize (MacKenzie and Cormier, 2012; Verweij et al., 2006). Red mangrove species cover habitat complexity through high interstitial space (Vorsatz et al., 2021), which creates microhabitats and protection against predation for small fish and shrimps. In contrast, black mangrove habitats hold high complexity because of a high surface-area-to-volume ratios-index of the pneumatophores and not because of high interstitial space (Vorsatz et al., 2021), which facilitates colonization of epiphytical biota (Verweij et al., 2006). This facilitation of other species through habitat complexity is described as non-trophic interactions in food web topology (Kéfi et al., 2012).

The facilitation of species, and often consequently biodiversity, by habitat complexity impacts food web topology (Borst et al., 2018). For example, species that are directly facilitated by mangrove habitat structure (i.e., non-trophic interaction) attract other species such as herbivores and predators (i.e., trophic interaction). In this way, foundation species such as mangroves and corals, facilitate species of diverse trophic levels as a result of habitat modification (Christianen et al., 2016; Kéfi et al., 2012; van der Zee et al., 2016). However, food webs in these ecosystems are highly sensitive to changes in habitat complexity, because with degradation of the habitat structure, biodiversity and food web complexity will also diminish (Borst et al., 2018; Medina Contreras et al., 2018). Little is known about the resilience of food web structure, as determined by its characteristics, with degradation of habitat structure provided by foundation species.

Food web metrics (e.g., species richness, link density or connectance) can be used to identify the effect of changes in habitat complexity on the resilience of the food web structure. These metrics can be used as indicators for food web size, complexity, robustness, and efficiency (Borst et al., 2018; Christianen et al., 2016; Dunne et al., 2002a). These food web metrics can be a useful tool to trace the role of foundation species in ecosystem functioning. Generally, foundation species affect food web topology by enhancing species richness. This higher species richness is often associated with an increased number of links per species (increased food web complexity) (Borst et al., 2018). These larger, more complex food webs are more robust and have a lower connectance (realized fraction of all possible links) because a high species richness leads to a lower probability of links between all species (Dunne et al., 2004; Dunne et al., 2002a; Dunne et al., 2002b). In addition, short path lengths are an indication of efficient energy transfer as it quantifies the average number of links necessary to transfer information along the shortest path length between nodes (Watts and Strogatz, 1998). As such, these food web metrics provide insight into complex trophic interactions and can be used to trace changes in food web resilience and functioning that may be overlooked when solely focusing on biodiversity metrics (Christianen et al., 2016).

Coastal foundation species are rapidly decreasing as a result of human activities leading to a loss of habitat complexity and associated

species (Anthony and Gratiot, 2012; Murray et al., 2022). However, little is known about how loss of habitat complexity affects complex trophic interactions (i.e., food web structure). We therefore aimed to explore food web network structures in mangrove forests with varying developmental stages, associated with differing levels of habitat complexity. For this, we analyzed food web network structures, stable isotopes and habitat complexity in four stages of mangrove forests along the coast of Suriname: climax, degrading, colonizing, and bare. The dynamics of Suriname's coast, part of the Guianas in South America, provide a unique opportunity to study the role of habitat complexity on food web structure, as different developmental stages (and thus stages of habitat complexity) naturally occur relatively close together.

2. Methods

2.1. Study site

The entire coast of Suriname consists of mangrove forests of different developmental stages dominated by black mangroves, *Avicennia germinans* (Toorman et al., 2018). These mangrove developmental stages are produced by a unique geomorphological cycle of sediment dynamics leading to high tidal wetland erosion and colonization (Anthony et al., 2014; de Vries et al., 2022; Murray et al., 2022). Sediment from the Amazon River is transported along the coast of French Guyana, Suriname, Guyana and ultimately ends up in de Orinoco delta in Venezuela (Anthony et al., 2014). These large deposits of sediment create mud banks that propagate along the shore (up to 2 km/year), due to the constant resuspension of mud on one side and the deposition of mud on the opposite side (Anthony et al., 2010). The coastal area that lies behind the bank is sheltered from wave stress and fine sediment can settle in the slower moving water, elevating the soil. This creates opportunities for mangroves to establish (Anthony and Gratiot, 2012; Toorman et al., 2018). On the side of the trailing edge, where the mud bank erodes, mangroves will degrade, as trees are no longer protected from the force of incoming waves. The leading edge, creates new opportunities for mangrove forests to establish, leading to a colonizing forest (de Vries et al., 2022). The study site was situated in the Coronie district of Suriname close to the town Totness (5° 53' NB, 56° 20' WL; Fig. 1a and b). In this district, we sampled four different developmental stage of black mangrove forests: climax, degrading, colonizing, bare ($n = 3$ per developmental stage). The vegetated developmental stages were located fringing between land and sea with a similar emergence time estimated by observations (Fig. 1b). Only the bare stages were positioned more seaward than the other stages because of i) the absence of unvegetated areas in the fringe of the other developmental stages and ii) little long-distance impact of the mangrove forests. Each replicate was divided into 9 plots to measure habitat characteristics.

2.2. Habitat characteristics

To investigate habitat complexity and heterogeneity, we measured environmental variables in 9 adjacent (0 m distance between the plots) 10 × 10 m plots per replicate ($n = 9$ per replicate). In each plot, we estimated microhabitats by assessing coverage (%) of shells, mud, water, pools, living and dead black mangrove trees, pneumatophores and canopy mangrove leaves. Black mangrove trees are structures that increase habitat complexity because of an enlarged surface-area-to-volume ratios-index of the pneumatophores (Verweij et al., 2006; Vorsatz et al., 2021). In this study, mangrove trees (dead and alive) with associated pneumatophore served as proxies for habitat complexity. The microhabitats such as shell-, mud-, water-cover and number of pools were characteristics of habitat heterogeneity. In addition, sediment samples were collected in every plot with a syringe (Ø 2.5 cm, ~5 cm deep), dried at ~60 °C for 48 h, and subsequently incinerated for 4 h at 550 °C in ovens to measure organic matter content by loss of ignition (LOI%) (Heiri et al., 2001).

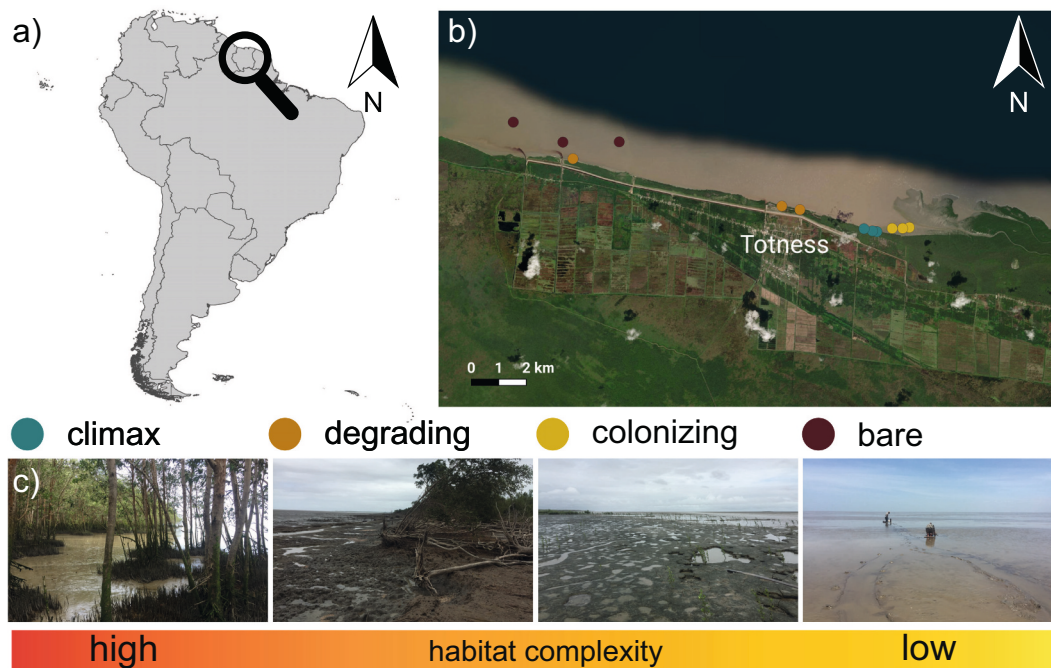


Fig. 1. Overview of sampling area along a) the Suriname's dynamic mangrove-mudflat tidal coast, b) sample locations of mangrove forests in different stages: climax, degrading, colonizing and bare, and c) pictures of sampled mangrove forests ordered from high to low complexity: climax, degrading, colonizing and bare.

2.3. Habitat classification

Along this dynamic mangrove coast, we sampled four developmental stages of mangroves classified by habitat complexity: climax > degrading > colonizing > bare ($n = 3$) between February and April 2018. We classified these stages in order of habitat complexity and heterogeneity: 1) climax mangroves (~30 years old) were the most complex and the selected plots included patches of black mangrove trees scattered across mud, fully grown and established mangrove forest with dense aggregations of pneumatophores and muddy creeks and zones of fluid mud, the term most commonly used to evoke the rheology of mud banks, (Anthony et al., 2010) (Fig. 1c), 2) degrading mangrove forests (~30 years old, degrading since ~20 years and completely degraded to bare in 2022) were characterized by dead mangrove trees and living mangrove trees with pneumatophores and shell ridges, fluid mud, dense layers of clay structured by bioturbation of *Uca* sp. fiddler crab species, clay with remnants of dead pneumatophores (Fig. 1c), 3) colonizing mangrove forest (0–5 years old) were characterized by a successional gradient from sea to land with early, mid and late succession of mangroves (based on tree density, height, diameter at breast height and canopy cover) on muddy tidal flats combined with pools and young pneumatophores (Fig. 1c), 4) the bare mudflat was characterized by the lowest structural complexity and consisted of only fluid mud (Fig. 1c; Anthony et al., 2010). All plots covered the seaward edge of the mangrove forest.

2.4. Sampling procedures for food web structure

To measure differences in food web structure, we sampled multiple trophic levels of the food web (i.e., carbon sources, macrozoobenthos, epibenthos and fish). Carbon sources, macrozoobenthos and epibenthos were sampled in 9 adjacent plots of 10×10 m in a square configuration within each replicate. In each plot ($n = 9$ per replicate), carbon sources (sediment organic matter, particulate organic matter, diatoms, leaves, macroalgae, detritus) were collected through a variety of methods. Sediment organic matter was sampled by sampling the upper 5 cm of the sediment surface layer with a $\varnothing 2.5$ cm corer (50 ml syringe). Particulate organic matter (POM) from the water column was collected in a 5 l jerry

can, left to precipitate and filtered using pre-combusted Whatman GF/F glass fiber filters. Diatoms were sampled covering an sediment surface area of 100 cm^2 (top 1 cm layer). These diatom (mixed with sediment) samples were plated out onto petri dishes and covered with a $250 \mu\text{m}$ mesh filter and filtered seawater. After a 12 h-incubation period in the sun, during which the diatoms were able to migrate through the filter, they were removed with a razor blade, collected and dried at $\sim 60^\circ \text{C}$ (Eaton and Moss, 1966). Mangrove leaves were collected at breast height. Mangrove tree trunks were covered by macroalgae (*Rhizoclonium riparium*), which were collected manually in an area of 100 cm^2 . Detritus layers were sampled by handpicking a sediment surface area of 100 cm^2 . Macrozoobenthos were sampled using a PVC core of $\varnothing 10.5$ cm to a depth of 20 cm (a total of 3 cores * 9 plots = 27 cores per replica) covering all microhabitats: close to a tree, covering the pneumatophores and on the muddy area (Compton et al., 2013). The samples were sieved over a 1 mm round mesh and all organisms were collected and identified up to order level and when possible, species level. Epibenthic organisms on mud and tree trunks were collected manually per plot ($n = 9$ per replicate). Fish species were sampled per replicate ($n = 3$ replicate study areas) using a fixed gill net, mesh 1.27 cm, with a height of 1 m and set up over a length of 10 m. The net was left for one high tide and collected afterwards. All organisms caught were identified to highest taxonomic level possible, mostly family-level. Worms (identified to family-level) were grouped based on their feeding type (predators, deposit-feeding, suspension-feeding and omnivores) (Hartmann-Schröder, 1996).

2.5. Stable isotope analyses

After species collection, we measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signals in the laboratory (>3 replicates per taxon group). Whenever possible, we used muscle tissue of fish, crustaceans and bivalves, and soft tissue of other invertebrates and macroalgae. For species too small (~ 2 cm) to separate calcified body parts from muscle and/or soft tissue, we used the entire organism. If the tissue contained calcified body parts, we decalcified the tissue with 3 M HCl (drop-by-drop technique, (Jacob et al., 2005). All tissue was rinsed with demineralized water, dried for 48 h at 60°C , ground with Mixer Mill (MM400) until homogenized. The subsamples were weighed in pre-burned tin cups and analyzed for $\delta^{13}\text{C}$ and

$\delta^{15}\text{N}$ isotope composition with Isotope Ratio Mass Spectrometry (Delta V Advantage IRMS, Thermo Fischer Scientific, Waltham, Massachusetts, USA). Isotope values were calibrated to a Vienna standard and Caffeine laboratory standard ($n = 14$ for both primary standards), and corrected for blank contribution. The target weights of the subsamples differed per tissue (in mg): diatoms 5, detritus 4, POM 1.5, zooplankton 1.5, sediment 50–60, macroalgae 0.5, plant tissue 0.8, animal tissue 0.3–0.4.

2.6. Food web construction

After sample collection and measuring isotopic values, we analyzed food web structure based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values and Stable Isotope Mixing Models, r-package: 'SIAR' (Parnell et al., 2010) per replicate ($n = 3$). First, we used a self-constructed maximized interaction matrix (who eats whom) with all potential trophic links between consumers and their food resources ('prey'). These trophic relations were determined based on scientific literature, databases and expert knowledge (World Register of Marine Species (Boxshall et al., 2014), FishBase (Froese and Pauly, n.d.)). Second, we constructed potential species interaction matrices per replicate (4 stages * 3 replicates = 12 interaction matrices) based on the observed species. Rare species (≤ 1 individual in total) were excluded from the matrix to exclude ecological irrelevant species interactions. Third, we used Stable Isotope Mixing Models, 'SIAR' to update the potential species interaction matrices by dietary proportions of each food resource per consumer from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values. In this process, food resources were combined based on their taxonomic relatedness (e.g., species of the same family) and overlapping isotopic value to reduce the total number of food resources per consumer to a maximum of ten. After combining and reducing resources, we removed resources (combinations) that contributed $< 5\%$ to the consumer's diet resulting in species interaction matrices per replicate (Appendix 1). In this procedure, missing food sources (e.g., mobile fish species feeding on food sources far away from the mangrove area) form a potential bias and results should therefore be interpreted with caution. If insufficient isotopic values per species were available, isotopic values were grouped per stage (climax, degrading, colonizing, bare). Finally, we use the interaction matrix obtained to calculate basic food web properties according to Borst et al. (2018) (Appendix 2).

2.7. Statistical analyses

We performed all statistical analyses in R (R Core Team, 2020, version 4.2.0 and 3.6.3): a language for statistical computing and graphics, using open-source R studio (version 1.2.1335). We validated all model assumptions by plotting 1) residuals versus fitted values to verify homogeneity, 2) QQ-plots of the residuals to test for normality and 3) residuals versus each explanatory variable to check for independence. In addition, Shapiro-Wilk's test ($p > 0.05$) and Bartlett's test ($p > 0.05$) were used to test for normality and homogeneity of variance, respectively.

We used linear models to compare individual food web metrics between the different stages.

The metrics 'vulnerability' and 'total number of links' were log transformed to meet model assumptions. We used generalized linear models (GLM) with negative binomial distribution to test for differences in 'basal' species, because the data did not meet linear model assumptions after transformation and overdispersion (tested with Levene's test). The differences among all four mangroves stages were tested with Tukey's post-hoc comparison (r-package: 'emmeans' (Lenth, 2019), except for 'link density'). For this metric, the overarching model indicated significant differences between climax and bare stages, but the Tukey post-hoc tests did not detect differences. Therefore, we ran the more liberal Fisher's Least Significant Difference (LSD; i.e., no correction of the significance level) to highlight weaker differences.

To test for the relation between habitat complexity variables and food web metrics, we used Principal Component Analysis (PCA), using

the different replicate food webs as samples and food web metrics as variables. The scores of the first Principal Component axis (PC1) were used to measure differences in food web structure and analyzed with a GLM with gaussian distribution and tested with Tukey's post-hoc comparison. Consequently, we analyzed multiple linear regressions of environmental variables onto these PCA ordination axes (envfit: r-package 'vegan' (Oksanen et al., 2019) with 999 permutations). Significances were tested by permutation test.

3. Results

3.1. Taxon observations

Only eight out of the thirty-nine taxon groups were commonly found in all stages: two carbon sources (POM and sediment), two worm groups distinguished by feeding type (predator and deposit-feeding worms), two crustaceans (juvenile Caridea and Tanaidacea) and one catfish species (*Cathorops spixii*). The presence of mangrove trees, in climax, degrading and colonizing, added two new carbon sources to the system (mangrove leaves and diatom mats), one species of swimming crab *Callinectes bocourti* and the four-eyed fish *Anableps microlepis*. Insects such as Gerridae, Lepidoptera, Coleoptera were exclusively found in the climax stage. In addition, taxon groups that relied on settlement substrate such as Actiniaria and the algae *Rhizoclonium riparium* were only found in the climax stage. Two fish species, *Cynoscion acoupa* and *Symphurus plagusia* were only caught in the bare stage and not in the other mangrove stages. So, most taxon groups related to the terrestrial food web (insects) or groups that need settlement substrate were found in the climax stage (see Appendix 3 for the complete species list).

3.2. Food web networks

We found that the food web networks supported higher species richness and more complexity in the climax stage of mangrove forests, followed by degrading $>$ colonizing $>$ bare development stages (Figs. 2 & 3, Appendix 4). These food web networks were characterized by +119, +74 and +56 % species richness in climax, degrading and colonizing mangrove forests compared to bare (Fig. 3a, ANOVA, $F_{3,8} = 14.94$, $p = 0.001$). In addition, link density was +39 % higher in the climax stage compared to bare (Fig. 3b, LSD = $p = 0.043$). Furthermore, the connectance, which is explained as the saturation of all possible links which is general lower in more complex networks, was -35% in the climax mangrove forests, followed by -31% in degrading and -27% in colonizing mangroves, compared to bare (Fig. 3c, ANOVA, $F_{3,8} = 39.47$, $p < 0.001$). Moreover, path length, the average amount of links necessary to transfer energy between a pair of nodes, was +19, +9 and +11 % higher in climax, degrading and colonizing, respectively, compared to bare (Fig. 3d, ANOVA, $F_{3,8} = 7.11$, $p = 0.010$). Effects of mangrove stages on various other food web metrics can be found in Appendix 4.

3.3. Linking food web networks to habitat complexity

We combined the food web metrics of the developmental stages within one principal component analysis (PCA) to analyze the overall response of food web networks on changes in habitat complexity. We found that most of the variation (97.61 %) between the developmental stages of mangrove forests could be condensed onto a single PCA axis (PC1). PC1 differentiated all developmental stages, except for degrading and colonizing (Tukey, $p = 0.80$, Fig. 4, see Appendix 5 for habitat complexity data). Since PC1 explained 97.61 % of the variation, we tested for a correlation between the environmental variables and food web metrics based on PC1 (Fig. 4). We found that this PC1 axis significantly correlated with environmental variables that indicate habitat complexity such as the number of trees ($r^2 = 0.55$, $p = 0.04$), leaf cover ($r^2 = 0.65$, $p = 0.01$), tree cover ($r^2 = 0.60$, $p = 0.03$), pneumatophore densities ($r^2 = 0.56$, $p = 0.02$) and mud cover (Fig. 4; $r^2 = 0.56$, $p =$

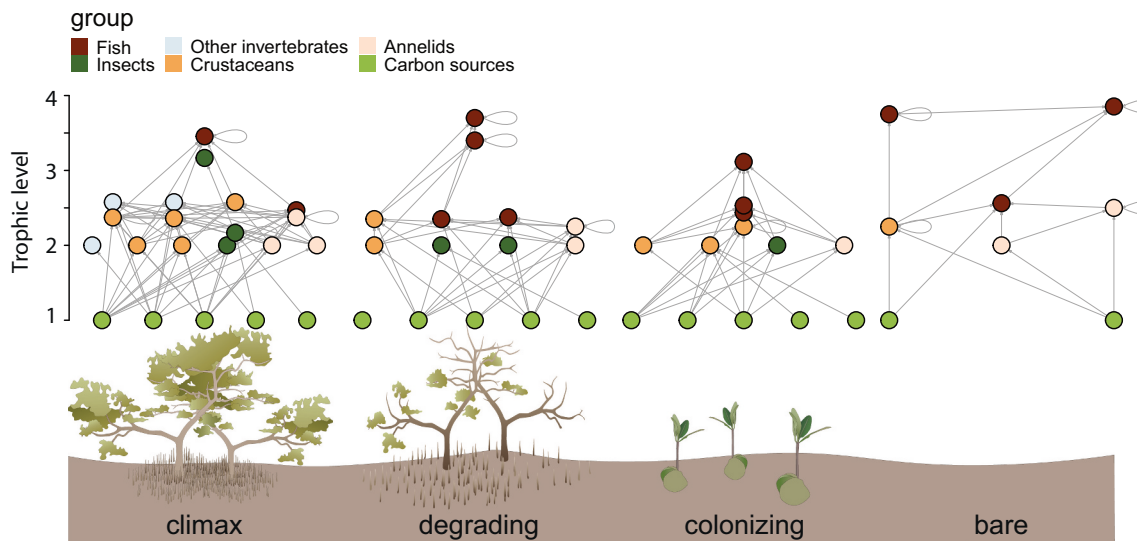


Fig. 2. Stable isotope-based food web network reconstruction shows a decrease of food web complexity along a gradient of decreasing mangrove habitat complexity from climax, degrading, colonizing to a bare stage. Nodes show species per functional group (fish, insects, other invertebrates, crustaceans, annelids and algae, depicted by different colors) and arrows are feeding links between species. Looped arrows show cannibalism within the species. These four food webs show the average amount of species per trophic level based on three sampled replicates per developmental stage.

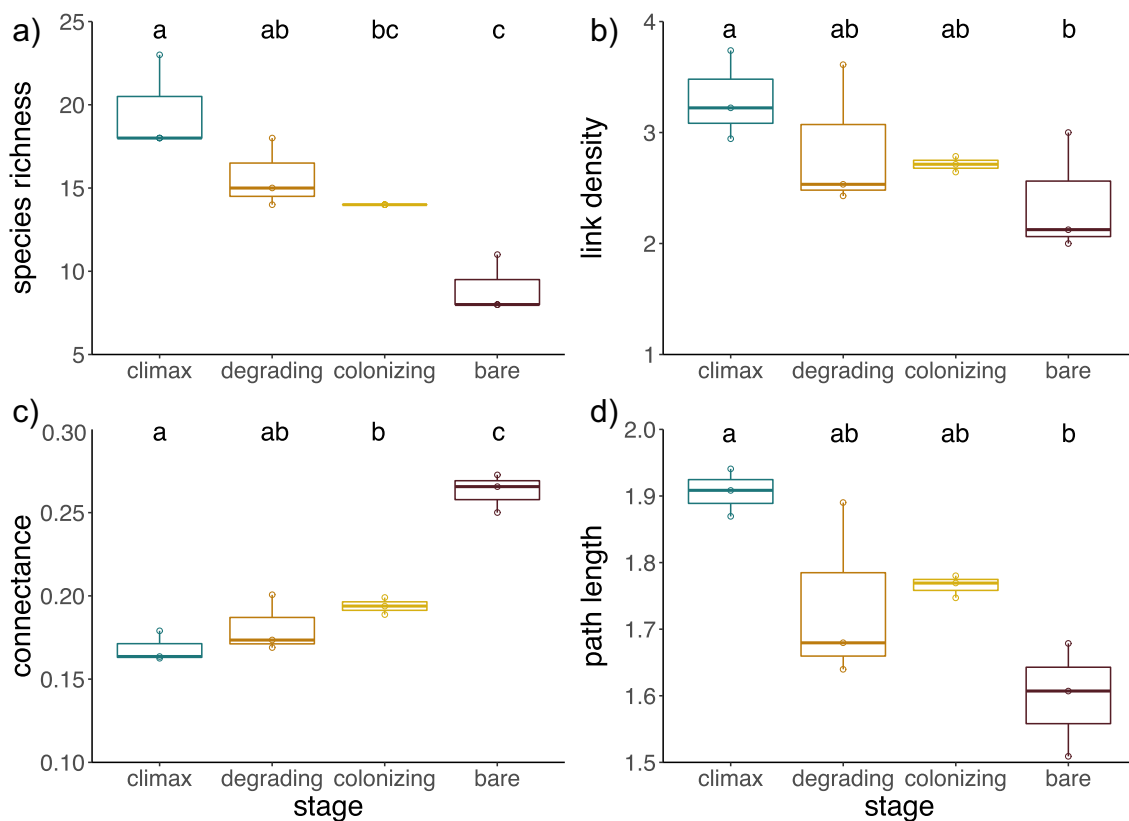


Fig. 3. Comparison of four food web metrics between climax - degrading - colonizing - bare mangrove forests food web size (species richness), complexity (link density), robustness (connectance) and efficiency of energy transfer (path length). Data are shown as raw data points (open circles) and boxplots with median, first and third percentile, minimum (10th percentile) and maximum (90th percentile) ($n = 3$) with linear models and Tukey post-hoc comparison (significant differences shown in letters), except for link density we used Fisher's Least Significant Difference (LSD; i.e., no correction of the significance level).

0.002). Characteristics of habitat heterogeneity such as shell-, water-cover and number of pools cover did not correlate significantly with the ordination axis PC1 of the food web metrics.

3.4. Carbon and nitrogen isotope values

We could not distinguish between the four mangrove stages based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values since their 95 % confidence intervals strongly overlapped (Fig. 5). However, the isotopic niche of bare was smaller

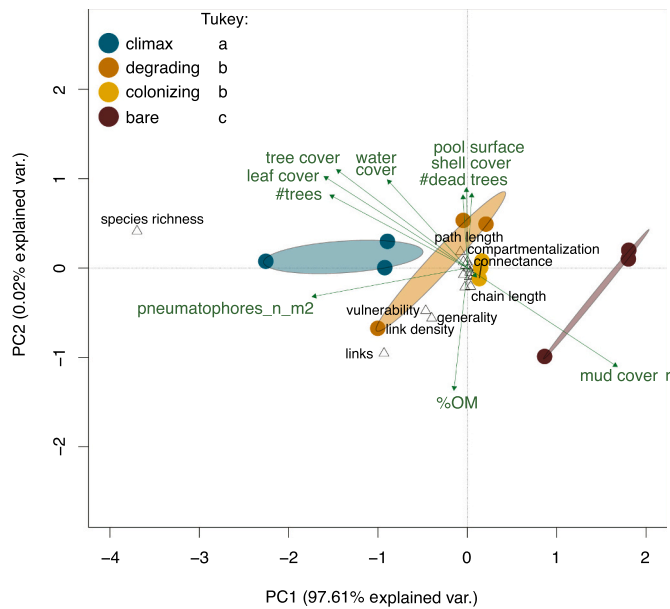


Fig. 4. Significant separation of the different stages of mangrove forests by food web metrics. Ellipses show ellipse area per habitat stage, triangles display food web metrics, and arrows in green indicate linear regression between environmental variable and ordination axes (r^2 projected in length of the arrow). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

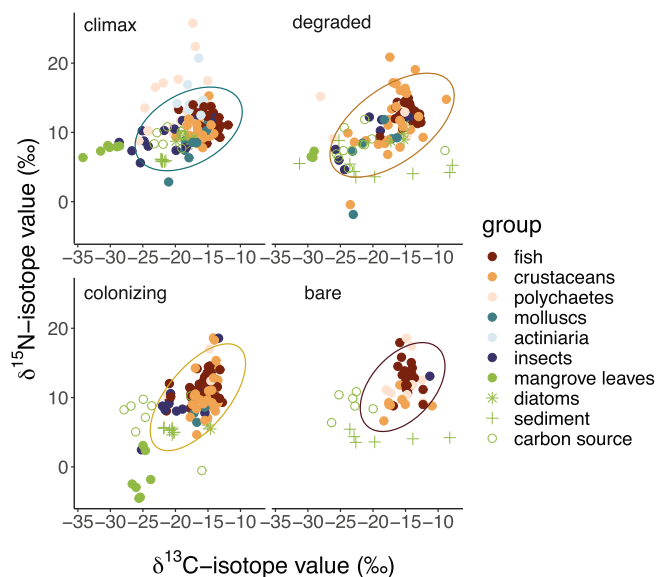


Fig. 5. Isotope values of all species (divided in functional group) indicate no separation between the isotopic niches of the different stages (ellipse with 95 % confidence interval). The position of all carbon sources (green) suggests that diatoms, sediment organic matter and other carbon sources (e.g., particulate organic matter) are a more dominant carbon source for the higher trophic levels than mangrove leaves. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

than that of the other stages with standard deviations of 3.62, 3.80, 4.18 and 4.74 $\delta^{13}\text{C}$ values for bare<colonizing<climax<degrading. The $\delta^{15}\text{N}$ values varied with standard deviations of 3.27, 3.34, 3.78, 4.16 for climax<bare<degrading<colonizing. In contrast, the food web metric trophic level did not detect any differences in trophic levels among the stages (Appendix 4). Furthermore, the $\delta^{13}\text{C}$ values (Fig. 5, light green) indicate that the most important carbon sources for most higher trophic

levels are diatoms, sediment and other carbon sources (POM, algae and detritus), and some species rely on mangrove leaves based on their position in the isotope biplot (Fig. 5).

4. Discussion

Foundation species promote biodiversity by providing habitat complexity (Jones et al., 1994), but little is known about how changes in habitat complexity can affect food web resilience. We here demonstrated that habitat complexity drives food web network structure along a gradient of successional stages of a dynamic mangrove coast. The study showed that mangrove food webs became more biodiverse (species richness), more complex (species richness and link density), more robust (connectance) with increasing complexity of the mangrove trees as foundation species (i.e., number of trees, leaf cover, pneumatophore densities). Food web complexity and robustness decreased from climax>degrading>colonizing> bare, but food web metrics of degrading mangrove forests were similar to the climax and colonizing stages (similar to the findings of Morillo-Velarde et al., 2018). An increase in the diversity of micro-habitats (i.e., habitat heterogeneity) did not affect food web structure. Thus, this study showed that food web network metrics are suitable to detect changes in trophic complexity in relation to habitat complexity. This can provide a useful tool for conservation and management of foundation species (e.g., mangroves, seagrasses and coral reefs) that are currently rapidly degrading and consequently leading to the loss of associated biodiversity and trophic complexity (Cabanillas-Terán et al., 2019).

This study showed that food web structure was linked to habitat complexity (black mangrove trees, leaves and pneumatophores). These trees (and associated structural complexity) were mostly present in the climax stage, followed by degrading and colonizing mangroves and accordingly facilitated a more complex food web. These complex food webs were mostly driven by a higher species richness. No differences in food web metrics were found between climax versus degraded and degraded versus colonizing. This could be explained by dead and young trees also providing habitat complexity, contributing to enlarging the surface-area-to-volume ratios-index of the pneumatophores, and settlement substrate and microhabitats (Loke and Todd, 2016; St. Pierre and Kovalenko, 2014; Vorsatz et al., 2021). In addition, the structure provided by dead and young trees will still mitigate waves and protect the remaining mangroves and associated fauna (Anthony and Gratiot, 2012; Toorman et al., 2018). When mangrove trees are present in the ecosystem, degrading or not, their structural complexity makes it suitable for a higher diversity of species to inhabit, allowing for higher biodiversity and food web complexity. This structural complexity is completely absent in bare stages of mangrove forests (Kovalenko et al., 2012; Loke and Todd, 2016).

In order to understand how biodiversity affects the functioning of ecosystems, an assessment of trophic complexity (within and across trophic levels) is needed (Duffy, 2002). Previous mangrove food web studies observed separation between cleared and natural mangrove forests based on the isotopic niche space of the macrozoobenthos, which are the low trophic levels (trophic levels between 2 and 3 in this study) (Fraga Bernardino et al., 2018; Sabeel et al., 2015). In contrast, this study could not detect such differences between bare and the vegetated stages exclusively based on traditional stable isotope biplots. Although the isotopic niche width in our study was smallest in the bare stage for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, indicating a loss of trophic diversity (Fraga Bernardino et al., 2018), it remains impossible here to assess trophic complexity solely using this traditional stable isotope approach, which would lead to erroneous conclusions. Furthermore, the added value of food web analyses to the more traditional biodiversity indices has been proven for other foundation species and artificial reefs in a comparison with reef structure versus bare (Borst et al., 2018; Christianen et al., 2016; Nauta et al., 2023; van der Zee et al., 2016). Where previous studies only compared habitat complex ecosystems versus nearby bare

control, we here emphasized the importance of assessing food web network interactions (i.e., food web metrics) and ecosystem functioning along a gradient of coastal foundation species with varying degrees of habitat complexity.

While our study includes complex food web networks, it simplified trophic and non-trophic interactions of mangrove forests, because we studied mangrove habitats in isolation. It is known, however, that mangroves are connected to adjacent marine ecosystems because they provide nursery grounds for shrimp and smaller fish (Nagelkerken et al., 2000). In addition, bird species that use mangrove habitats are an important linkage between terrestrial and marine ecosystems (Nagelkerken et al., 2008). Focusing on these mobile species in food web structure would increase the size, complexity and robustness of mangrove food webs. We were unable to include birds, shrimp and small fish species because of the mesh size used in our study. Therefore, it is possible that we did not completely cover the nursery function of mangrove habitats. Nevertheless, the presence of mangrove trees enhanced food web complexity by facilitating taxon groups related to the terrestrial food web such as insects.

Our study highlights the importance of mangrove habitat complexity for food web structure along a dynamic mangrove coast such as on the geomorphologically active coastline of the Guianas. This northern coast of South America supports extensive mangrove forests that are under high anthropogenic pressures (Anthony and Gratiot, 2012). The loss of structural complexity due to habitat degradation is currently an urgent global problem as other foundation species such as corals and seagrasses are also highly threatened (Reaka-Kudla, 1997; Valiela et al., 2001; Waycott et al., 2009), and strongly contributes to ongoing biodiversity losses. The food web metrics used in this study may be an important tool to assess trophic complexity, robustness, resilience and efficiency of food webs. Therefore, we recommend restoration practitioners to use this food web network approach to quantify habitat restoration successes in addition to traditional biodiversity methods. Our study provides vital information on trophic structure in ecosystems shaped by habitat complexity and can be used by nature practitioners to prevent further degradation of ecosystem functioning.

CRediT authorship contribution statement

Janne Nauta: Writing – original draft, Conceptualization, Methodology, Formal analysis, Investigation, Visualization. **Carlijn Lammers:** Writing – review & editing, Conceptualization, Methodology, Formal analysis, Investigation. **Robin Lexmond:** Writing – review & editing, Conceptualization, Methodology, Formal analysis, Investigation. **Marjolijn J.A. Christianen:** Writing – review & editing, Conceptualization. **Annieke Borst:** Writing – review & editing, Conceptualization. **Leon P. M. Lamers:** Writing – review & editing, Conceptualization. **Hanneke van Lavieren:** Writing – review & editing, Resources. **Sieuwnath Naipal:** Resources. **Laura L. Govers:** Writing – review & editing, Conceptualization, Investigation, Supervision.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

Data will be made available on request.

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Appendices. Supplementary data

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