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Essay

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Rise and Fall of Caribbean Mangroves

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Abstract: Mangrove forests, which are essential for the maintenance of terrestrial and marine biodiversity in tropical coasts and constitute the main blue-carbon ecosystems for the mitigation of global warming, are among the world's most threatened ecosystems. Mangrove conservation can greatly benefit from paleoecological and evolutionary studies, as past analogs documenting the responses of these ecosystems to environmental drivers such as climate change, sea level shifts and anthropogenic pressure. A database (CARMA) encompassing nearly all studies on mangroves from the Caribbean region, one of the main mangrove hotspots, and their response to past environmental shifts has recently been assembled and analyzed. The dataset contains over 140 sites and ranges from the Late Cretaceous to the present. The Caribbean was the cradle of Neotropical mangroves, where they emerged in the Middle Eocene (~50 million years ago; Ma). A major evolutionary turnover occurred in the Eocene/Oligocene transition (34 Ma) that set the bases for the shaping of modern-like mangroves. However, the diversification of these communities leading to their extant composition did not occur until the Pliocene (~5 Ma). The Pleistocene (the last 2.6 Ma) glacial-interglacial cycles caused spatial and compositional reorganizations with no further evolution. Human pressure on Caribbean mangroves increased in the Middle Holocene (~6000 years ago), when pre-Columbian societies began to clear these forests for cultivation. In the last decades, deforestation has reduced the Caribbean mangrove cover by one third and it has been estimated that, if urgent and effective conservation actions are not undertaken, these 50 million-year-old ecosystems might disappear in little more than half a century. A number of specific conservation and restoration applications based on the results of paleoecological and evolutionary studies are suggested.

Keywords: Caribbean; mangroves; evolution; paleoecology; deforestation; conservation

1. Introduction

Mangroves form a distal continental fringe along the tropical/subtropical coasts (Figure 1), which marks the extent of normal tides. Mangrove forests protect coasts and other coastal ecosystems (corals, seagrasses, salt marshes) from erosion and develop a complex physical structure that favors habitat and niche diversification, which allows many terrestrial and aquatic species to thrive, thus enhancing biodiversity and ecological complexity (Laegdsgaard & Johnson 2001; Saenger 2002; Nagelkerken et al., 2008). Mangroves not only provide ecological and cultural services (fisheries, cultivation, aquaculture, timber, fuel, aesthetics, ecotourism) but also contribute to the mitigation of global warming. These communities, along with seagrasses and salt marshes, are among the most important blue-carbon ecosystems – i.e., marine ecosystems that sequester and immobilize carbon, thus removing it from the global cycle – acting as efficient carbon sinks and contributing to the alleviation of atmospheric CO_2 increase (Nellemann et al., 2009; Mcleod et al., 2011; Fest et al. 2022). Presently, mangrove forests are among the world's most threatened ecosystems (Worthington et al. 2020). According to the latest estimates, the global mangrove extent was reduced by ~25% in only three decades (1980-2010) due to natural and anthropogenic deforestation (Bunting et al. 2022). If these rates are maintained, these ecosystems will be severely reduced during this century and could disappear from the face of the Earth within the next century (Duke et al. 2017).
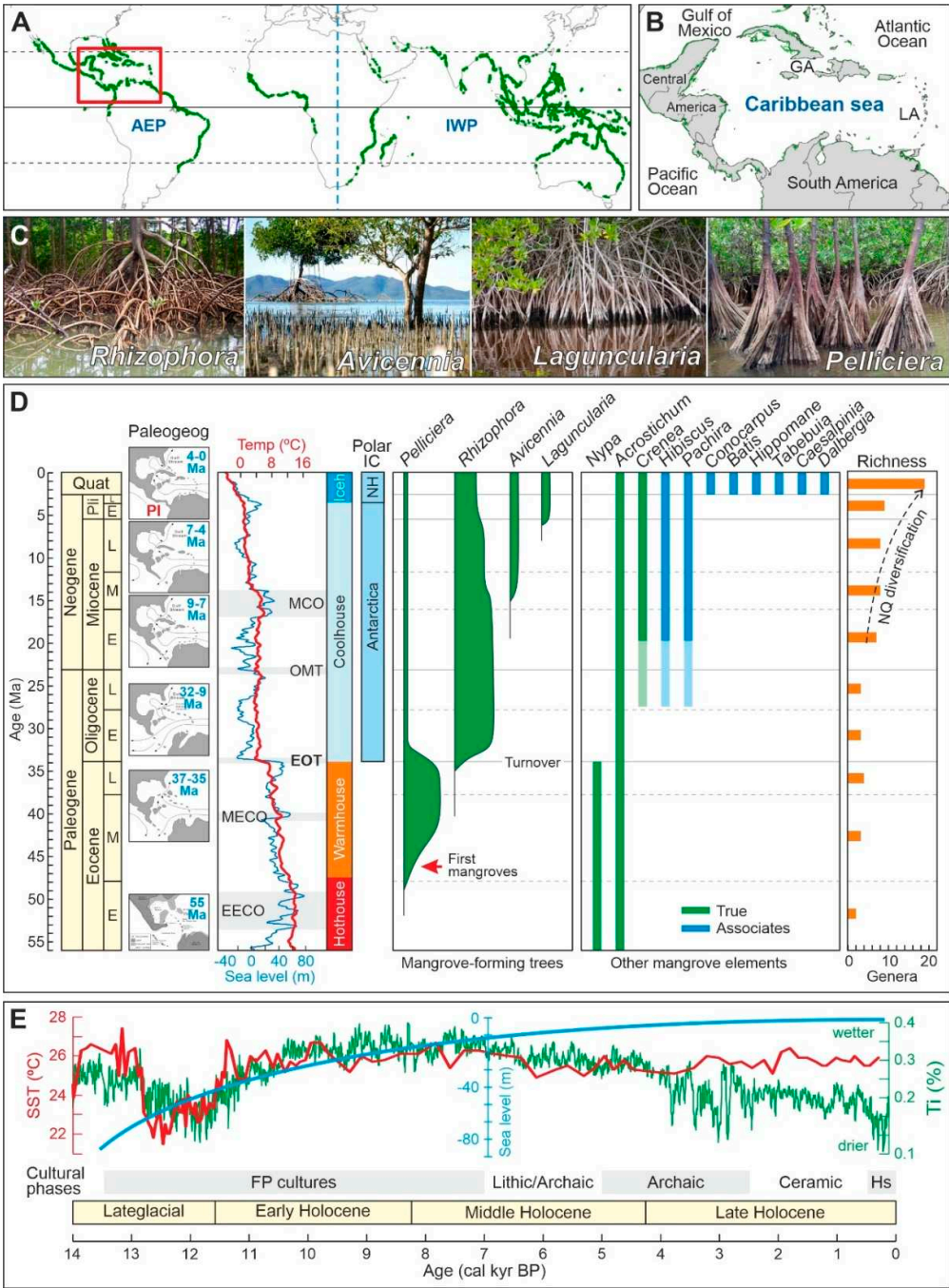
Figure 1. Present patterns and past trends of Caribbean mangroves. A) Present worldwide mangrove distribution (green patches) (Spalding et al., 2010) and the two main biogeographical regions (AEP, Atlantic-East Pacific; IWP, Indo-West Pacific). The location of the Caribbean region is indicated by a red box. B) The Caribbean region, as considered in this study (GA, Greater Antilles; LA, Lesser Antilles). C) The main genera of mangrove-forming trees (Rull, 2022a, b). D) Paleogene and Neogene evolution of Caribbean mangroves (Rull, 2022a, c, 2023a) in relation to paleographic (Iturralde-Vinent, 2006), paleoclimatic (Westerhold et al., 2020) and paleoeustatic (Miller et al., 2020) shifts. Chronology: Quat, Quaternary; Pli, Pliocene; E, Early, M. Middle; L, Late. Paleogeography: PI, Panama Isthmus. Paleoclimates: EECO, Early Eocene Climatic Optimum; MECO, Middle Eocene Climatic Optimum; EOT, Eocene–Oligocene Transition; OMT, Oligocene/Miocene Transition; MCO, Miocene Climatic Optimum; Iceh, Icehouse; NQ, Neogene-Quaternary. Polar Ice Caps (IC): NH, Northern Hemisphere.

Richness: NQ, Neogene-Quaternary. E) Holocene paleoclimatic (Haug et al., 2002, Lea et al., 2003), paleoeustatic (Khan et al., 2017) and cultural trends and events (Rull, 2022b). SST, Sea Surface Temperature; Ti, Titaniun concentration as a moisture proxy.

The Neotropical Caribbean region is one of the main mangrove hotspots (Duke, 2017; Bryan-Brown et al., 2020), and the most relevant threats are urbanization, damming, agriculture, forestry, tourism, fisheries, salt production and shrimp farming (Lacerda et al., 2019). A significant amount of basic ecological information is still needed to properly address the conservation and restoration of Caribbean mangroves. Part of this information may be retrieved from paleoecological and evolutionary records, which provide a natural laboratory where to study the responses of Neotropical ecosystems to long-term natural and anthropogenic drivers of ecological change (Vegas-Vilarrúbia et al., 2011). In the last couple of years, the paleoecological and evolutionary study of Caribbean mangroves has experienced a significant burst with the compilation of a nearly exhaustive database of >140 sites (CARMA, for CARibbean MAngroves) encompassing the whole history of these communities from their origin, ~50 million years ago (Ma), to their anthropization during the last millennia (Figure 2). The detailed analysis of this dataset has provided new clues on the origin, evolution and biogeography of Caribbean mangroves that challenge classical views and have been published in a collection of recent papers, sorted chronologically (Rull, 2022a, b, c; 2023a, b). A synthetic update of this new information is still unavailable and is the main target of this paper, which highlights the most relevant findings for understanding the shaping of these ecosystems and for informing their conservation.
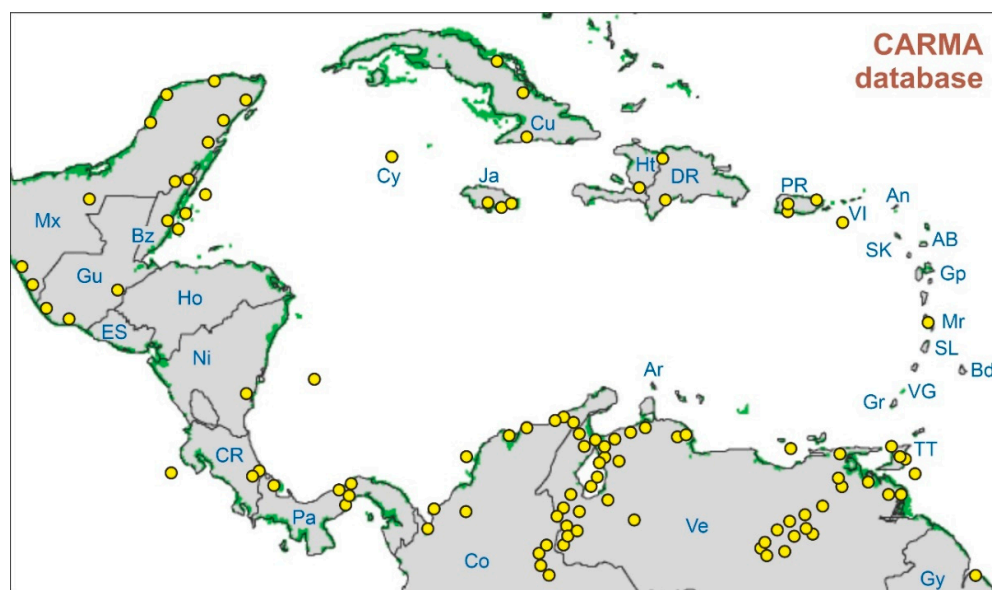

Figure 2. Sketch-map indicating the location of the study sites compiled in the CARMA (CARibbean MAngroves) database (yellow dots). In a number of cases, a dot corresponds to more than one site (see the Supplementary Material for details and references). Present-day mangroves are indicated by green patches (Spalding et al. 2010). Country/island abbreviations as in Table 2.

2. Extant mangroves

The extant Caribbean mangroves are characterized by three main tree genera, known as mangrove-forming trees: *Rhizophora* (Rhizophoraceae), *Avicennia* (Acanthaceae) and *Laguncularia* (Combretaceae) (Figure 1). The first is the most abundant and widespread and is represented by two species (*R. mangle, R. racemosa*), whereas the second has three Caribbean species (*A. germinans, A. bicolor, A. shaueriana*) and the third is monospecific (*L. racemosa*) (Table 1). These trees are known as major true-mangrove elements, as they are restricted to mangrove ecosystems, play a major structural role and are able to develop pure stands, possess special morphological adaptations to tidal

environments and bear physiological mechanisms of salt exclusion (Tomlinson, 2016). Minor true-mangrove elements share the same features but occupy peripheral habitats, rarely form pure stands and are not major structural elements; they are the tree *Pelliciera rhizophorae* (Tetrameristaceae), the herb *Crenea patentinervis* (Lythraceae) and the ferns *Acrostichum aureum* and *A. danaefolium* (Pteridaceae). Other 25 species (Table 1) are known as mangrove associates, as they are characteristic of these communities but are not restricted to them and lack the adaptations that characterize true-mangrove elements (Tomlinson, 2016). Some important mangrove associates are *Conocarpus erectus* (Combretaceae), *Mora oleifera* and *Muellera moniliformis* (Fabaceae), *Pavonia paludicola* and *P. rhizophorae* (Malvaceae), and *Tabebuia palustris* (Bignoniaceae) (Duke, 2017).

Table 1. True (in bold) and associate Neotropical mangrove elements. Habitats: BC, beach communities; BM, back mangrove; BC, beach communities; CC, coastal communities; CS, coastal swamps; MF, mangrove fringe; RB, river banks; SM, Salt marshes; W, wetlands. Summarized from Tomlinson (2016).

Genus	Family	Mangrove species	Life form
Acrostichum	**Pteridaceae**	**A. aureum, A. danaefolium**	**Fern**
Amoora	Meliaceae	A. cucullata	Tree
Amphitecna	Bignoniaceae	A. latifolia	Tree
Anemopaegna	Bignoniaceae	A. chrysoleucum	Vine
Avicennia	**Acanthaceae**	**A. germinans, A. bicolor, A. shaueriana**	**Tree**
Batis	Batidaceae	B. maritima	Shrub
Caesalpinia	Fabaceae	C. bonduc	Vine
Conocarpus	Combretaceae	C. erectus	Tree
Crenea	**Lythraceae**	**C. patentinervis**	**Herb**
Dalbergia	Fabaceae	D. ecastophyllum, D. amerimnion	Tree/Shrub
Hibiscus	Malvaceae	H. tiliaceum	Tree
Hippomane	Euphorbiaceae	H. mancinella	Tree
Laguncularia	**Combretaceae**	**L. racemosa**	**Tree**
Mora	Fabaceae	M. oleifera	Tree
Muellera	Fabaceae	M. moniliformis	Tree
Pachira	Bombacaceae	P. aquatica	Tree
Pavonia	Malvaceae	P. paludicola, P. rhizophorae	Shrub
Pelliciera	**Tetrameristaceae**	**P. rhizophorae**	**Tree**
Phryganocydia	Bignoniaceae	P. phellosperma	Vine
Pluchea	Asteraceae	P. odorata	Herb
Rhabdadenia	Apocynaceae	R. biflora	Vine
Rhizophora	**Rhizophoraceae**	**R. mangle, R. racemosa**	**Tree**
Rustia	Rubiaceae	R. occidentalis	Tree/Shrub
Scaevola	Goodeniaceae	S. plumieri	Shrub
Tabebuia	Bignoniaceae	T. palustris	Tree
Thespesia	Malvaceae	T. populnea, T. populneiodes	Tree
Tuberostylis	Asteraceae	T. axillaris, T. rhizophorae	Shrub

The Neotropical mangrove forests show a characteristic sea-inland zonal pattern with no herbaceous understory, characterized by the sequence *Rhizophora-Avicennia-Laguncularia* in the more saline zone dominated by normal tides, *Acrostichum* and *Conocarpus* in the brackish back-mangrove swamps and elevated areas under the influence of spring tides, and *Mauritia* and other palms in the more inland freshwater swamps, which mark the transition to the interior savannas and rainforests (Figure 3). Mangrove zonation is influenced by a diversity of biotic and abiotic factors, notably geomorphology, inundation frequency/intensity, salinity, propagule sorting and competition (Tomlinson, 2016). Biogeographically, Caribbean mangroves belong to the Atlantic-East Pacific (AEP)

region (Figure 1), which is significantly less diverse (17 typical mangrove species belonging to 11 genera and 9 families) than the Indo-West Pacific region, with 54 species (24 genera and 17 families) characteristic of mangroves (Duke, 2017). Among mangrove-forming trees, the genera *Rhizophora* and *Avicennia* occur in both the AEP and IWP but are represented by different species, whereas *Laguncularia* and *Pelliciera* occur only in the AEP, with the second restricted to a relictual patch around the Central American Panama Isthmus (Duke, 2020).
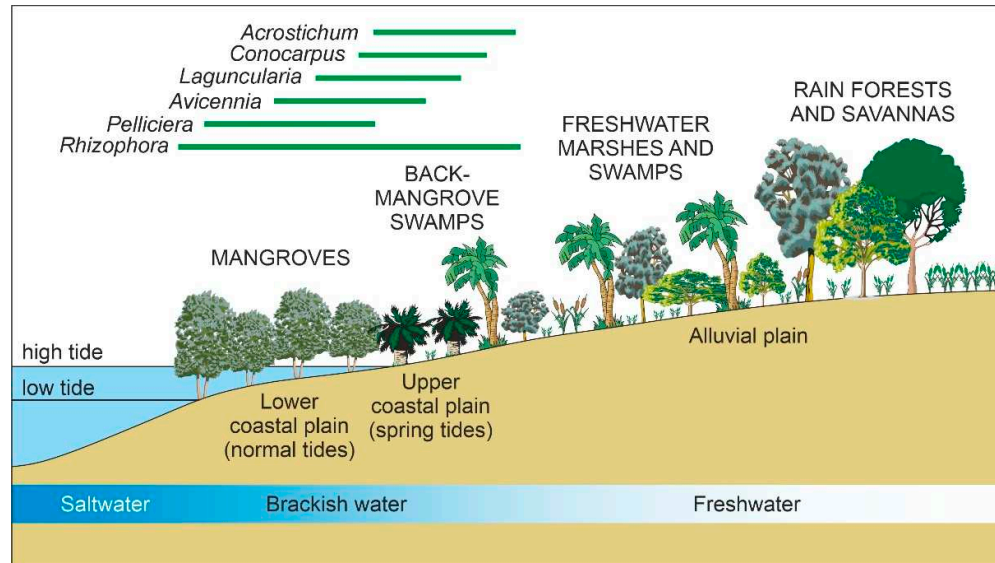

Figure 3. Idealized transect showing the typical coastal zonation of Caribbean mangroves. The approximate ranges of the most important mangrove elements are indicated. After Rull (2022a).

3. Evolution

3.1. Eocene origin

According to the classical and more accepted view, the Neotropical mangroves would have originated by regional differentiation from a hypothetical Late Cretaceous (>65 Ma) pantropical mangrove belt along the coasts of the Tethys Sea after the formation of the African barrier by continental drift (Figure 1). This idea was based on qualitative evidence, usually the presence of pollen and other fossils from assumed mangrove elements, notably *Spinizonocolpites* (the fossil representative of the palm *Nypa*, characteristic of the IWP mangroves) and *Deltoidospora* (the fossil representative of *Acrostichum*) (Srivastava & Prasad, 2018). However, a recent analysis of the quantitative palynological evidence has shown that Neotropical mangroves, as ecosystems, likely originated much later, between 50 and 40 Ma (Lutetian, Middle Eocene) (Rull, 2022a). Rather than the evolutionary descendants of a former hypothetical pantropical belt, the Caribbean mangroves signified an evolutionary innovation that emerged de novo, thanks to the evolutionary appearance of *Pelliciera*, the oldest known mangrove-forming tree, represented in the fossil record by the pollen morphospecies *Lanagiopollis crassa* (also *Psilatricolporites crassus*). This tree dominated the Eocene mangrove communities, with *Nypa* in the understory, *Acrostichum* in the back-mangrove belt and *Mauritia* (represented by the fossil pollen *Mauritiidites franciscoi*) in the inland freshwater swamps. The communities quickly dispersed across the region and were distributed across the Caribbean area by the Middle/Late Eocene. According to the updated Caribbean database, evidence for mangrove communities before the Middle Eocene is lacking, and the scattered individual appearances of fossil pollen from nonmangrove-forming elements, such as the palm *Nypa* or the fern *Acrostichum,* are insufficient to support the occurrence of mangrove forests (Rull, 2022a).

3.2. Oligocene revolution

The newly assembled Caribbean database also allowed the identification of a major evolutionary shift that occurred in the Eocene/Oligocene transition, hereafter EOT (~34 Ma), characterized by the replacement of ancient *Pelliciera* mangroves by modern-like *Rhizophora* mangroves (Figure 1). *Rhizophora* (represented by the fossil pollen *Zonocostites ramonae*) was absent from the Neotropics during the Eocene (Graham, 1995) and reached the Caribbean region in the EOT, likely by trans-Atlantic dispersal from the IWP, where it originated (Takayama et al., 2021). Quantitative pollen records showed that the dominance shifted abruptly from *Pelliciera* to *Rhizophora* in the EOT, coinciding with global cooling and sea-level fall, along with an intense biotic turnover, although not as catastrophic as the Big Five mass extinctions, characterized by enhanced Eocene extinction and Oligocene radiation rates (Coxall & Pearson, 2007; Hutchinson et al., 2021). Noteworthy, *Nypa* disappeared from the EAP region during the EOT (Figure 1). This major community turnover did not signify the disappearance of *Pelliciera*, which remained a minor component of the new *Rhizophora* mangroves since the Oligocene and expanded its range to the whole Neotropcis in the Miocene, always as a subordinate component represented by small and diffuse populations (Rull, 2023b). It has been suggested that the continuity and further expansion of *Pelliciera*, a stenothermic taxon with low dispersal power, was facilitated by the protection offered by *Rhizophora*, a more eurthermic and vagile element, whose canopy would have created a microhabitat for the first to endure the new less favorable environments created by the EOT global disruption, as occurs today (Dangremond et al., 2015). After the Miocene, *Pelliciera* underwent a significant reduction in its range to an area similar to the Middle Eocene equatorial distribution, which led to its present-day residual distribution (Rull, 2023b).

3.3. Neogene diversification

The main diversification trend of Caribbean mangroves occurred in the Neogene (Mio-Pliocene), when the remaining true mangrove elements (*Crenea*, *Avicennia*, *Laguncularia*) and most of the associated taxa (>20 genera) emerged (Rull, 2023a), thus conforming the present-day richness patterns (Figure 1). This represented a diversity increase of almost 80% with respect to the Paleogene (Eocene–Oligocene), when only half of the present-day true-mangrove elements (*Rhizophora, Pelliciera, Acrostichum*) were present. No extinctions have been recorded since the Miocene in Caribbean mangroves at the genus level (Graham, 1995). The potential influence of climatic and sea-level fluctuations on the Neogene-Quaternary diversification trend (NQDT) remains unclear.

4. Paleoecology

4.1. Pleistocene reorganization

A significant gap exists in the Caribbean mangrove record for most of the Pleistocene (the last 2.6 Ma), the oldest records dating from ~130,000 years before present (yr BP), which corresponds to the Eemian Interglacial or the Marine Isotopic Stage (MIS) 5e, occurred just before the Last Glaciation (Weichselian). This has been attributed to the lack of full Pleistocene records for the Caribbean region, and the need for developing extensive coring campaigns, especially in marine environments, has been emphasized (Rull, 2022b). In the Caribbean, the Eemian interstadial was characterized by sea-surface temperatures (SST) a few degrees above the present ones and sea levels at least 3 m (maximum estimates of 20 m) higher than today. During the Last Glacial Maximum (LGM), which occurred ~21,000 yr BP, SSTs were 2-4 °C lower than today, and sea levels were up to 120 m below their present position (Schmidt et al., 2006; Hearthy et al., 2007). The extrapolation of these trends to former Pleistocene glacial-interglacial cycles suggests that full Pleistocene records should be sought in deep (>120 m) marine environments beyond the present continental shelf, where the Caribbean coasts were located during glacial maxima. Otherwise, glacial records would be lost due to coastal erosion. The available records suggest that all extant mangrove elements (true and associate) were already present at the beginning of the Pleistocene, and this period was characterized by spatial and

community reorganization driven by climatic and eustatic fluctuations (Rull, 2022b), but more studies are needed to test this hypothesis.

4.2. Holocene anthropization

A new external environmental driver, anthropogenic pressure, was added in the Holocene. Although Paleoindian settlements as old as ~13,000 yr BP (Lateglacial) are known for the southern Caribbean coasts (Bryan et al., 1978), the first significant disturbances on mangrove ecosystems did not occur until the Middle Holocene (~6000 yr BP), when Mesoamerican Maya societies cleared these forests using fire, mainly for maize and squash cultivation (Neff et al., 2006; López-Angarita et al., 2016). The Greater and Lesser Antilles (Figure 1) were colonized by humans between approximately 6000 and 2000 yr BP (Napolitano et al., 2019), and therefore, mangrove disturbance was posterior. Superimposed on the growing Holocene human influence were the maintained temperature and sea level increases and the nondirectional moisture variability (Figure 1), along with the corresponding feedbacks and synergies among these drivers (Rull, 2020b). Rising sea levels were a major influence on mangrove communities, which responded in different ways, according to the particular features of each locality. The balance between sediment input from the continent and sea-level rise seems to have been crucial for mangrove dynamics. When this balance was biased toward continental terrigenous input, coastal progradation overcame sea-leevel rising and favored seaward mangrove migration of mangrove communities. Conversely, when sea-level rise was dominant, landward migration was favored. Regional moisture declines and increases in drought frequency/intensity were especially important during the Late Holocene, causing significant mangrove reductions by salinity stress caused by increasing evaporation and reduced freshwater input from the continent (Rull, 2022b). Human disturbance has grown during the last millennia, as shown in paleoecological records documenting increased mangrove deforestation for wood extraction, fisheries, coconut plantations and rice crops (González et al., 2010; Urrego et al., 2019).

5. Historical decline

In recent decades, the Caribbean mangrove extent has been drastically reduced by natural and anthropogenic deforestation. According to the most updated data, the total mangrove cover of this region dropped from ~21,000 km² in 1980 to ~14,000 km² in 2010 (Table 3). This represents a one-third reduction in three decades, at an average rate of >2300 km² per decade. If these deforestation rates were maintained, the Caribbean mangroves would totally disappear within the next 60 years. Warming and aridification driven by ongoing anthropogenic climate change, along with the associated acceleration of sea-level rise, can aggravate the situation and exacerbate mangrove loss in the Caribbean and the Neotropics, in general (Ellison & Farnsworth, 1996, Godoy & Lacerda, 2015). In addition to removal, fragmentation is also a threat for Caribbean mangroves, as it increases exposure to environmental stresses and reduces the capacity of these ecosystems to provide ecological services such as coastal protection and carbon sequestration (Bryan-Brown et al., 2020).

Table 2. Mangrove extent (km²) by country/island in the Caribbean region, comparing the most updated estimates (2010) with those of 1980 (Rull, 2022b). Country/island codes correspond to Figure 2.

Country/island	Code	1980 (FAO, 2007)	2010 (Bunting et al., 2022)
Anguilla (UK)	An	0.90	1.00
Antigua & Barbuda	AB	15.70	8.63
Aruba	Ar	4.20	0.26
Barbados	Bd	0.30	0.14
Belize	Bz	785.00	445.07
Cayman Islands (UK)	Cy	10.10	41.48
Colombia	Co	4400.00	2622.12
Costa Rica	CR	634.00	364.75
Cuba	Cu	5374.00	3328.16

Dominican Republic	DR	344.00	187.41
El Salvador	ES	467.00	375.89
Grenada	Gr	2.95	1.90
Guadeloupe (France)	Gp	30.00	37.13
Guatemala	Gu	186.00	235.23
Guyana	Gy	910.00	286.40
Haiti	Ht	178.00	144.32
Honduras	Ho	1525.00	597.32
Jamaica	Ja	120.00	94.11
Martinique (France)	Mr	19.00	20.52
Nicaragua	Ni	1034.00	739.88
Panama	Pa	2500.00	1533.37
Puerto Rico	PR	76.50	86.85
Saint Kitts & Nevis	SK	0.85	0.28
Saint Lucia	SL	2.00	16.40
Saint Vincent & The Grenadines	VG	0.55	0.31
Trinidad & Tobago	TT	75.00	76.96
Venezuela	Ve	2600.00	2753.25
Virgin Islands (US and UK)	VI	10.10	20.53
Caribbean Total		**21,295.05**	**13,999.14**

6. Conservation insights

It is often said that what evolution has taken millions of years to develop might be lost in just centuries. In the case of Caribbean mangroves, this assessment may be quantified, as these ecosystems originated ~50 million years ago and, if current loss rates are maintained, they may disappear in barely half a century. Given the importance of mangroves for terrestrial and marine biodiversity and ecology, as well as for climate change mitigation, the preservation of these ecosystems has been considered a priority in the Caribbean region and a number of local and regional conservation and restoration initiatives have been undertaken that have contributed to alleviate the situation, although they have been insufficient to revert the regional trend toward mangrove loss and fragmentation (Barker, 2002; Polidoro et al., 2010; Lacerda et al., 2019; Bryan-Brown et al., 2020; Grimm et al., 2022; Walker et al., 2022). According to Lacerda et al. (2019), regional assessments and politically coordinated initiatives including the Latin America and Caribbean (LAC) mangrove-bearing countries are fundamental for mangrove conservation and sustainable use. In this framework, empirically-based ecological knowledge is essential for establishing the suitable conservation and restoration baselines. Part of this knowledge may emerge from past paleoecological and evolutionary studies like those summarized above. The below points could contribute to set suitable and realistic conservation/restoration targets and to guarantee their success.

6.1. Evolutionary hints

The Caribbean mangroves were dominated by single mangrove-forming tree species for tens of million years – during the Mid-Late Eocene, when *Pelliciera* was the dominant tree, and the Oligocene/Early Miocene, under the dominion of *Rhizophora*. The remaining structural mangrove trees, *Avicennia* and *Laguncularia*, did not appear until the Middle and Late Miocene, respectively. This means that preserving the dominant species would be enough to guarantee the continuity of mangroves, as communities, and the preservation and/or restoration of other species may be addressed gradually. An important lesson of the fossil record is that ecological communities do not emerge instantaneously as a whole but by progressive enrichment due to evolutionary innovations and community assembly. Any new species successfully incorporates to the community when the ecological conditions are suitable for them. This would especially useful in restoration practices

where the short-term reconstruction of a whole community is difficult or unfeasible and the reproduction of the natural process of community assembly would seem more suitable.

Long-term range expansions and contractions may also be informative for conservation purposes. A characteristic example is that of *Pelliciera*, which dominated the primeval Eocene mangroves and today is endemic of a small relict equatorial patch. The long-term range shifts of this taxon have been considered to be an example of taxon cycle (Wilson, 1961), characterized by an expansion from its original equatorial range (Eocene) to the whole Neotropics (Miocene) and a further contraction to its extant area of distribution. According to the taxon cycle predictions, *Pelliciera* could be in its last steps before natural extinction (Rull, 2023b), which could be accelerated by current urban expansion (Blanco-Libreros et al., 2021). Currently, this species is listed as "Vulnerable" in the IUCN Red List of Threatened Species (Polidoro et al., 2010) but it has been suggested that it could be transferred to the "Critically Endangered" category if the predictions of the taxon cycle are considered (Rull, 2023b).

6.2. Paleoecological contributions

Another clue identified in Quaternary studies is the importance of the balance between sedimentation and sea-level shifts, which controls coastal dynamics, with the corresponding lateral mangrove migrations and spatial ecological reorganizations. This point is especially important today, as the Caribbean sea level is rising at rates of 1.8-2.5 mm per year (Palanisamy et al., 2012; Torres & Tsimplis, 2013). In these conditions, in situ mangrove conservation is largely dependent on sedimentation, which is a function of climate and the features of the local fluvial network. As climate cannot be managed, conservation actions should focus on the maintenance of a regular sediment supply able to overcome sea-level rising. This would be especially important in arid climates and areas with insufficient drainage, which might require engineering solutions. Local records of mangrove colonization or degradation under rising or falling sea levels may also be useful to identify the species involved in each successional stage, which can inform restoration practices.

Paleoecological and evolutionary studies also provide evidence-based past analogs to assess the effects of climatic changes on mangrove communities. This study can be addressed regionally or locally. At a regional level, the Caribbean mangroves have been sensitive to long-term temperature and moisture variations but this is hardly applicable to specific conservation problems, as is more dependent on worldwide policies to mitigate the ongoing anthropogenic global warming. At a local level, studies on particular mangrove communities and their response to climatic shifts are highly informative, as they provide site-specific responses to temperature and hydrological balance shifts. These responses could be used as straightforward inputs for forecasting possible future developments or may be incorporated into more general predictive models of regional, continental or global scope, in the search for potential regularities (Anderson et al., 2006). Numerous examples of particular case studies dealing with mangrove responses to climatic and sea-level shifts can be found in the above-quoted database (Figure 2 and Supplementary Material).

6.3. Anthropogenic pressure

Paleoecological records of anthropization processes are usual for the Mid-Late Holocene, especially for the last centuries. Human activities affecting the Caribbean mangroves may be local and direct (deforestation) or general and indirect (global warming, sea-level rise). The most effective conservation measures are legislation (including the creation of protected areas) and restoration, which are of more local scope, as well as general policies of global change mitigation. Once more, local assessments and actions may benefit from the known history of each particular site in relation to human disturbance, whereas global initiatives may be able to found past analogs in long-term paleoecological and evolutionary studies, along with global paleoecological databases.

7. Conclusions

The conservation of Caribbean mangroves may benefit from paleoecological and evolutionary studies, which have shown the influence of environmental drivers such as paleogeographical shifts, climate changes, sea-level fluctuations and anthropogenic pressure on the biodiversity, biogeography, ecology and evolution of these ecosystems. The lessons learned from these studies may be useful to inform conservation and restoration actions, as they provide evidence-based past analogs that can be incorporated into predictive models aimed at forecasting the responses of these communities to future environmental changes. The availability of a newly assembled and updated database encompassing virtually all the paleoecological and evolutionary studies developed to date on Caribbean mangroves provides an advantage with respect to other mangrove-bearing tropical/subtropical areas that should not be neglected. It is hoped that contributions such as the present will help raise awareness of the importance of past records for conservation and restoration purposes.

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