

# 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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## Research Article

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# Abstract

Urbanization represent 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 through 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 the majority of all taxa (65%) were non-indigenous species whose presence is related with known stressors in urbanized systems. Hence, we suggest that urban mangrove forests are emerging 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 communities dominated by non-indigenous biota.

## 1. Introduction

Habitat loss and invasive species have long been heralded as major causes of biodiversity loss in conservation biology (e.g., Pimm & 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 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-native species (Santana et al. 2020; Gonzalez-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).

Through centuries, mangrove forests have provided 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 species introductions commonly associated with 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 biotas are interacting through time. Particularly, mangrove-root fouling communities are suitable 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 native and non-native 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 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 García and Palacios (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, reflecting its urban character and thus a more diverse arrange of human activities and introduction vectors in this bay.

## 2. 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 basing mangroves (Urrego et al. 2014). The gulf is part of the Chocó-Darien Global Ecoregion, a globally recognized biodiversity hotspots prioritized for conservation due to the high levels of biodiversity and endemism (Fagua and Ramsey 2019). Despite this, the coalescence of outrages and conflicts that characterized the aftermath of European invasion in Latin America is epitomized in this

region. The region witnessed the rise and fall of the oldest founded Spanish city of the Americas in *terra firma* (Sarcina, 2017), the spread of African-descendant peoples that displaced indigenous groups after slavery abolition and the growth of coca cultivation and the linked problem of illegal armed groups that turned the region into a major trafficking illegal immigration corridor. These historic processes have resulted in a region displaying a complex mosaic of land covers, ethnic groups and legal and illegal economic activities.

Mangroves in Turbo Bay have been characterized as “peri-urban” because they are structurally and functionally affected by its proximity to the Turbo port city (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 have been cleared for expanding lands for agriculture (mainly comprising plantain crops) and cattle ranching, a typical example of a rural-agricultural transition (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-20th century (Blanco-Libreros et al. 2013, Alcántara-Carrió et al. 2019).

#### Field work

This work builds on a previous work on the structure of macrobenthic communities associated to prop roots of *R. mangle* performed by García and Correa (2006), which was later published by García and Palacio (2008). 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 single sampling in June 2021, taking ten *R. mangle* prop roots in the same zones (east, north, west) in each bay (Fig. 1). Following the criteria established by García and Palacio (2008), roots were selected by i) belonging to mature trees ( $\geq 10$ 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 registered: trampling (the number of human footprints), logging (number of trees cut), litter (number of litter items) and urban structures (number of urban structures, i.e. houses, roads, peers, etc.). All these counts were performed by a single dedicated observer in the area 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 hours. Roots were weighted 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:

1. 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.
2. Alien species: a species introduced outside its natural past or present distribution.
3. Invasive-alien species: an alien species whose introduction and/or spread threaten biological diversity

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

### Data analysis

As sampled prop roots had distinct weight, the abundance of species was calculated as the number of individuals per gram of 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 of sessile animals. Data on environmental factors 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 to 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 (Sommerfield et al. 2021). This preliminary analysis confirmed that there were no significant differences between zones.

To assess our hypothesis on changes in the structure of epibenthic macrofauna associated to 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 size and origin (native/non indigenous) to

discuss our findings. 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).

### 3. Results

Our study reports 40 taxa of invertebrates associated to prop roots of *Rhizophora mangle* (Table 1) 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 dominguensis* and *Tanais dulongii*) made up nearly half of the total abundance. 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 (12), alien (7), invasive alien (5) and cryptogenic (2) (Table S1).

Table 1

Abundance (expressed as percentage of total abundance shown in the last row) of invertebrate species associated to prop roots of *Rhizophora mangle* in 2005 and 2021 at El Uno bay and Turbo bay, Colombian Caribbean. Note that total abundances for 2005 at the two bays represent the average for the period September to December.

Taxa	Percentage of total abundance					
	2005		2021		Total	Cumulative
	El Uno	Turbo	El Uno	Turbo		
<i>Brachidontes domingensis</i> (Lamarck. 1819)	33.762	38.844	7.368	10.979	26.555	26.555
<i>Tanais dulongii</i> (Audouin. 1826)	23.138	20.255	13.158	19.643	20.169	46.725
<i>Crassostrea rhizophorae</i> (Guilding. 1828)	13.571	16.533	2.105	2.447	10.375	57.100
<i>Leptocheirus rhizophorae</i> (Ortíz & Lalana. 1980)	0.000	0.000	27.237	26.257	9.734	66.834
<i>Apocorophium acutum</i> (Chevreux. 1908)	1.930	0.130	25.658	16.138	7.739	74.573
<i>Mytilopsis sallei</i> (Récluz. 1849)	3.030	4.869	3.553	8.598	5.021	79.594
<i>Exaiptasia diaphana</i> (Rapp. 1829)	11.724	1.320	0.000	0.000	4.203	83.798
<i>Biflustra tenuis</i> (Desor. 1848)	0.000	0.022	6.447	7.341	2.585	86.383
<i>Alitta succinea</i> (Leuckart. 1847)	1.556	2.683	0.921	1.786	1.884	88.267
<i>Sphaeroma terebrans</i> (Bate. 1866)	1.619	0.887	5.395	0.992	1.701	89.968
<i>Amphibalanus amphitrite</i> (Darwin. 1854)	2.200	2.380	0.395	0.331	1.579	91.548
<i>Panopeus herbstii</i> H. Milne Edwards. 1834	1.473	3.008	0.132	0.000	1.426	92.974
<i>Bankia fimbriatula</i> (Moll & Roch. 1931)	0.062	2.813	0.000	0.000	0.893	93.867
<i>Aratus pisonii</i> (H. Milne Edwards. 1837)	1.349	0.692	0.658	0.463	0.845	94.712
<i>Vitta virginea</i> (Linnaeus. 1758)	0.083	2.337	0.395	0.000	0.800	95.512
Chaetopteridae (Audouin & Milne Edwards. 1833)	0.000	0.000	4.737	0.860	0.790	96.302
<i>Brachidontes</i> (Swainson. 1840)	2.137	0.000	0.000	0.000	0.692	96.993
Sabellidae (Latreille. 1825)	0.000	0.000	1.053	1.720	0.548	97.541

	Percentage of total abundance					
<i>Thaisella coronata</i> (Lamarck. 1816)	0.166	0.216	0.263	0.860	0.363	97.904
<i>Littoraria angulifera</i> (Lamarck. 1822)	0.498	0.433	0.000	0.000	0.295	98.199
<i>Chthamalus</i> (Ranzani. 1817)	0.519	0.390	0.000	0.000	0.289	98.488
<i>Nereis</i> (Linnaeus. 1758)	0.623	0.130	0.000	0.000	0.242	98.730
<i>Pachygrapsus gracilis</i> (de Saussure. 1857)	0.042	0.714	0.000	0.000	0.235	98.965
<i>Neoteredo reynei</i> (Bartsch. 1920)	0.000	0.260	0.000	0.529	0.209	99.174
<i>Ligia</i> (Fabricius. 1798)	0.042	0.606	0.000	0.000	0.201	99.376
Ascidia (Linnaeus. 1767)	0.000	0.022	0.000	0.661	0.168	99.543
<i>Neopanope</i> A. Milne-Edwards. 1880 [in A. Milne-Edwards. 1873–1880]	0.042	0.303	0.000	0.000	0.107	99.651
Hirudinea (Savigny. 1822)	0.000	0.022	0.000	0.265	0.071	99.722
<i>Polymesoda arctata</i> (Deshayes. 1855)	0.145	0.022	0.000	0.000	0.054	99.776
<i>Pyrgophorus</i> (Ancey. 1888)	0.104	0.000	0.000	0.000	0.034	99.809
<i>Stenoninereis</i> (Wesenberg-Lund. 1958)	0.000	0.000	0.000	0.132	0.032	99.842
<i>Martesia striata</i> (Linnaeus. 1758)	0.000	0.043	0.132	0.000	0.030	99.871
Diptera (Linnaeus. 1758)	0.000	0.022	0.132	0.000	0.023	99.894
<i>Sphaeroma</i> (Bosc. 1801)	0.062	0.000	0.000	0.000	0.020	99.914
<i>Culex pipiens</i> (Linnaeus. 1758)	0.000	0.000	0.132	0.000	0.016	99.930
<i>Platynereis mucronata</i> (León-González. Solís-Weiss & Valadez-Rocha. 2001)	0.000	0.000	0.132	0.000	0.016	99.946
<i>Pyrgophorus parvulus</i> (Guilding. 1828)	0.042	0.000	0.000	0.000	0.013	99.960
<i>Macrobrachium acanthurus</i> (Wiegmann. 1836)	0.021	0.022	0.000	0.000	0.013	99.973
<i>Callinectes sapidus</i> (Rathbun. 1896)	0.021	0.022	0.000	0.000	0.013	99.987

	Percentage of total abundance					
<i>Callinectes bocourti</i> A. Milne-Edwards. 1879 [in A. Milne-Edwards. 1873–1880]	0.042	0.000	0.000	0.000	0.013	100
<b>Richness (number of taxa)</b>	<b>28</b>	<b>29</b>	<b>20</b>	<b>18</b>	<b>40</b>	
<b>Total abundance (Number of individuals-all taxa)</b>	<b>201</b>	<b>193</b>	<b>76</b>	<b>151</b>	<b>621</b>	

The abundance and species composition of macrobenthic assemblages associated to roots of *R. mangle* did not show significant differences among zones, neither in El Uno bay (ANOSIM;  $R = 0.012$ ;  $p = 0.34$ ) nor in El Uno Bay (ANOSIM;  $R = 0.116$ ;  $p = 0.06$ ), although a higher spatial segregation in nMDS ordination plots was observed in Turbo bay (Fig. 2). This result was surprising, because PCA ordinations of anthropogenic pressures (Fig. 3) showed a clear spatial structure within each bay, with the density of litter and urban structures being key structuring factors.

In contrasts, our results rendered 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. 4), 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 2). Of these species, only five were categorized as indigenous species, while the majority where either, alien, invasive alien or cryptogenic species (Fig. 5; Table S1). Of special importance was the fact that two of the most abundant species observed in 2005 where replaced as dominant species in 2020 by two previously unregistered species.

Table 2  
Results of Similarity Percentage Analysis showing the main benthic species contributing to the dissimilarity in community structure between 2005 and 2021

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

## 4. Discussion

In a classical work on ecosystem ecology, Odum (1985) suggested that in a system submitted to external disturbances or stressors, species diversity would decrease while dominance increase. Direct, comparisons of species diversity of fouling communities associated to 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 1996 = 59 taxa), Mexico (Hemández-Alcántara and Solís-Weiss 1995 = 86 taxa; Tunell and Withers 1996 = 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). 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 is in line with the observed variation of faunal and plant

species richness along rural-urban gradients (Alberti 2008). However, a second explanation for the low richness may also lie in the fact that estuarine conditions in the study area restrict stenohaline species.

In contrast, we could not suggest a link between the high dominance of a few species and disturbances associated to urbanization –remarkably high dominances in fouling communities or specific taxonomic assemblages in mangrove roots have been observed in relatively undisturbed areas (Hemández-Alcántara and Solís-Weiss 1995; Farnsworth and Ellison 1996; Tunell and Withers 1996; Vilarity and Polania 2002; Molina et al. 2017).

Mangrove-root epibenthic communities have long been recognized as spatially structured communities controlled by physical and biological factors (Binham 1992; Farnsworth and Ellison 1996). At local scales, 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 (Binham 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 it seems not the case: for example, *Tanais dulongii* (which alone comprised 20% of the total abundance), is a brooding crustacean with a strictly benthic life cycle and low dispersion rate (Rumboldt et al. 2015).

The lack of spatial variability in community structure seems more likely related to i) the surprising finding that non-indigenous species outnumber indigenous species and ii) the local expression of a widely observed effect of species invasions: biotic homogenization (*sensu* McKinney and Lockwood 1999). Significant increases in the number of non-indigenous plant species as a response to urbanization have been observed in forested urban wetlands (Ehrenfeld and Schneider 1991, Paquin et al. 2021) and urban mangroves (Branoff and Martuzzi 2020). In our knowledge, this is the first study showing that animal assemblages associated to mangrove forests in urban areas are dominated by non-indigenous species; hence, we suggest that urban mangroves may be emerging hotspots for non-indigenous biota. Some of the most abundant species in our study are invasive species associated to 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 Tay 2018, ); *Apocorophium acutum* is an invasive species associated 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 2022) and *Tanais dulongii* is a cryptogenic species commonly found in eutrophic waters (Wildsmith et al. 2009).

A second striking results 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 show 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 & Henderson 2003). Therefore, the observed turnover in core species is unexpected and hard to explain within the scope of our data. As 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 comparing start and end conditions without knowledge of e.g. long-term or cyclic environmental or oceanographic changes between these conditions that may be independent of urban expansion.

The unusually high proportion of non-indigenous species in mangrove-root epibenthic communities and the difficult to understand the significant species turnover of core species most probably reflect potential synergistic effects of multiple co-occurring stressors on the establishment and impact of non-native species—a current research priority to advance invasion science in the face of rapid environmental change (Ricciardi et al. 2021)

## **Declarations**

### **Author Contributions**

All authors contributed to the study conception and design. Field work was conducted by José M. Riascos and Enis Mosquera. Material preparation, data collection and analysis were performed by José M. Riascos and Enis Mosquera. The first draft of the manuscript was written by José M. Riascos and Enis Mosquera, and all authors commented on previous versions of the manuscript.

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### **Competing 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.

### **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.

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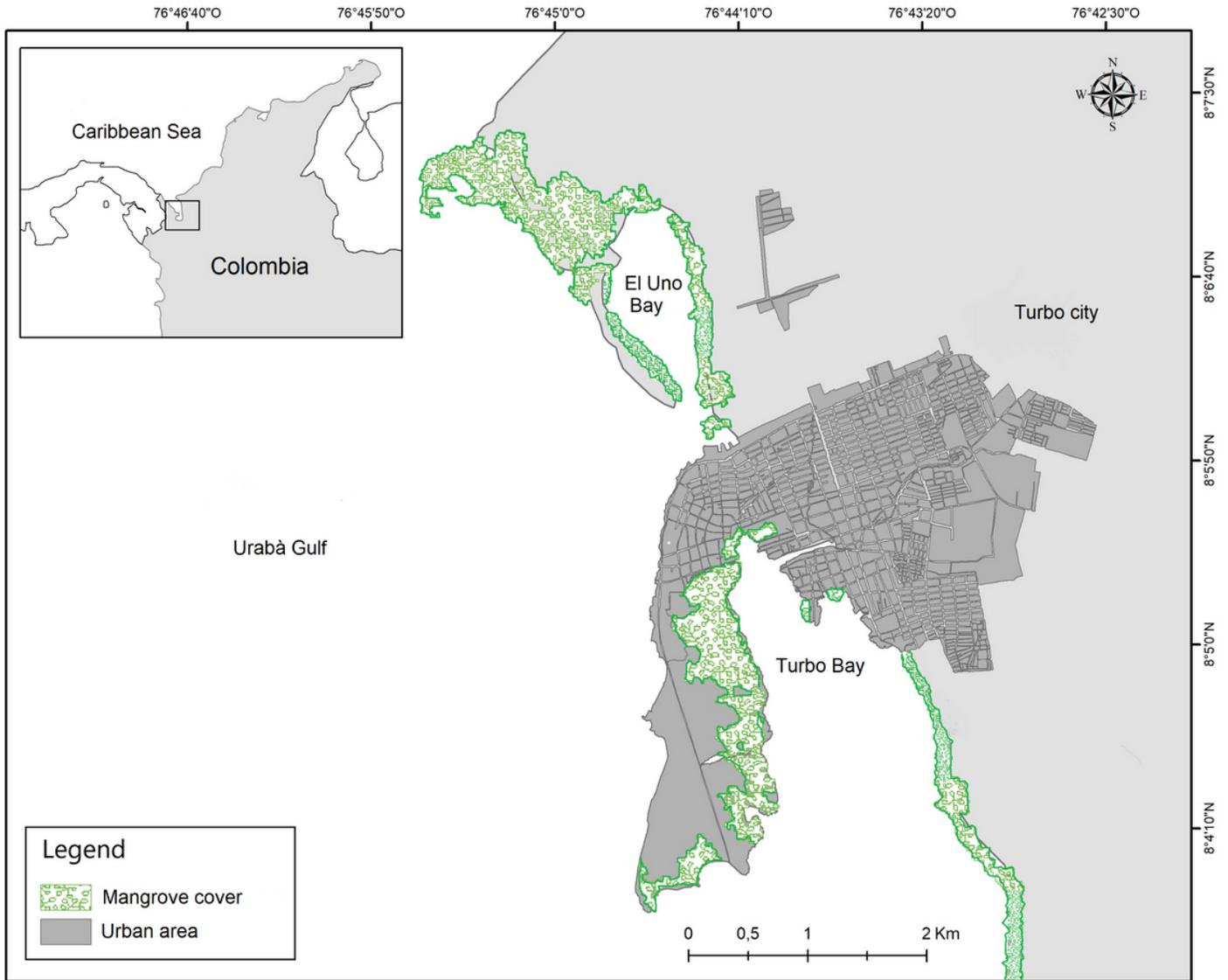
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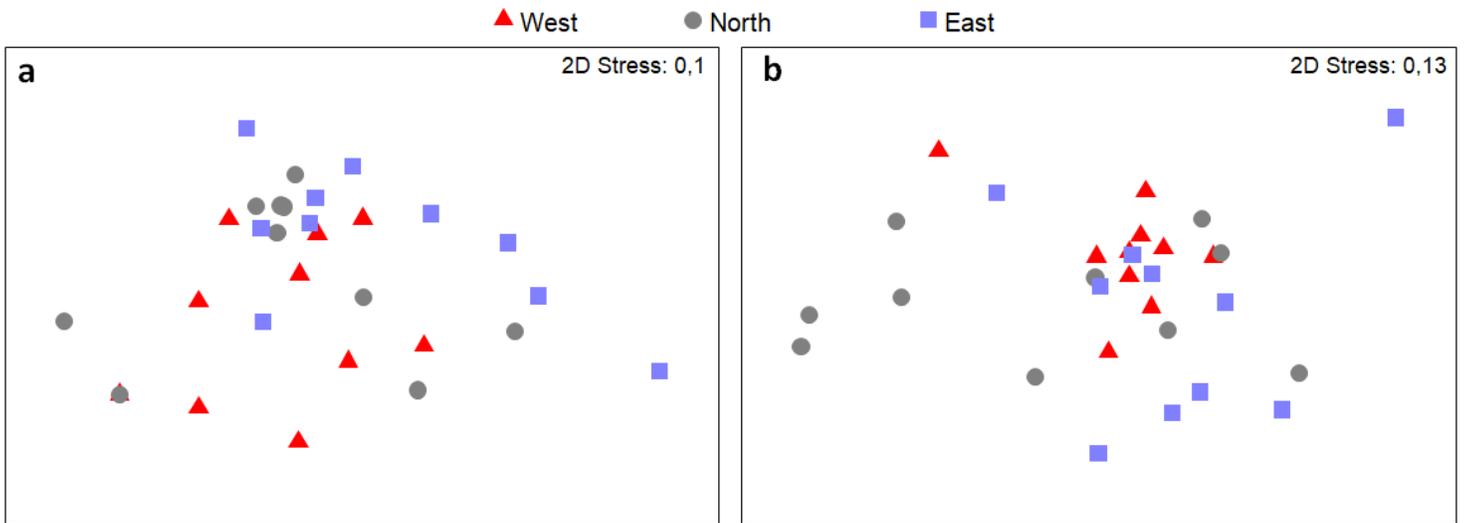
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## Figures



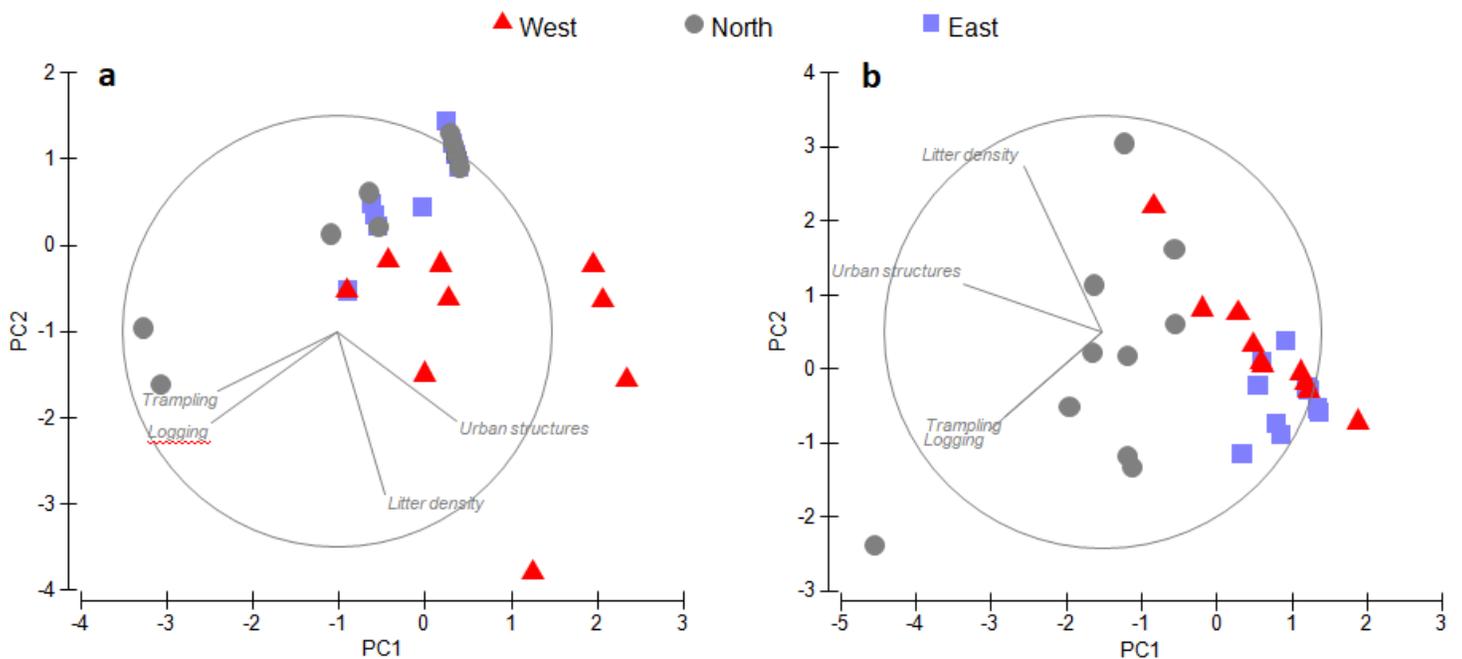
**Figure 1**

Map of the Urabá gulf and the study sites. Shape of mangrove forests provided by Valencia-Palacios and Blanco-Libreros (2021)



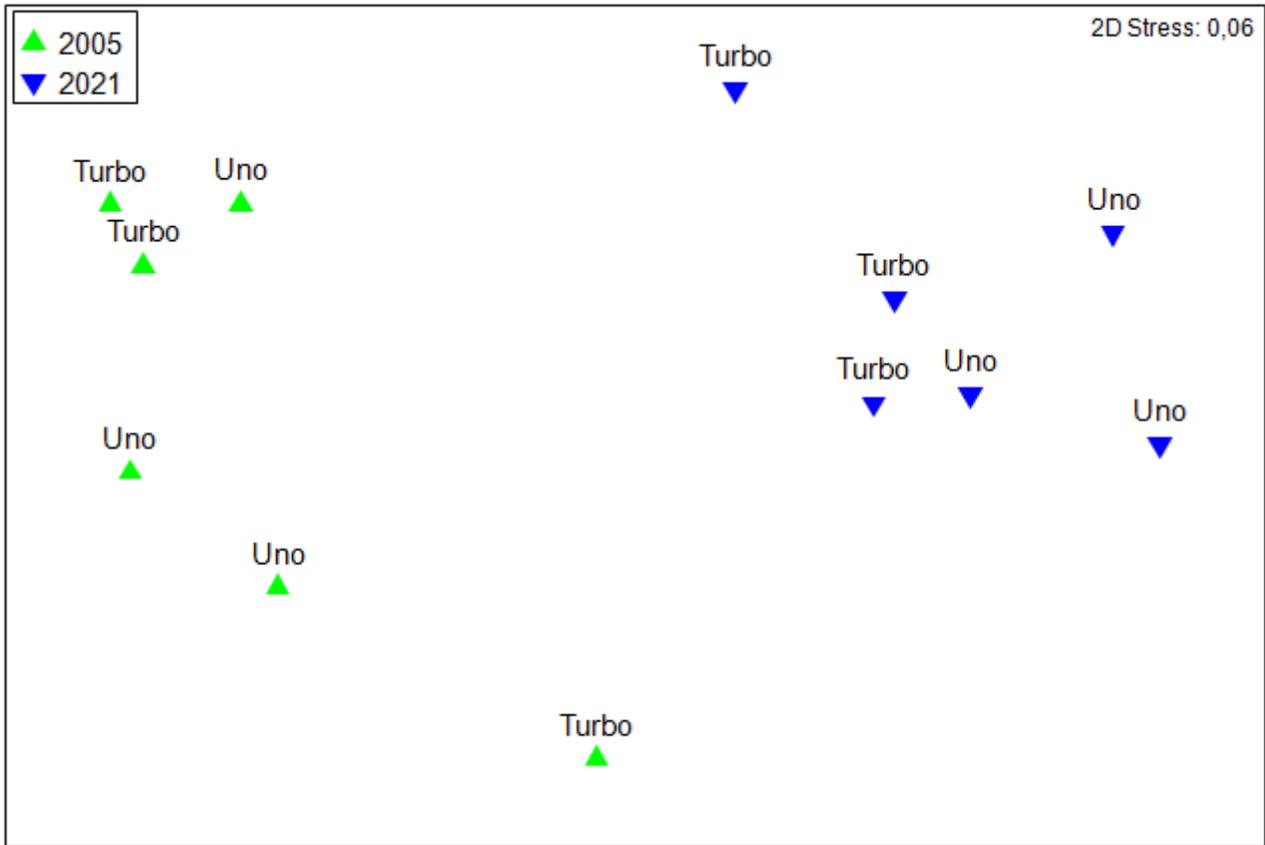
**Figure 2**

Ordination by non-metrical Multidimensional Scaling of composition and abundance of macrobenthic communities associated to 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.



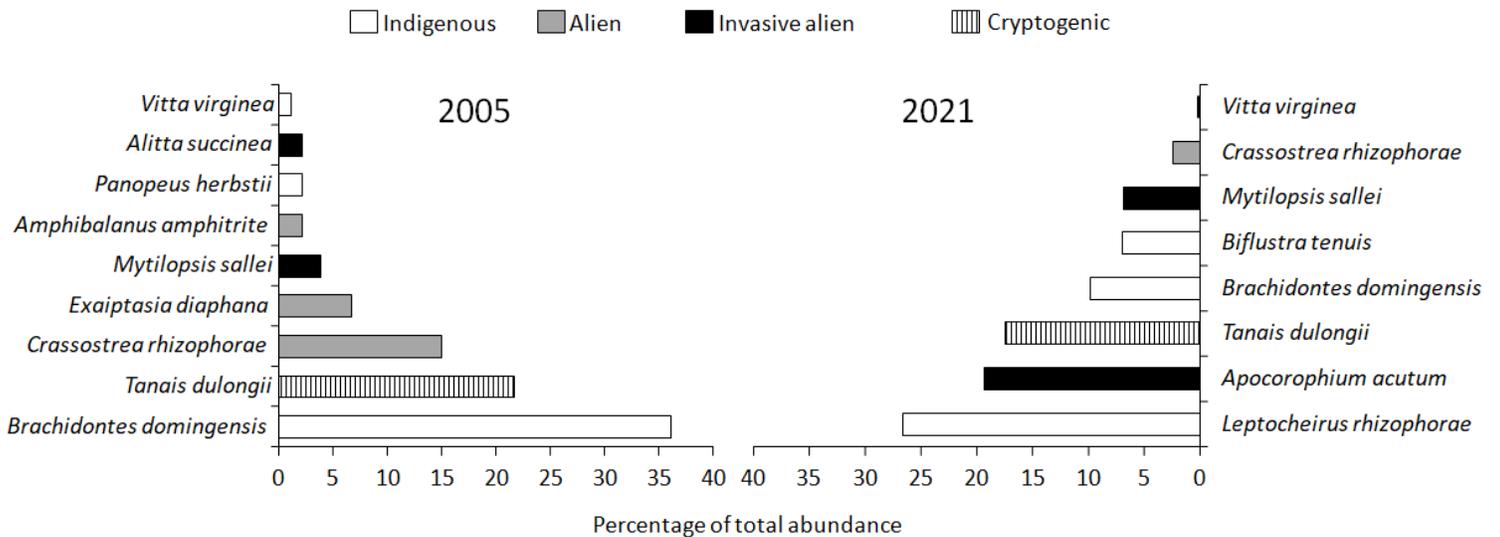
**Figure 3**

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) and the superimposed vectors (grey lines) of anthropogenic factors.



**Figure 4**

Ordination by non-metrical Multidimensional Scaling (nMDS) of composition and abundance of macrobenthic communities associated to prop roots of *Rhizophora mangle* in El Uno Bay and Turbo bay, Colombian Caribbean coast. nMDS was built on Bray-Curtis dissimilarity measures.



**Figure 5**

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 S1; note that *Crassostrea rhizophorae* and *Mytilopsis salsalei* are native to the Caribbean, but they have been introduced to other regions and hence are reported here as alien and invasive-alien species, respectively.

## Supplementary Files

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- [TableS1.xlsx](#)