



Are urban mangroves emerging hotspots of non-indigenous species? A study on the dynamics of macrobenthic fouling communities in fringing red mangrove prop roots

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Received: 14 March 2022 / Accepted: 3 October 2022 / Published online: 29 December 2022
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Abstract Urbanization represents a radical transformation of natural habitats that alters all the biotic and abiotic properties governing ecosystems. Urban expansion often results in oversimplified communities, where most specialists decline or disappear and a few generalist or exotic species become dominant. The consequences of urban expansion in mangrove forests are understudied, although these systems have been altered by humans for centuries and the growth of human population in tropical coasts is expected to be faster than in higher latitudes. To assess the importance of indigenous and non-indigenous species in driving temporal and spatial changes in community

structure of red-mangrove prop-root macrobenthic communities, we studied heavily altered mangrove forests from two bays from the Caribbean coast of Colombia in 2005 and 2021. In all places/periods, the community richness was low, a few taxa were dominant (11 taxa, out of 40, comprised ~90% of the total abundance) and 35% of those taxa were non-indigenous species whose presence is related with known stressors in urbanized systems. Hence, call for efforts to assess whether urban mangrove forests are emerging as hotspots for non-indigenous biota. Community structure did not change within or between bays, there was a clear, significant turnover of core species between 2005 and 2021, with non-indigenous species playing a prominent role in this variability. This was puzzling—ecological theory asserts that the abundance of a species is related to their permanence: core species are relatively stable through time, while rare species appear or disappear—but this may not apply for stressed communities influenced by non-indigenous biota.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10530-022-02944-x>.

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Resumen La expansión urbana es una transformación radical de un hábitat natural; prácticamente altera todas las propiedades bióticas y abióticas que definen la estructura y función de un ecosistema. El conjunto de estas alteraciones usualmente se traduce en comunidades simplificadas, donde unas pocas especies generalistas o exóticas proliferan exitosamente a expensas de muchas especialistas, que declinan o desaparecen. El estudio de las consecuencias de la ur-

banización en bosques de manglar es precario a pesar del milenar proceso de transformación humana en esos ecosistemas y de las tendencias de crecimiento de la población humana, más acelerado que en otros sistemas. Para evaluar la participación relativa de especies nativas y no nativas en la definición de cambios espaciales y temporales en las comunidades macrobentónicas asociadas a las raíces de mangle estudiamos bosques fuertemente alterados en dos bahías del Caribe colombiano en 2005 y 2021. En general, la comunidad se caracterizó por una baja riqueza, la alta dominancia de unas pocas especies y por una alta proporción de especies exóticas, exótico-invasoras y crípticas (35% del total de las especies) típicamente indicadoras de perturbaciones en zonas costeras urbanizadas. En ese contexto, sugerimos que es urgente evaluar si los bosques de manglar en zonas urbanizadas se estarían convirtiendo en puntos focales de especies no nativas. Aunque la estructura de esta comunidad no presentó variaciones espaciales, si se observa una significativa rotación de las especies más abundantes entre 2005 y 2002, muchas de ellas no nativas. Esto fue inesperado; la teoría ecológica indica que la abundancia de especies en una comunidad está relacionada con su permanencia: las especies núcleo tienden a mantenerse mientras las especies raras van y vienen –pero esto podría no aplicar para el caso de una comunidad influenciada por especies exóticas en un ambiente perturbado.

Keywords Urban ecology · Urban expansion · Invasive alien species · Biotic homogenization · *Rhizophora mangle*

Introduction

Habitat loss and invasive species have long been heralded as major causes of biodiversity loss in conservation biology (e.g., Pimm and Raven 2000; Sala et al. 2000; Molnar et al. 2008). Among the vast array of human transformations of natural habitats, cities represent the heart of our human enterprise and perhaps the most radical source of ecological disturbances: urbanization alters all of the abiotic and biotic properties that govern ecosystems (Alberti 2008). Recent evidence suggest that the multifarious human pressures clustered in cities is creating oversimplified communities where specialized species decline and

generalist tolerant species prevail (Faeth et al. 2011; Santana et al. 2020). This, and the transport of people and goods—a major vector for species translocation—interact to foster cities as emerging hotspots for the arrival, establishment and expansion of non-indigenous species (Santana et al. 2020; González-Lagos et al. 2021).

In urban ecology, much of the existing methods, principles, frameworks and knowledge come from developed countries in the so-called Global North (Shackleton et al. 2021), where studies have been traditionally focused in terrestrial socio-ecological systems. Fixing this imbalance is critical for two main reasons. First, major biodiversity hotspots in pan-tropical areas from developing countries are forecasted to experience the fastest rates of urbanization by 2030, with consequences for biodiversity loss (Seto et al. 2012). Second, coastal or riverine ports near coasts account for a considerable number of the major cities of the Global South: 32 of the 77 largest cities in the world are located on coastal areas of the Global South (Myers 2021). Third, population density is much higher in coastal areas (Faulkner 2004) and compositional reorganizations related to human pressures are faster and more variable in marine than in terrestrial ecosystems (Blowes et al. 2019).

Mangrove forests provide a multitude of ecosystem services and significant aesthetic, educational, cultural, recreational and spiritual benefits for humans—more than any other tropical coastal ecosystem (Millennium Ecosystem Assessment 2005). Yet for the same reason, mangroves are highly threatened systems: mangrove forests are being lost at a fast rate in recent decades, driven primarily by aquaculture development, deforestation, freshwater diversion and urban expansion (Duke et al. 2007; Chakraborty 2019; Branoff 2017). Therefore, mangrove forests in urban settings are ideal systems to assess how indigenous and non-indigenous biota are interacting through time. Particularly, mangrove-root fouling communities are species-poor and accessible model systems to study the dynamics of community structure related to environmental changes at different spatial scales, ranging from individual roots to whole mangrove islands (e.g. Farnsworth and Ellison 1996; Hay et al. 2004).

In this study we assessed the relative importance of indigenous and non-indigenous species in driving temporal and spatial changes in community structure

of mangrove-root associated biota in the Urabá Gulf, southern Caribbean coast of Colombia. Mangrove forests in this area have been heavily altered by land reclamation for agricultural expansion in El Uno bay and urban expansion of the Turbo city port (Blanco-Libreros and Estrada-Urrea 2015). Owing to the intensification and heterogeneity of the anthropogenic impacts in these areas during the last 15 years, we hypothesized that the structure of epibenthic macrofauna associated with the roots of *R. mangle* will differ between periods (2005–2021) and bays (El Uno—Turbo), with invasive species being important drivers of those differences. We built on previous historical work performed by Garcia and Palacio (2008) in the study area and predicted that the number of alien and alien-invasive species will be consistently higher through time in Turbo bay. The bays are closely located and influenced by human activities as to be considered urban. However, urban areas are mainly surrounding Turbo bay and the associated impacts (including land use changes, pollution, deforestation and harvesting) are concentrated around Turbo bay. Hence a more diverse array of introduction vectors for non-indigenous species might be expected in this region.

Materials and methods

Study area

The study was performed in the southeastern coast of the Urabá Gulf (Fig. 1). Located near the Colombia-Panama border, the gulf is a north-facing embayment that represents the southernmost region of the Caribbean Sea. The gulf is home to the most developed mangrove forests in the Colombian Caribbean, which are probably the most productive in the Americas (Riascos and Blanco-Libreros 2019). Fringe forest is the dominant physiographic type of mangroves in the region, which mostly comprise monospecific stands of *Rhizophora mangle*, while *R. mangle*, *Laguncularia racemosa* and *Avicennia germinans* occur in basin mangroves (Urrego et al. 2014). The gulf is part of the Chocó-Darien Global Ecoregion, a globally recognized biodiversity hotspot prioritized for conservation due to the high levels of biodiversity and endemism (Fagua and Ramsey 2019). Nowadays the region comprises a complex mosaic of land covers,

ethnic groups and legal and illegal economic activities and is considered a deforestation hotspot in the Colombian Caribbean coast. The estimated cover of 4908 ha in 2009 represent a reduction of 29.8% of the previous estimation in 2003 (Blanco-Libreros et al. 2012). The eastern coast of the gulf, which includes the study area, have been dramatically shrunk due to expanding agricultural and pasture lands and urban areas, particularly near the Turbo Municipality.

Mangroves in Turbo Bay are exposed to mesohaline to polyhaline waters (0.5–10‰) and have been characterized as “peri-urban” because they are structurally and functionally affected by their proximity to the Turbo port city (Ortiz and Blanco 2012; Blanco-Libreros and Estrada-Urrea 2015). During the last 15 years, the number of homes in the Turbo District increased by 18.12%, most of them concentrated in Turbo city that currently is home to 48,787 people (DANE 2018). Moreover, the ongoing development of major port facilities will further boost urban expansion and the associated pressures on mangrove forests in coming years. In turn, mangroves at El Uno Bay grow in oligohaline to mesohaline conditions (10–35‰) and their areal coverage have been reduced for expanding lands for agriculture (mainly comprising plantain crops) and cattle ranching, illustrating a typical example of a rural-agricultural transition (Ortiz and Blanco 2012; Blanco-Libreros and Estrada-Urrea 2015). The bay is a coastal lagoon whose formation is linked to the evolution of the Turbo River delta since the transfer of its mouth to this region in the mid-twentieth century (Blanco-Libreros et al. 2013; Alcántara-Carrió et al. 2019).

Field work

This work builds on previous work on the structure of macrobenthic communities associated with prop roots of *R. mangle* performed by García and Correa (2006), which was later published by Garcia and Palacio (2008); hence their methods were replicated to warrant comparability. They sampled six prop roots in the eastern, western and northern zones of each bay between September and December 2005. They found that diversity of macrobenthic communities did not significantly change through time or zones. Moreover 12 species comprised 90% of the total abundance and these species were found in all sampling points through the study period. Hence, we performed a

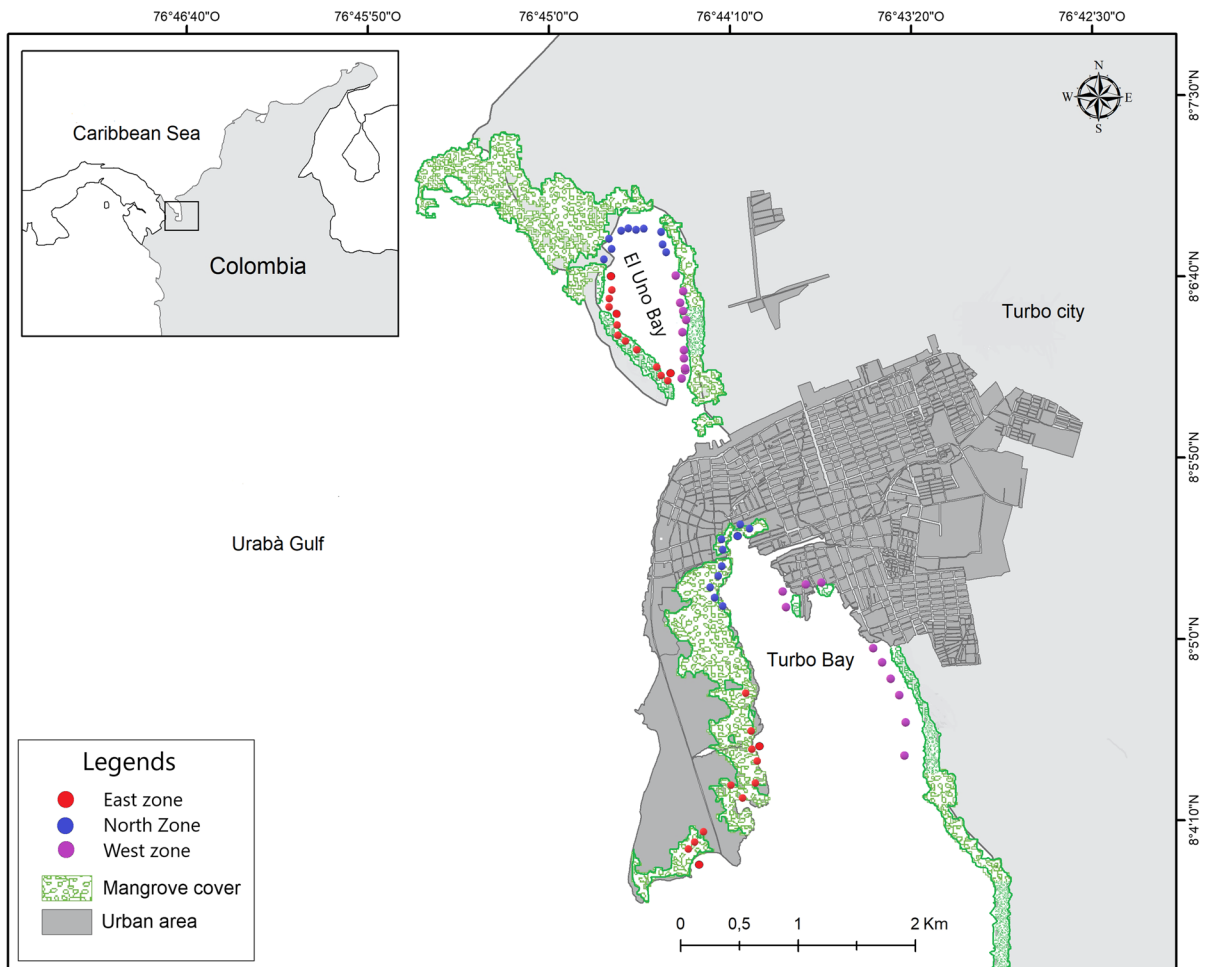


Fig. 1 Map of the Urabá gulf and the study zones and specific sampling points. Shape of mangrove forest cover provided by Valencia-Palacios and Blanco-Libreros (2021)

single sampling in June 2021, taking ten *R. mangle* prop roots in the same zones (east, north, west) in each bay (Fig. 1), thus 60 prop roots were sampled in this study. Following the criteria established by Garcia and Palacio (2008), roots were haphazardly selected by (i) belonging to mature trees (≥ 10 cm in diameter at breast height), (ii) having a significant portion submerged into the water and (iii) harboring easily seen sessile organisms. The roots were cut at the high-tide mark and immediately stored in labeled plastic bags. Additionally, the following factors related to anthropogenic disturbances were measured: trampling (presence/absence), logging (number of trees cut), litter (number of litter items per plot) and urban structures (number of urban structures, e.g.

houses, roads, piers, etc. per plot). All these counts were performed by a single dedicated observer in a 10 m diameter plot surrounding each sampling point.

Samples were immediately taken to the Marine Ecology laboratory (Universidad de Antioquia, Marine Science Campus in Turbo), refrigerated at 3–5 °C and processed within the next 12 h. Roots were weighed and placed on plastic trays, cut into small parts and dissected. Observed macroinvertebrates were removed and stored in alcohol. Oysters in particular were carefully reviewed under a stereoscope to record attached organisms. Plastic bags and root pieces were washed and sieved through a 250-micron mesh sieve. The retained material was stored in labeled plastic jars with 95% ethanol for

further analysis. The samples were sorted under a stereomicroscope and the resulting organisms identified to the minimum possible taxonomic level. Following the criteria and definitions used by the Convention on Biological Diversity on invasive alien species (<https://www.cbd.int/invasive/terms.shtml>), all taxa identified to the species level were categorized as:

- (i) Indigenous species: a species living within its natural range (past or present) including the area which it can reach and occupy using its natural dispersal systems.
- (ii) Alien species: a species introduced outside its natural past or present distribution.
- (iii) Invasive-alien species: an alien species whose introduction and/or spread threatens biological diversity

Finally, a species that was not demonstrably indigenous or introduced based on current knowledge was classified as a cryptic species.

Data analysis

The abundance of each taxon was calculated as the number of individuals per root. These data were organized in biological (species abundances per root) or environmental (anthropogenic disturbances in each sampling point) matrices. Abundance data were square-root transformed to balance the contribution of abundant and rare species in further analysis, thus accounting for the fact that some fast-moving animals had a chance to escape during samplings, as opposite to sessile animals. Data on environmental factors (see Table S3) were first normalized (subtracting the mean and dividing by the standard deviation for each variable) to account for the different scales among variables. The Bray–Curtis dissimilarity index was later estimated from abundance data for each pair of samples in the matrix and Non-metric multidimensional scaling (nMDS; Clarke and Gorley 2006) was used to build ordination plots of the structure of macrobenthic communities in mangrove roots for each zone and bay. In turn, Euclidean distances were calculated between sampling points to describe abiotic differences among zones in each bay, using bi-dimensional plots of Principal Component Analyses.

To test for changes in the structure of epibenthic macrofauna associated with roots between zone (east, north, west) and bays (El Uno, Turbo) we used a two-way ANOSIM test. This approach performs a permutation test of the null hypothesis of no differences among a priori defined groups of samples, based on the ranks of the sample dissimilarity matrix (Sommerfeld et al. 2021).

To assess our hypothesis on changes in the structure of epibenthic macrofauna associated with roots, samples from each zone were pooled and treated as replicates. A crossed two-way ANOSIM test was used to test for differences between periods (2005–2021) and bays (El Uno–Turbo). For samples found to be significantly different, the Similarity Percentage Analysis (SIMPER) implemented in PRIMER software was used to evaluate which species contributed most to the differences between periods and bays. This biota was further characterized according to origin (indigenous and non-indigenous) to discuss our findings and differences in the abundance and richness of indigenous and non-indigenous species between years were tested using the Mann–Whitney U-tests. A significance level of $\alpha=0.05$ was chosen for all the tests performed. All multivariate analyses were performed using PRIMER v.6 software (Clarke and Gorley 2006).

Results

Our study reports 40 taxa of invertebrates associated with prop roots of *Rhizophora mangle* (Table S1) in El Uno and Turbo. We found 225 specimens in 2021 (El Uno=75; Turbo=150), which was nearly half of the 394 specimens found in 2005 (El Uno=201; Turbo=193). Richness (number of taxa) also decreased in 2021 (El Uno=20; Turbo=18) with respect to 2005 (El Uno=28; Turbo=29). A few taxa were highly dominant in all places/times: 11 species comprised more than 90% of the abundance. In fact, two species (*Brachidontes dominguiensis* and *Tanais dulongii*) made up nearly half of the total abundance (Fig. 2). In contrast, there were 28 taxa that contributed less than 1% of the total abundance. Of the 40 taxa found in our study, 26 (65%) were identified to the species level and categorized as indigenous (17), alien (3), alien-invasive (4) and cryptogenic (2) (Table S2). Moreover, El

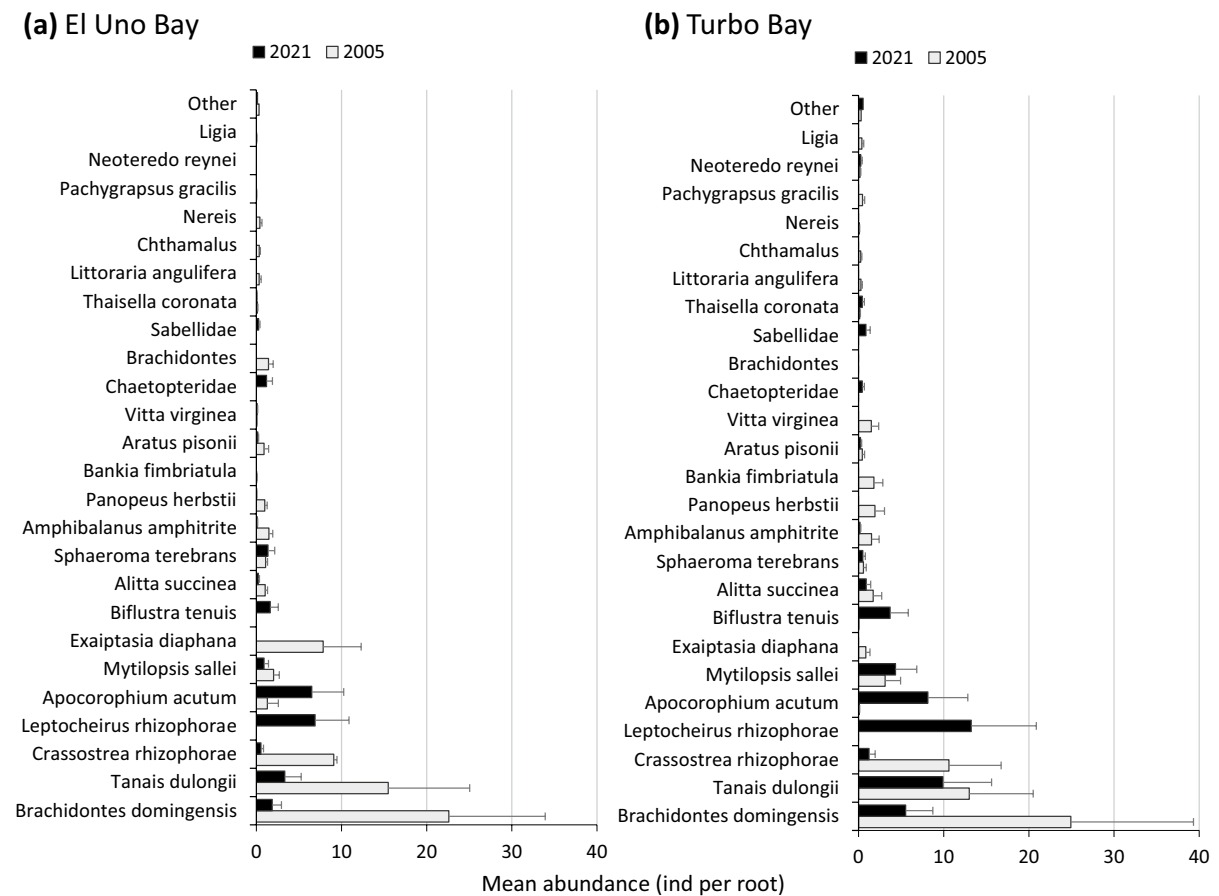


Fig. 2 Spatial and temporal comparisons of the mean abundance of taxa associated to roots of *Rhizophora* mangle. Taxa displaying lower abundances (<0.01 ind per root) are shown as “other”

Uno and Turbo had almost the same number of non-indigenous species in 2005 and 2021, which was not in line with our prediction that Turbo would harbor more non-indigenous biota.

The abundance and species composition of macrobenthic assemblages associated with roots of *R. mangle* did not show significant differences between zones, neither in El Uno bay (ANOSIM; $R=0.012$; $p=0.34$) nor in El Uno Bay (ANOSIM; $R=0.116$; $p=0.06$), which was also reflected in a lack of spatial segregation of communities in nMDS ordination plots (Fig. 3). This result was surprising, because PCA ordinations of anthropogenic pressures (Fig. 4) showed a clear spatial structure within each bay, with the density of litter and urban structures being key structuring factors (see also the environmental data matrix—Table S3).

In contrast, our results revealed significant differences in the structure of benthic assemblages between periods (ANOSIM; $R=0.853$; $p=0.02$) but not between bays (ANOSIM; $R=0.000$; $p=0.45$). These results are also illustrated in the nMDS ordination plot (Fig. 5), which show that samples from 2005 clustered to the left of the plot while samples from 2021 clustered to the right. In turn, between-bays distances were less consistent. Results of SIMPER analysis showed that 12 species explained more than 90% of dissimilarity in abundance and species composition between samples taken in 2005 and 2021 (Table 1). Of these species, the third and fifth species contributing most to the dissimilarity were cryptogenic (*Tanais dulongii*) and alien-invasive species (*Apocorophium acutum*). Besides, the fourth, sixth and eighth species, contributing most

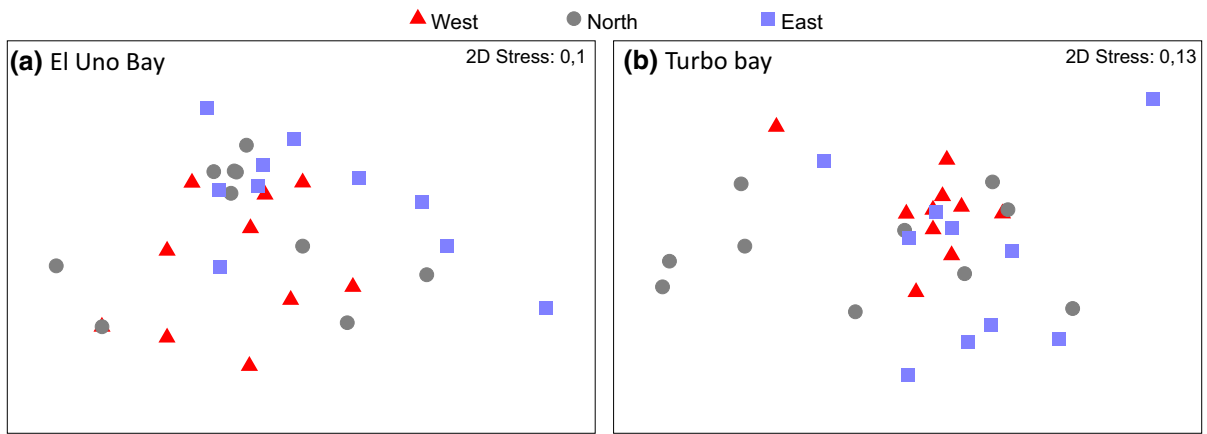


Fig. 3 Ordination by non-metric Multidimensional Scaling of composition and abundance of macrobenthic communities associated with prop roots of *Rhizophora mangle* in El Uno

Bay (a) and Turbo bay (b), Colombian Caribbean coast. Ordination maps were calculated from Bray–Curtis dissimilarity measures

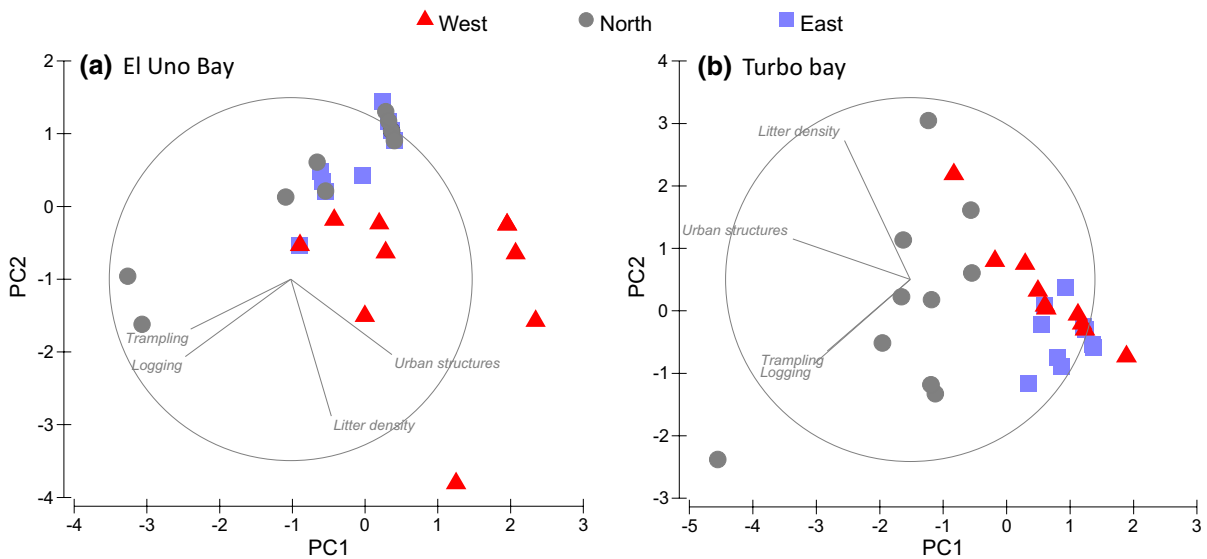


Fig. 4 Bi-dimensional plots of Principal Components (PC1 and PC2) after the Principal Component Analyses of anthropogenic factors registered in sampling spots in western, northern and eastern zones at El Uno Bay (a) and Turbo Bay (b)

in 2021 and the superimposed vectors (grey lines) of anthropogenic factors. PC1 and PC2 together explained 70.8% of the observed variance in El Uno and 76.5% in Turbo

to the dissimilarity are indigenous species to the study area that however have been reported as introduced or alien-invasive species in other regions of the globe (Table 1, Table S2). Temporal changes in abundance and species composition are clearly seen in Fig. 6. Of special importance was the fact that two of the most abundant species observed in 2005 (*Tanais dulongii* and *Brachidontes dominguensis*)

were replaced as dominant species in 2021 by two previously unregistered species (*Apocorophium acutum* and *Leptocheirus rhizophorae*). Finally, the abundance and richness of indigenous species was significantly higher in 2005 than in 2021 (Fig. 7), but that of non-indigenous species did not significantly change over time.

Fig. 5 Ordination by non-metrical Multidimensional Scaling (nMDS) of composition and abundance of macrobenthic communities associated with prop roots of *Rhizophora mangle* in El Uno Bay and Turbo bay, Colombian Caribbean coast. nMDS was built on Bray–Curtis dissimilarity measures. Each point represent data on species composition and abundance pooled by zone

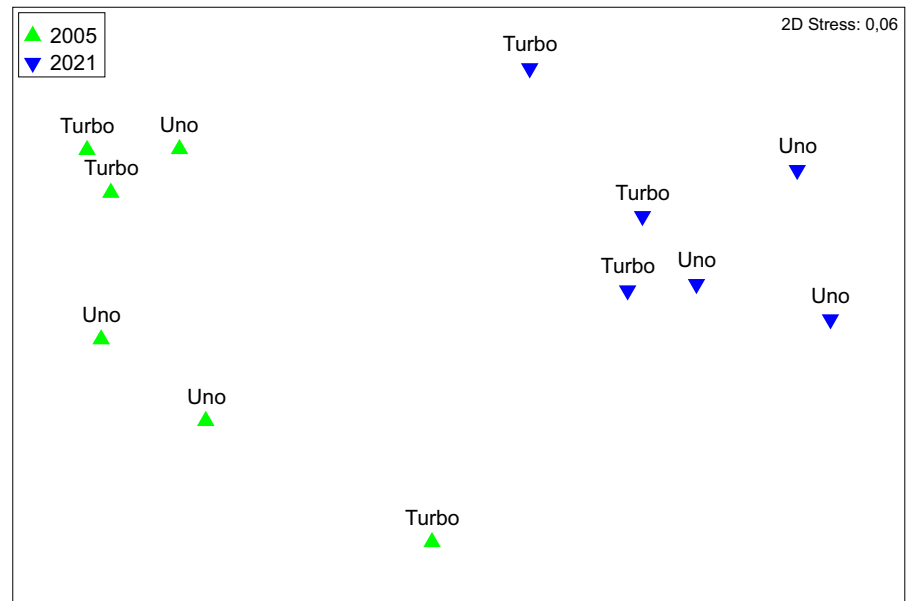


Table 1 Results of similarity percentage analysis showing the main benthic species contributing to the dissimilarity in community structure between 2005 and 2021

Main discriminating species	Classification	Abundance average		Dissimilarity average	Contribution (%)	Cumulative (%)
		2005	2021			
<i>Branchidontes domingensis</i>	Indigenous	23.76	3.70	18.6	24.96	24.96
<i>Leptocheirus rhizophorae</i>	Indigenous	0.00	10.07	9.96	13.36	38.31
<i>Tanais dulongii</i>	Cryptogenic	14.24	6.62	9.46	12.69	51.00
<i>Crassostrea rhizophorae</i>	*Indigenous	9.85	0.88	8.46	11.34	62.35
<i>Apocorophium acutum</i>	Alien-invasive	0.69	7.32	6.87	9.21	71.56
<i>Exaiptasia diaphana</i>	*Indigenous	4.35	0.00	4.72	6.34	77.90
<i>Biflustra tenuis</i>	Indigenous	0.01	2.67	2.53	3.40	81.30
<i>Mytilopsis sallei</i>	*Indigenous	2.58	2.62	2.17	2.91	84.20
<i>Panopeus herbstii</i>	Indigenous	1.46	0.02	1.38	1.85	86.05
<i>Vitta virginea</i>	Indigenous	0.78	0.05	1.31	1.76	87.81
<i>Amphibalanus amphitrite</i>	Alien	1.50	0.13	1.26	1.69	89.50
<i>Alitta succinea</i>	Alien-invasive	1.38	0.57	1.09	1.47	90.97

Species signaled by an asterisk are indigenous species to the study area that are currently reported as introduced (*Crassostrea rhizophorae*, *Exaiptasia diaphana*) or alien-invasive species (*Mytilopsis sallei*) beyond their native geographic range (see Table S2)

Discussion

In a classical work on ecosystem ecology, Odum (1985) suggested that in a system exposed to external disturbances or stressors, species diversity would decrease while dominance would increase. Direct, comparisons of species diversity of fouling communities associated with roots between

different places are difficult to make because of differences in sampling effort, spatial coverage, taxonomic expertise, abiotic conditions, large scale trends in biodiversity, among others. Despite this, the richness of taxa in our work was much lower than that typically found in non-urban spots of the Caribbean Sea, including Belize (Ellison and Farnsworth 1992 = 46 taxa; Farnsworth and Ellison

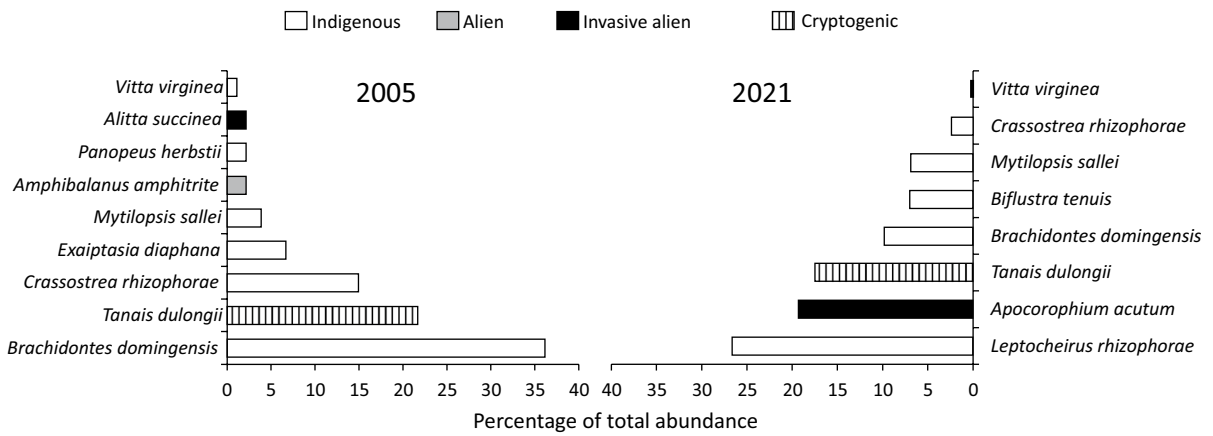


Fig. 6 Abundance of Indigenous, alien, alien-invasive and cryptic macrobenthic species mainly contributing to the dissimilarity in community structure between 2005 and 2021 (after SIMPER analysis) in Turbo and El Uno. Note that,

together these species comprised about 90% of the total abundance in each study period. References for the categorization of this, and the full set of species found in this study, are given in Table S2

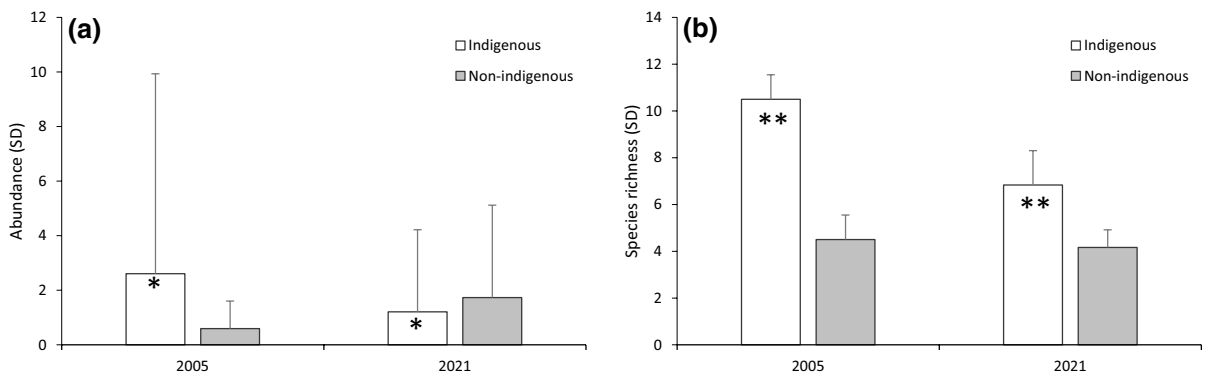


Fig. 7 Temporal changes in the **a** abundance (ind per root) and **b** species richness of indigenous and non-indigenous species of microbenthic communities associated with prop roots of *Rhizophora mangle* in Turbo and El Uno. Vertical bars displaying asterisks denote significant differences (* $p < 0.05$; ** $p < 0.01$) after Mann–Whitney *U* tests. Error bars are standard deviations

Vertical bars displaying asterisks denote significant differences (* $p < 0.05$; ** $p < 0.01$) after Mann–Whitney *U* tests. Error bars are standard deviations

1996 = 59 taxa), Mexico (Hemández-Alcántara and Solís-Weiss 1995 = 86 taxa; Tunnell and Withers 2009 = 47–56 taxa; Lucas and de la Cruz-Francisco 2018 = 26 taxa; Ruiz and López-Portillo 2014 = 28 taxa), Venezuela (Guerra-Castro et al. 2011 = 115 taxa that included algae). In the Urabá Gulf, Fernandez-Rodríguez et al. (2016) studied polychaete assemblages in Rionegro Cove and Marirrí Bay, areas not clearly affected by urbanization, and found ten taxa, which exceeds the five taxa reported in our study. Because of this, and the decreasing richness observed between in 2021 compared to 2005, we suggest that the low richness of taxa of

fouling communities in red mangrove roots might be a response to impacts of increased urbanization in Turbo and related human activities that spill-over in El Uno. More importantly, this would be in line with the commonly observed reduction of faunal and plant species richness along rural–urban gradients in diverse terrestrial and aquatic ecosystems (e.g. Alberti 2008). A further explanation for the low richness may also lie in the fact that estuarine conditions in the study area is known to restrict stenohaline species, thus reducing diversity (Blanco-Libreros et al. 2016), although higher species richness have been reported for mangrove root

fouling communities in other estuarine systems in Panama (Cubit et al. 1987) and the Gulf of Mexico (Tunnell and Withers 2009).

The high dominance of a few taxa is a general feature of mangrove root epibiotic communities; it has been consistently reported in relatively undisturbed areas of the Caribbean Sea (Hemández-Alcántara and Solís-Weiss 1995; Farnsworth and Ellison 1996; Tunell and Withers 1996; Vilardy and Polania 2002; Molina 2017). Thus, if the dominance is further increased as a response to the disturbances connected to urban expansion in El Uno and Turbo, we could not discriminate that response in a system characterized by a high dominance regardless of whether the habitat is disturbed or not.

Mangrove-root epibenthic communities have long been recognized as spatially structured communities controlled by physical and biological factors that operate at different scales (Bingham 1992; Farnsworth and Ellison 1996). While large spatial differences are largely influenced by physical factors, at local scale, as that used in our study, changes in community structure are known to be mainly controlled by larval supply: the patchiness seen in many mangrove epifaunal communities is largely a result of the importance of short-lived lecithotrophic species (e.g., sponges, bryozoans, ascidians), while homogeneous communities result from the dominance of species with long-lived planktotrophic larvae (Bingham 1992). Thus, given the lack of spatial differences in the structure of mangrove-root benthic communities in our study we would expect that species with long-lived planktotrophic larvae are dominant. But an analysis of the four species comprising nearly 75% of the total abundance suggest that it is not the case in our study: *Tanais dulongii* and *Leptocheirus rhizophorae* are brooding crustaceans with benthic life cycles and low dispersion rates (Rumbold et al. 2015; Arfianti 2020). In turn, while *Brachidontes domingensis* and *Crassostrea rhizophorae* are broadcast spawners, *C. rhizophorae* have short-lived larvae (10–12 d; Rampersad and Ammons 1992) and although *B. domingensis* does have long larval stage it commonly display heterogeneous spatial distributions at local stages (Bennett et al. 2011).

The lack of spatial variability in community structure seems more likely related to (i) the observed drop in the number and abundance of indigenous species as compared with non-indigenous biota and (ii) the

local expression of a widely observed effect of species invasions: biotic homogenization (sensu McKinney and Lockwood 1999). Significant shifts in the balance of indigenous and non-indigenous plant species as a response to urbanization have already been observed in forested urban wetlands (Ehrenfeld and Schneider 1991; Paquin et al. 2021) and urban mangroves (Branoff and Martinuzzi 2020). Some of the most abundant species in our study are invasive species associated with conditions commonly found in urbanized coasts: *Balanus amphitrite*, *Mytilopsis sallei* and *Alitta succinea* are common elements of encrusting communities in human-made structures worldwide or in invasive mangroves (Neves and Rocha 2008; Demopoulos and Smith 2010; Aguilera et al. 2018; Tan and Tay 2018); *Apocorophium acutum* is an invasive species associated with algal mats in jetties and aquaculture facilities (Hossain and Hughes 2016; Giménez-Delcamp 2021); *Exaiptasia diaphana* is an alien species covering artificial and natural surfaces (Durán-Fuentes et al. 2022) and *Tanais dulongii* is a cryptogenic species commonly found in eutrophic waters (Wildsmith et al. 2009). Unfortunately, the establishment of non-indigenous animal species in urban mangrove forests has been rarely addressed. Hence, we urge ecologist and conservationist to further assess whether urban mangroves are emerging as hotspots for non-indigenous biota.

A second striking result in our study was a clear turnover of core species between 2005 and 2021, with non-indigenous species playing a prominent role in this variability. A fairly common feature of ecological communities is that a few (core) species are exceptionally abundant, whereas most are rare, transient species (Gaston and Blackburn 2000). Empirical evidence shows that core species tend to be present for a longer period than rare species, thus implying that the commonness and rarity of species in the assemblage is related to their permanence (e.g. Magurran and Henderson 2003). Therefore, the observed turnover in core species is unexpected and hard to explain within the scope of our data. A species invasion is not an event but a species-specific and site-specific process occurring in consecutive stages including transport, establishment, spread and impact (Lockwood et al. 2013). Thus, we hypothesize that the observed turnover may reflect the progress or failure of each species to go through these stages. This, however, is rather speculative because our data have intrinsic

limitations mostly related with the fact that we are comparing start (2005) and end conditions (2021) without knowledge of e.g. seasonality in demographic processes and/or longer-term or cyclic oceanographic changes between these years, which may be independent of urban expansion.

The difficult to relate the presence of non-indigenous species to specific stressors in mangrove-root epibenthic communities and explain the turnover of core species also reflects our limitation to assess synergistic effects of multiple co-occurring stressors in this system—a current research priority to advance invasion science in the face of rapid environmental change (Ricciardi et al. 2021).

Acknowledgements María José Pacheco contributed to fieldwork. Thanks to local communities in El Uno and Turbo bay for allowing access to their territories. Fieldwork and collection of biological samples was conducted in under the permit 0524 provided by Autoridad Nacional de Licencias Ambientales to Universidad de Antioquia. We acknowledge the thoughtful and constructive work performed by two anonymous reviewers.

Author contributions All authors contributed to the study conception and design. Field work was conducted by JMR and EM. Material preparation, data collection and analysis were performed by JMR and EM. The first draft of the manuscript was written by JMR and EM, and all authors commented on previous versions of the manuscript.

Funding Open Access funding provided by Colombia Consortium. This work was financially supported by a ICETEX scholarship for black minorities and Esperanza Afro foundation, awarded to Enis Mosquera.

Data availability All data generated or analysed during this study are included in this published article [and its supplementary information files]. Any further information regarding the database supporting this work is available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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