Essay

Rise and Fall of Caribbean Mangroves

Valenti Rull [*]

Keywords: Caribbean; mangroves; evolution; paleoecology; climate; sea level; anthropization; conservation

Essay

Rise and Fall of Caribbean Mangroves

Valentí Rull

1   Spanish National Research Council (CSIC), 08038 Barcelona, Spain; vrull@csic.es
2   Catalan Institute of Paleontology (ICP), 08193 Cerdanyola del Vallès, Spain

Abstract: Mangrove forests, which are essential for the maintenance of terrestrial and marine biodiversity on 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 biodiversity 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 reorganization 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 recent decades, deforestation has significantly reduced Caribbean mangrove cover and it has been estimated that, if urgent and effective conservation actions are not undertaken, these 50 million-year-old ecosystems might disappear in a few centuries. 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 continental fringe along the tropical/subtropical coasts (Figure 1), which marks the extent of normal (semidiurnal) tides. Mangrove forests protect coasts and other coastal ecosystems 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 ecosystem 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; Macreadie et al., 2021; Fest et al., 2022). Globally, mangrove forests have been considered to be among the world's most threatened ecosystems (Worthington et al., 2020). According to the latest estimates, the global mangrove extent was reduced by 3.4% in less than three decades (1996-2020) 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 their long-term survival is at great risk (Duke et al., 2007). However, other authors, enrolled in the so-called Conservation Optimism movement, consider these predictions to be too catastrophic (Friess et al., 2020).
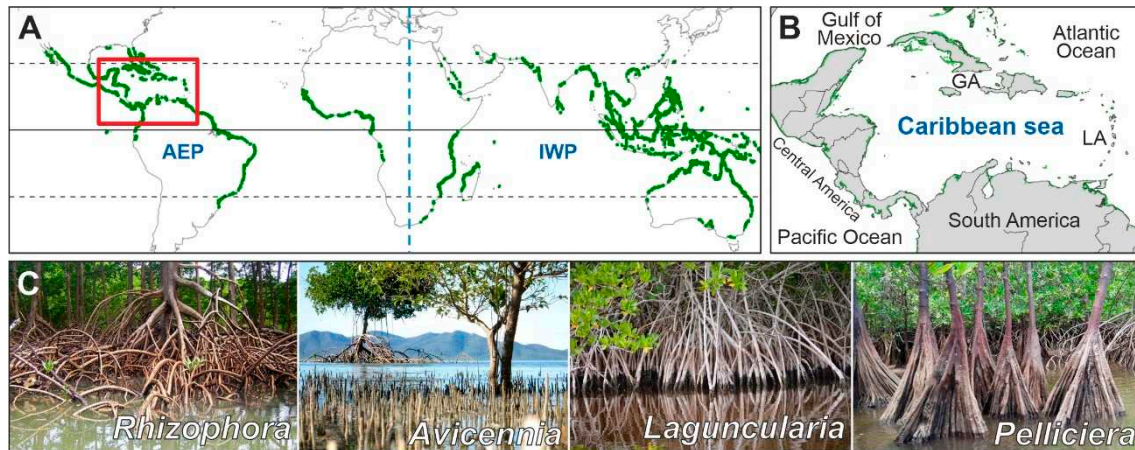
Figure 1. Present patterns of Caribbean mangroves. (**A**) Worldwide mangrove distribution (green patches) (Spalding et al., 2010) and the two main biogeographical regions (AEP, Atlantic-East Pacific; IWP, Indo-West Pacific). The location of the Caribbean region is indicated by a red box. (**B**) The Caribbean region, as considered in this study (GA, Greater Antilles; LA, Lesser Antilles). (**C**) The main genera of mangrove-forming trees (Rull, 2022a, b).

The Neotropical Caribbean region is one of the main mangrove biodiversity hotspots (Duke, 2017; Bryan-Brown et al., 2020; Goldberg 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.

The central tenet of this discussion is that paleoecological and evolutionary background on how extant ecosystems have been shaped is useful to inform biodiversity and ecosystem conservation by providing past analogs on the ecological responses to external environmental drivers such as paleogeographical, climatic, eustatic and anthropogenic shifts. Knowing these biotic responses may be important to forecast potential future ecosystem developments under increasing natural and anthropogenic stress, as prognosticated by current global change estimates (IPCC, 2022). In this way, conservation and restoration programs may benefit from past empirical evidence to optimize their outputs (Willis et al., 2010). The usefulness of this paleostrategy to the Neotropics was extensively discussed by Vegas-Vilarrúbia et al., (2011), and this discussion illustrates how it can be applied to a particular example, mangroves, for which fairly complete paleoecological and evolutionary information exists after the author's compilation mentioned above. This discussion builds on previous author's reviews summarized in sections 3 and 4 as sources for paleoecological and evolutionary information, and combines this past background with the current state of Caribbean mangroves (section 2) and their recent deforestation trends affected by both natural and anthropogenic drivers (section 5) to extract lessons that may inform mangrove conservation and restoration (section 6).
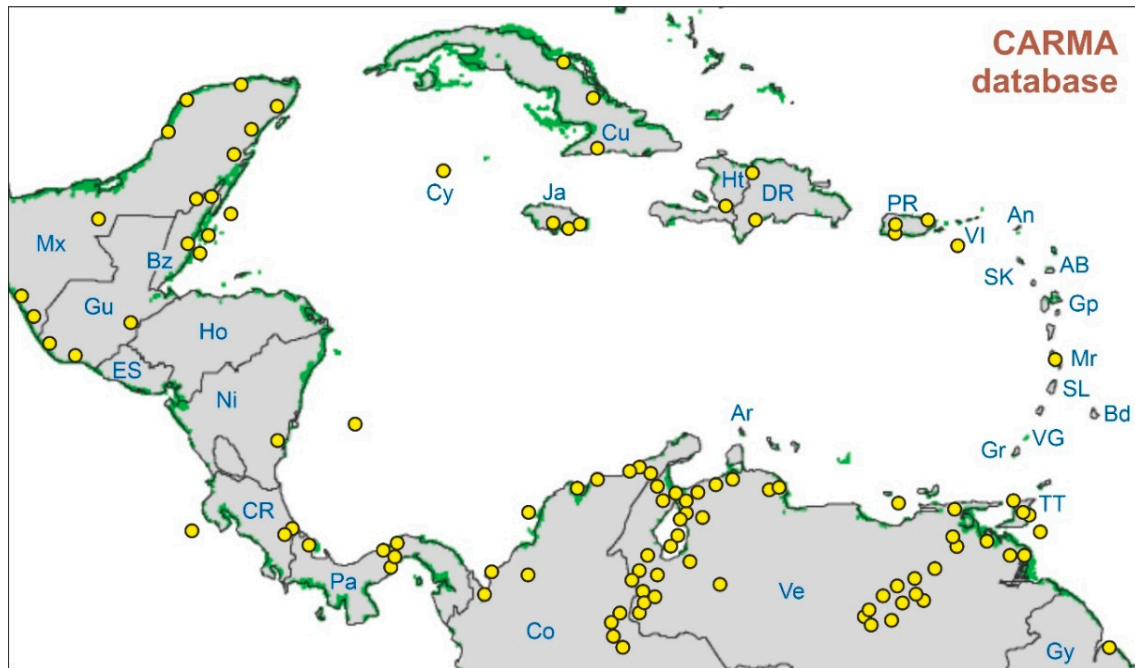
Figure 2. Sketch-map indicating the location of the study sites compiled in the CARMA (CARibbean MAngroves) database (yellow dots). In a number of cases, a dot corresponds to more than one site (see the Supplementary Material for details and references). Present-day mangroves are indicated by green patches (Spalding et al., 2010). AB, Antigua & Barbuda; An, Anguilla; Ar, Aruba; Bd, Barbados; Bz, Belize; Co, Colombia; CR, Costa Rica; Cy, Cayman Islands;   Cu, Cuba; DR, Dominican Republic; ES, El Salvador; Gr, Grenada; Gp, Guadeloupe; Gu, Guatemala; Gy, Guyana; Ho, Honduras; Ht, Haiti; Ja, Jamaica; Mr, Martinique; Mx, Mexico; Ni, Nicaragua; Pa, Panama; PR, Puerto Rico; SK, Saint Kitts & Nevis; SL, Saint Lucia; TT, Trinidad & Tobago; Ve, Venezuela; VG, Saint Vincent & The Grenadines; VI, Virgin Islands.

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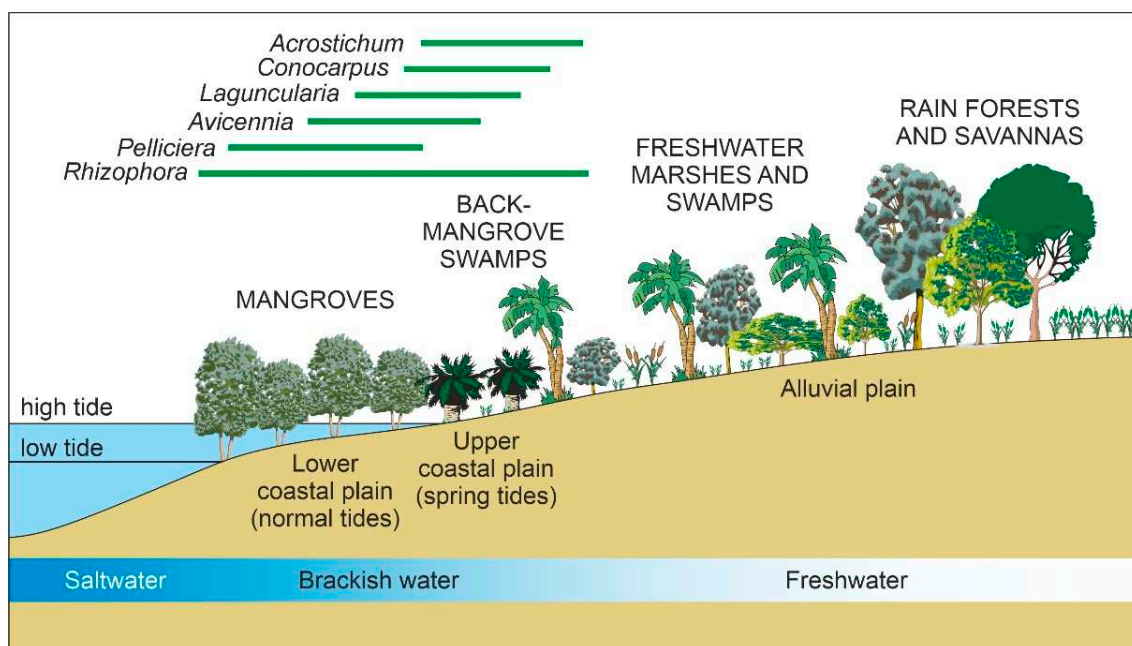
Figure 3. Idealized transect showing the typical coastal zonation of Caribbean mangroves. The approximate ranges of the most important mangrove elements are indicated. After Rull (2022a).

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*) (Figure 4). 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).
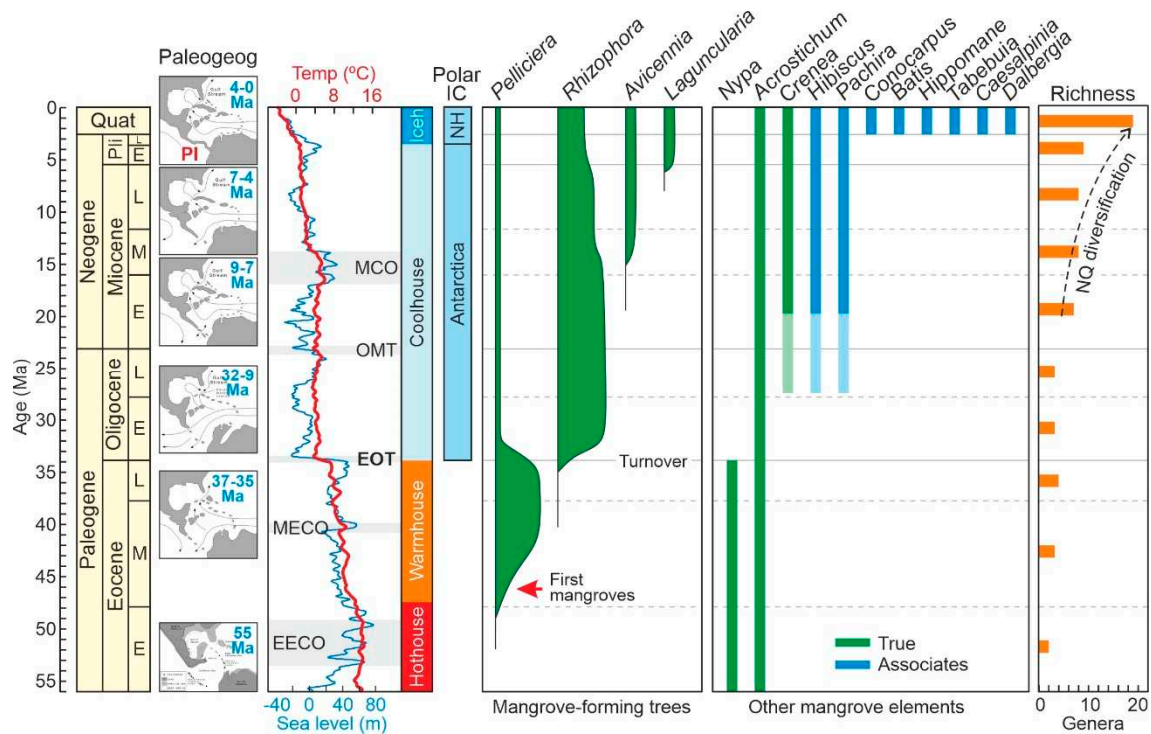
Figure 4. Paleogene and Neogene evolution of Caribbean mangroves (Rull, 2022a, c, 2023a) in relation to paleographic (Iturralde-Vinent, 2006), paleoclimatic (Westerhold et al., 2020) and paleoeustatic (Miller et al., 2020) shifts. Chronology: Quat, Quaternary; Pli, Pliocene; E, Early; M. Middle; L, Late. 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.

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 4). *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 4). 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 eurythermic taxon with greater dispersal power, 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 4). 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). These records are from the Pacific coasts of present-day Mexico and Guatemala (Figure 2), and therefore, they fall outside the Caribbean region sensu stricto. However, they have been included in the CARMA database because of their importance in the history of anthropogenic mangrove disturbance and because they were the most likely place of origin of the cultures that participated in the first wave of colonization of the Caribbean islands (review in Rull, 2022b). 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 5), 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-level rise 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).
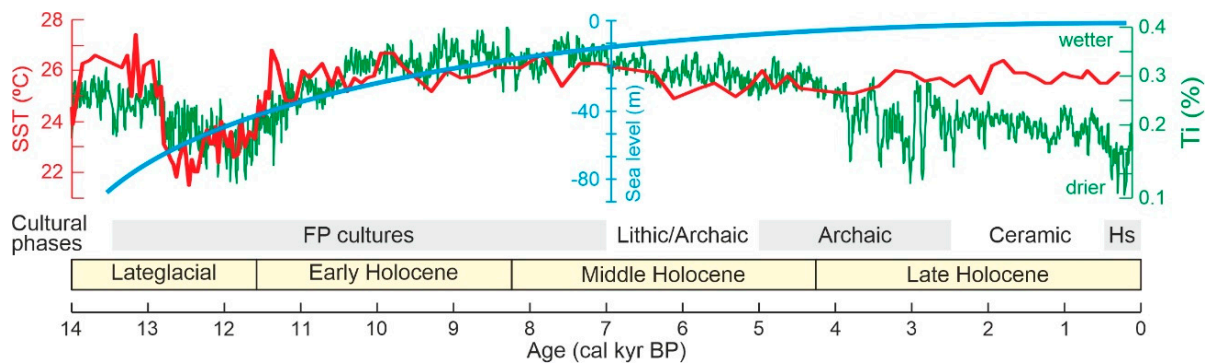
Figure 5. Holocene paleoclimatic (Haug et al., 2002, Lea et al., 2003), paleoeustatic (Khan et al., 2017) and cultural trends and events (Rull, 2022b). SST, Sea Surface Temperature; Ti, Titaniun concentration as a moisture proxy.

5. Recent Decline and Near-Future Projections

In recent decades, the Caribbean mangrove extent has been significantly reduced by natural and anthropogenic deforestation. According to the most updated data, from the Global Mangrove Watch, the total mangrove cover of this region dropped from 6545.1 km² in 1996 to 6031.3 km² in 2020 (Bunting et al., 2022). This represents a reduction of 7.9% in a couple of decades (24 years), at an average rate of 21.4 km² (0.33%) per year. If these deforestation rates were maintained, which is not guaranteed, the Caribbean mangroves would totally disappear within the next three centuries (303 years). A number of studies exist on this potential mangrove reduction for specific Caribbean areas – e.g., Central America (Tuhilske et al., 2017), South America (Daza et al., 2020) or the Antilles (Fitzpatrick et al., 2021) – that may be useful for local/regional conservation planning. 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). This could be compensated by protection measures and the fact that deforestation drivers change as economies change.

Current global change estimates for the Caribbean region predict a warming of 1–3.5 °C by the end of this century in both land and sea environments, with the highest warming rates in terrestrial settings, along with an increased frequency of temperature extremes. Additionally, a moderate drying trend consisting of a 20–30% reduction in rainfall will likely occur, accompanied by increases in heavy rainfall events and in the number of consecutive hot and dry days (Campbell et al., 2011; Stenneth-Brown et al., 2017; Taylor et al., 2018). It is estimated that storms and hurricanes will also increase in frequency and intensity, as predicted by global projections. Regarding sea levels, Caribbean forecasts are also in agreement with global estimates of a 0.4–0.6 m increase relative to 1986–2005, although a few studies suggest that increases above 1 m should not be disregarded (Rahmstorf, 2007; Perrette et al., 2013). In addition to a multitude of human affairs, these events may impact terrestrial and marine ecosystems, and biodiversity. For example, increasing temperatures may foster coral bleaching, promote blooms of invasive species, or favor the northern migration of Caribbean fish and coral reefs. Decreasing rainfall may affect patterns of seed production,

germination survival and development, thus increasing seedling mortality. Increased flood, storm and hurricane frequency may enhance the degradation of coastal wetlands and forests (notably mangroves), and reduce their natural filtering and buffering capacity. This may enhance habitat loss and contribute to the degradation of other ecosystems, such as coral reefs, ultimately leading to biodiversity depletion. Sea-level rise may also affect mangroves by promoting their landward migration of coastal ecosystems and enhancing coastal erosion.

Hurricanes, or tropical cyclones, are among the most destructive natural hazards affecting mangroves, especially in the Caribbean region, where a significant activity increase has been observed since 1995 (Webster et al., 2005; Palmieri et al., 2006; Burgess et al., 2018). Some mangrove-rich parts of the Caribbean region (e.g., Mexico and Cuba) are especially prone to the action of hurricanes, whereas others (e.g., South America) are rarely affected. Tropical cyclones affect mangrove forests mainly by increasing tree mortality, changing forest structure and spatial distribution, and modifying biogeochemical cycles (review in Krauss & Osland, 2020). The influence of hurricanes on mangroves depends on storm characteristics, geomorphic location and structural features of the affected forests, as well as on regeneration ability before the storm, which is linked to seed and propagule dispersal potential, nutrient conditions and ecophysiological properties of the involved species. Mangroves show relatively high resilience to hurricane activity, and regeneration is common, although the output of postcyclonic secondary succession may be different from the original forest composition, which enhances spatial heterogeneity. The expected consequences of the ongoing global change in tropical cyclones include increases in the frequency of the most intense events, in the amount of rainfall near the cyclone center and in the poleward distribution of hurricanes. As a consequence, cyclones will likely amplify their effects on several regions, including the Caribbean. In addition, fragmentation caused by anthropogenic activities will likely affect the capacity of mangrove regeneration (Krauss & Osland, 2020).

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 a few centuries. 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 alleviating 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 suitable conservation and restoration baselines. Part of this knowledge may emerge from past paleoecological and evolutionary studies such as those summarized above. The points below could contribute to set suitable and realistic conservation/restoration targets and to guaranteeing 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 into the community when the ecological conditions are suitable for them. This would be 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 to a small relict equatorial patch. The long-term range shifts of this taxon have been considered to be an example of the 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 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). Under 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 rise. 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, Caribbean mangroves have been sensitive to long-term temperature and moisture variations but this is hardly applicable to specific conservation problems, as it is more dependent on worldwide policies to mitigate 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 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 find past analogs in long-term paleoecological and evolutionary studies, along with global paleoecological databases.

Anthropogenic pressure is added to the action of natural forces and sometimes both are into play in a synergistic fashion. One of the main aims of paleoecological research applied to global

change study is to disentangle natural and human drivers by studying past times when human impact was absent or negligible and natural agents were dominant (Willis et al., 2010; Vegas-Vilarrúbia et al., 2011). In our case, preanthropic times could have been identified, and therefore, this allowed the attribution of mangrove shifts to the action of paleogeographic, climatic and eustatic drivers. This is a significant output per se that may be informative for mangrove protection, as discussed in the above sections. These factors, especially climatic and eustatic shifts, continued to be present before the anthropization of the Caribbean region and can be identified in past records by correlating mangrove shifts with evidence for climatic and/or sea-level shifts, in the absence of anthropogenic indicators, notably cultivated plants and charcoal, as a proxy for human-lighted fires. The reverse is also true and the predominance of human over natural drivers of mangrove change may be deduced from the occurrence of anthropogenic proxies in the absence of significant environmental change. When mangrove shifts coincide with evidence for both natural and anthropogenic agents, the possibility of synergistic actions and amplification feedbacks should be considered. An example is the combination of anthropogenic fires and arid climates, which may lead to nonlinear responses resulting in an exacerbation of forest loss.

In summary, the incoming of human agency is not a constraint for past records to produce useful ecological information. On the contrary, it may contribute not only to separating the effects of environmental and anthropogenic drivers, but also to identifying potential feedbacks and synergies that may be useful for prognosticating future developments. In addition, past records, whatever their nature, are evidence-based records of long-term ecological processes that are unattainable from present day ecological studies.

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.

Acknowledgments: This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. The comments and suggestions by two of the three anonymous reviewers are appreciated, as they greatly contributed to the improvement of the manuscript.

References

Anderson, H.J., Bugmann, H., Dearing, J.A., Gaillard, M.-J. 2006. Linking palaeoenvironmental data and models to understand the past and to predict the future. Trends Ecol. Evol. 21, 696-704.

Barker, D.R. 2002. Biodiversity conservation in the wider Caribbean region. Rev. Europ. Comp. Int. Environ. Law 11, 1.

Blanco-Libreros, J.F., Ramírez-Ruiz, K. 2021. Threatened mangroves in the Anthropocene: habitat fragmentation in urban coastalscapes of *Pelliciera* spp. (Tetrameristaceae) in northern South America. Front. Mar. Sci. 8, 670354.

Bryan, A.L., Casamiquela, R.M., Cruxent, J.M., Gruhn, R., Ochsenius, C. 1978. A El Jobo mastodon kill at Taima-taima, Venezuela. Science 200, 1275–1277.

Bryan-Brown, D.N., Connolly, R.M., Richards, D.R., Adame, F., Friess, D.A., Brown, C.J. 2020. Global trends in mangrove forest fragmentation. Sci. Rep. 10, 7117.

Bunting, P., Rosenqvist, A., Hilarides, L., Lucas, R.M., Thomas, N., et al., 2022. Global mangrove extent change 1996-2020: Global Mangrove Watch version 3.0. Remote Sens. 14, 3657.

Burgess, C., Taylor, M., Spencer, N., Jones, J., Stephenson, T. 2018. Estimating damages from climate related natural disasters for the Caribbean at 1.5 °C and 2 °C global warming above preindustrial levels. Reg. Environ. Change 18, 2297–2312.

Campbell, J.D., Taylor, M.A., Stephenson, T.S., Watson, R.A., Whyte, F.S. 2011. Future climate of the Caribbean from a regional climate model. Int. J. Climatol. 31, 1866–1878.

Coxall, H.K., Pearson, P.N. 2007. The Eocene–Oligocene transition. In: Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N. (Eds.), Deep-Time Perspectives on Climate Change: Marrrying the Signal from Computer Models and Biological Proxies. The Geological Society, London, pp. 351-387.

Dangremond, E.M., Feller, J.C., Souza, W.P. 2015. Environmental tolerance of rare and common mangroves along light and salinity gradients. Oecologia 179, 1187-1198.

Daza, D.A.V., Sánchez, H., Portz, L., Portantiolo, R., Bolívar-Anillo, H.J., Anfus, G. 2020. Mangrove forests evolution and threats in the caribbean sea of Colombia. Water 12, 1113.

Duke, N.C. 2017. Mangrove floristics and biogeography revisited: further deductions from biodiversity hot spots, ancestral discontinuities and common evolutionary processes. In: Rivera-Monroy, V.H., Lee, S.Y., Kristensen, E., Twilley, R.R. (Eds.), Mangrove Ecosystems: a Global Biogeographic Perspective. Springer, Cham, pp. 17-53.

Duke, N.C. 2020. A systematic revision of the vulnerable mangrove genus Pelliciera (Tetrameristaceae) in equatorial America. Blumea 65, 107-120.

Duke, N.C., Meyneccke, J.-O., Dittman, S., Ellison, A.M., Anger, K., Berger, U., et al., 2007. A world without mangroves? Science 317, 41b-42b.

Ellison, A.M., Farnswworth, E.J. 1996. Anthropogenic disturbance of Caribbean mangrove ecosystems: past impacts, present trends, and future predictions. Biotropica 28, 549-565.

Fest, B.J., Swearer, S.E., Arndy, S.K. 2022. A review of sediment carbon sampling methods in mangroves and their broader impacts on stock estimates for blue carbon ecosystems. Sci. Total Environ. 816, 151618.

Fitzpatrick, S.M., Glovas, C.M. 2021. Tropical islands of the Anthropocene: deep histories and anthropogenic terrestrial-marine entanglemnt in the Pacific and the caribbean. Proc. Natl. Acad. Sci. USA 27, e202209118.

Friess, D.A., Yando, E.S., Abuchahla, G.M.O., Adams, J.B., Cannicci, S., Canty, S.W.J., et al., 2020. Mangroves give cause for conservation optimism, for now. Curr. Biol. 30, R153-R154.

Godoy, M.D.P., Lacerda, L.D. 2015. Mangrove responses to climate change: a review of recent findings on mangrove extension and distribution. Ann. Acad. Bras. Ciên. 87, 651-667.

Goldberg, L., Lagomasino, D., Thomas, N., Fatoyinbo, T. 2020. Global declines in human-driven mangrove loss. Glob. Change Biol. 26, 5844-5855.

González, C., Urrego, L.E., Martínez, J.I., Polanía, J, Yokohama, Y. 2010. Mangrove dynamics in the southwestern Caribbean since the 'Little Ice Age': A history of human and natural disturbances. Holocene 20, 849–861.

Graham, A. 1995. Diversification of Caribbean/Gulf mangrove communities through Cenozoic time. Biotropica 27, 20-27.

Grimm, K.E., Archibald, J.L., Axelsson, E.P., Grady, K.C. 2022. Follow the money: understanding the Latin America and Caribbean mangrove restoration funding landscape to assist organizations and funders in improved social-ecological aoutcomes. Cons. Sci. Pract., doi 10.1111/csp2.12815.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C., Röhl, U. 2001. Southward migration of the Intertropical Convergence Zone through the Holocene. Science 293, 1304–1308.

Hearthy, P.J., Hollin, J.T., Neumann, A.C., O'Leary, M.J., McCulloch, M. 2007. Global sea-level fluctuations during the Last Interglaciation (MIS 5e). Quat. Sci. Rev. 26, 2090–2112.

Hutchinson, D.K., Coxall, H.K., Lunt, D.J., Steinthorsdottir, M., de Boer, A.M., Baatsen, M., et al., 2021. The Eocene–Oligocene transition: a review of marine and terrestrial proxy data, models and model-data comparisons. Clim. Past 17, 269-315.

IPCC. 2022. Climate Change 2022: Impacts, Adaptation and Vulnerability. Cambridge University Press, Cambridge.

Iturralde-Vinent, M.A. 2006. Meso-Cenozoic Caribbean paleogeography: implications for the historical biogeography of the region. Int. Geol. Rev. 48, 791-827.

Khan, N.S., Ashe, E., Horton, B.P., Dutton, A., Kopp, R.E., Bocard, G., et al., 2017. Drivers of Holocene sea-level change in the Caribbean. Quat. Sci. Rev. 155, 13–36.

Krauss, K., Osland, M.J. 2020. Tropical cyclones and the organization of mangrove forests: a review. Ann. Bot. 125, 213-234.

Lacerda, L.D., Borges, R., Ferreira, A.C. 2019. Neotropical mangroves: conservation and sustainable use in a scenario of global climatic change. Aquat. Cons. 29, 1347-1364.

Laegdsgaard, P., Johnson, C. 2001. Why do juvenile fish utilize mangrove habitats? J. Exp. Mar. Biol. Ecol. 257, 229-253.

Lea, D.W., Pak, D.K., Peterson, L.C., Hughen, K.A. 2003. Synchroneity of tropical and high-latitude Atlantic temperatures over the Last Glacial Termination. Science 301, 1361–1364.

López-Angarita, J., Roberts, C.M., Tilley, A., Hawkins, J.P., Cooke, R.G. 2016. Mangroves and people: lessons from a history of use and abuse in four Latin American countries. Forest Ecol. Manag. 368, 1151-162.

Macreadie, P.I., Costa, M.D.P., Atwood, T.B., Friess, D.A., Kelleway, J.J., Kennedy, H., et al., 2021. Blue carbon as a natural climate solution. Nature Rev. 2, 826-839.

Mcleod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., et al., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Front. Ecol. Environ. 9, 552-560.

Miller, K.G., Browning, J.V., Schmetz, W.J., Kopp, R.E., Mountain, G.S., Wright, J.D. 2020. Cenozoic sea level and chryospheric evolution from deep-sea geochemical and continental margin records. Sci. Adv. 6, eaaz1346.

Nagelkerken, I., Blaver, S.J.N., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., et al., 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. Aquat. Bot. 89, 155-185.

Napolitano, M.F., DiNapoli, R., Stone, J.H., Levin, M.J., Jew, N.P., Lane, B.G., et al., 2019. Reevaluating human colonization of the Caribbean using chronometric hygiene and Bayesian modeling. Sci. Adv. 5, eaar7806.

Neff, H., Pearsall, D.M., Jones, J.G., Arroyo, B., Collins, S.K., Freidel, D.E. 2006. Early Maya adaptive patterns: Mid-Late Holocene paleoenvironmental evidence from Pacific Guatemala. Lat. Am. Antiq. 17, 287–315.

Nellemann, C., Corcoran, E., Duarte, C., Valdés, L., De Young, C., Fonseca, L., et al., 2009. Blue Carbon. A Rapid Response Assessment. UNEP, GRID-Arendal.

Palanisamy, H., Becker, M., Meyssignac, B., Henry, O., Cazenave, A. 2012. A regional sea level change and variability in the Caribbean Sea since 1950. J. Geodet. Sci. 2, 125-133.

Palmieri, S., Teodonio, L., Siani, A.-M., Casale, G.R. 2006. Tropical storm impact in Central America. Meteorol. Appl. 13, 21–28.

Perrette, M., Launderer, F., Riva, R., Frieler, K., Meinshausen, M.A. 2013. Scaling approach to project regional sea level rise and its uncertainties. Earth Syst. Dyn. 4, 11–29.

Polidoro, B.A., Carpenter, K.E., Collins, L., Duke, N.D., Ellison, A.M., Ellison, J.C., et al., 2010. The loss of species: mangrove extinction risk and geographic areas of global concern. PLoS ONE 5, e10095.

Rahmstorf, S. 2007. A semi-empirical approach to projecting future sea level rise. Science 315, 368–370.

Rull, V. 2022a. The Caribbean mangroves: an Eocene innovation with no Cretaceous precursors. Earth-Sci. Rev. 231, 104070.

Rull, V. 2022b. Responses of Caribbean mangroves to Quaternary climatic, eustatic and anthropogenic drivers of ecological change: a review. Plants 11, 3502.

Rull, V. 2022c. Eocene/Oligocene global disruption and the revolution of Caribbean mangroves. EarthArxiv, doi 10.31233/X5835T.

Rull, V. 2023a. The Neogene-Quaternary diversification trend in the shaping of Caribbean mangroves. Quat. Sci. Rev. 300, 107920.

Rull, V. 2023b. Taxon cycles in Neotropical mangroves. Plants 12, 244.

Saenger, P. 2002. Mangrove Ecology, Silviculture and Conservation. Dordrecht: Kluwer.

Schmidt, M.W., Vautravers, M.J., Spero, H.J. 2006. Western Caribbean sea surface temperatures during the late Quaternary. Geochem. Geophys. Geosys. 7, 2.

Spalding, M., Kainuma, M., Collins, L. 2010. Wolrd Atlas of Mangroves. London: Routledge.

Srivastava, J., Prasad, V. 2018. Evolution and paleobiogeography of mangroves. Mar. Ecol. 40, e12571.

Stennett-Brown, R.K., Jones, J.J., Stephenson, T.S., Taylor, M.A. 2017. Future Caribbean temperature and rainfall extremes from statistical downscaling. Int. J. Climatol. 2017, 37, 4828–4845.

Takayama, K., Tateishi, Y., Kaijita, T. 2021. Global biogeography of a pantropical mangrove genus Rhizophora. Sci. Rep. 11, 7228.

Taylor, M.A. Clarke, L.A., Centella, A., Bezanilla, A., Stephenson, T.S., Jones, J.J., et al., 2018. Future Caribbean climates in a world of rising temperatures: The 1.5 vs 2.0 dilemma. J. Clim. 31, 2907–2926.

Tomlinson, P.B. 2016. The Botany of Mangroves. Cambridge Univ. Press, Cambridge.

Torres, R.R., Tsimplis, N.M. 2013. Sea-level trends and interannual variability in the Caribbean Sea. J. Geophys. Res. 118, 2934-2947.

Tuholske, C., Tane, Z., López-Carr, D., Roberts, D., Cassels, S. 2017. Thirty years of land use/cover change in the caribbean: assessing the relationship between urbanization and mangrove loss in Roatán, Honduras. Appl. Geogr. 88, 84-93.

Urrego, L.E., Prado, M.A., Bernal, G., Galeano, A. 2019. Mangrove responses to droughts since the little ice age in the Colombian Caribbean. Est. Coast. Shelf Res. 230, 196432.

Vegas-Vilarrúbia, T., Rull, V., Montoya, E., Safont, E. 2011. Quaternary palaeoecology and nautre conservation: a general review with examples from the Neotropics. Quat. Sci. Rev. 30, 2361-2388.

Walker, J.E., Ankersen, T., Barchiesi, S., Meyer, C.K., Altieri, A.H., Osborne, T.Z., et al., 2022. Governance and the mangrove commons: advancing the cross-scale, nested framework for the global conservation and wise use of mangroves. J. Environ. Manag. 312, 114823.

Webster, P.J., Holland, G.J., Curry, J.A., Chang, H.-R. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. Science, 309, 1844–1846.

Westerhold, T., Marwan, N., Drury, A.J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J.S., et al., 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years. Science 369, 1383-1387.

Willis, K.J., Bailey, R.M., Bhagwat, S.A., Birjs, H.J.B. 2010. Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. Trends Ecol. Evol. 25, 583-591.

Worthington, T.A., zu Ermgassen, P.S.E., Fries, D.A., Krauss, K.W., Lovelock, C.E., Thorley, J., et al., 2020. A global biophysical typology of mangroves and its relevance for ecosystem structure and deforestation. Sci. Rep. 10, 15652.