REVIEW ARTICLE

Changes in Mangrove Blue Carbon under Elevated Atmospheric CO₂

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While there is consensus that blue carbon ecosystems, such as mangroves, have an important role in mitigating some aspects of global climate change, little is known about mangrove carbon cycling under elevated atmospheric CO_2 concentrations (eCO_2). Here, we review studies in order to identify pathways for how eCO_2 might influence mangrove ecosystem carbon cycling. In general, eCO_2 alters plant productivity, species community composition, carbon fluxes, and carbon deposition in ways that enhance mangrove carbon storage with eCO_2 . As a result, a negative feedback to climate change exists whereby eCO_2 adds to mangrove's ability to sequester additional carbon, which in turn reduces the rate by which CO_2 builds. Furthermore, eCO_2 affects warming and sea-level rise (SLR) through alternate pathways, which coinfluence the mangrove response in both antagonistic (i.e., warming = greater carbon loss to decomposition) and synergistic (i.e., SLR = greater soil carbon burial) ways. eCO_2 is projected to become a more prominent driver in the future before reaching a steady state. However, given the complexity of the interactions of biological and environmental factors with eCO_2 , long-term field observations and in situ simulation experiments can help to better understand the mechanisms for proper model initialization to predict future changes in mangrove carbon sequestration.

Introduction

Forests are known to be prominent drivers of Earth's climatic environment [1–3]. Forest-based natural climate solutions have experienced a growing interest in recent years as a potential major contributor to meeting nationally determined carbon targets set forth by the 2015 Paris Agreement [4]. "Blue carbon ecosystems" are of particular importance in this context because of their extraordinarily high carbon sequestration capacity per unit area. Established blue carbon ecosystems are mangrove forests, tidal marshes, and seagrass beds [5]. Mangroves are much better studied and are well known for their high carbon sequestration rate in both biomass and sediments. Therefore, the restoration and management of mangroves are recognized as a key potential and self-sustaining forest-based natural climate solution to mitigate global climate change [6,7]. In addition to carbon sequestration, mangrove communities provide critically important habitat and feeding grounds for a range of invertebrates, water birds, and fish as well as other ecosystem services, including coastal protection, filtration, and trapping of pollutants [8]. Mangroves are also sensitive to temperature change, elevated atmospheric CO_2 concentrations (eCO_2), sea-level rise (SLR), and extreme climatic events [9–11], in part because the rate of change that occurs in the coastal zone [12] is high and exacerbated by human activity.

Currently more focus is placed on the response of mangroves to atmospheric warming and SLR, but the cause of these 2 factors, namely eCO_2 , directly affects mangrove carbon cycling by increasing photosynthesis and influencing the allocation of carbon biomass to different plant and ecosystem pools. eCO_2

Citation: Gu X, Qiao P, Krauss KW, Lovelock CE, Adams JB, Chapman SK, Jennerjahn TC, Lin Q, Chen L. Review: Changes in Mangrove Blue Carbon under Elevated Atmospheric CO₂ *Ecosyst. Health Sustain.* 2023;9:Article 0033. https://doi. org/10.34133/ehs.0033

Submitted 18 June 2022 Accepted 21 February 2023 Published 17 March 2023

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Table 1. Number of Web of Science core collection references of global change studies in coastal wetlands that were published between 1980 and 2022. Based on the Web of Science Core Collection of Clarivate Analytics, studies from 1980 January 1 to 2022 April 30 have been conducted on TS = eCO_2 , TS = sea-level rise (SLR), TS = Warming, TS = eCO_2 *SLR, TS = eCO_2 *Warming, TS = SLR*Warming, and TS = eCO_2 *SLR*Warming.

Factor type	Factors Coastal Mangrove		Salt marsh	
Single factor	eCO ₂	87	74	100
	SLR	1,718	1,284	1,845
	Warming	387	495	343
	eCO ₂ *SLR	47	23	45
Two factors	eCO ₂ *Warming	16	17	14
	Warming*SLR	124	115	100
Multifactors	eCO ₂ *SLR*Warming	7	8	5

also has indirect effects on a range of plant properties, such as nutrient stoichiometry [13–15]. CO_2 has rapidly increased in the atmosphere since long-term instrumental measurements first began in the 1950s [16]. Depending on different Shared Socio-economic Pathways (SSPs), atmospheric CO_2 is projected to rise to between 445 (SSP1-1.9) and 1135 (SSP5-8.5) ppm (parts per million) by the end of the 21st century [17].

The very likely, but not well-known, influence of eCO_2 on mangrove carbon cycling contributes to the uncertainty of future blue carbon sequestration in mangroves, or the permanence of carbon already buried. Early studies of mangroves' responses to eCO_2 focused largely on CO_2 fertilization in seedlings, a concept that refers to the potentially beneficial effects of eCO_2 on plant growth over short time intervals [18,19]. However, nearly half of the existing studies have focused on mangrove responses to the combined effects of other factors (e.g., atmospheric warming and SLR) (Table 1). The lack of clarity on the links between species attributes and their responses to eCO_2 and additional environmental factors gives rise to failures in predicting growth and physiological responses to eCO_2 or seedling recruitment under eCO_2 and other environmental conditions [20–22].

Thus, predicting the responses of mangrove blue carbon storage, the majority of which occurs in the soil, in future climate scenarios with eCO_2 is complicated by the uncertainty of ecosystem responses [23]. As a feature of the anthropocene, eCO_2 is occurring simultaneously with other anthropogenic impacts (e.g., land use and land cover change, regulations of hydrology, and coastal development), which will also influence blue carbon sequestration.

However, only a few studies have been conducted on the effects of eCO_2 at the scale of the mangrove community over the long term because of the difficulty in imposing eCO_2 experiments in coastal environments (Table 1). Currently, there is a critical gap in our knowledge of how climate-associated environmental factors interact to affect mangroves and their carbon accounting.

Here, we focus on assessing how mangroves respond to eCO_2 , aiming to (a) discover the key processes in mangrove carbon cycling; (b) explore the combined effects of eCO_2 and other

anthropogenic factors on mangrove carbon sequestration; and (c) project the change in mangrove blue carbon storage under different eCO₂ scenarios. Based on the Web of Science Core Collection of Clarivate Analytics, studies from 1980 January 1 to 2022 April 30 have been conducted on $TS = eCO_2$, TS = SLR, TS = Warming, $TS = eCO_2*SLR$, $TS = eCO_2*Warming$, TS =SLR*Warming, and $TS = eCO_2$ *SLR*Warming, locating a total of 74 papers involving mangrove response to eCO_2 (Table 1). There were no restrictions on language, document type, data category, or a document's year. To avoid misquotation, we read each paper (including gray literature) comprehensively and performed an integrated analysis of all data from the literature with original experimental data (only 9 papers). In order to understand the effects on the carbon sequestration capacity of mangroves under eCO_2 , we compared the differences among various parameters related to carbon sequestration capacity under different atmospheric CO₂ concentrations. If the literature did not have original data about the mangrove responds to *e*CO₂, they were not included in data analysis (Tables 2 and 3). However, we have also reviewed their relevant comments in the discussion section. This review also aims to identify critical knowledge gaps in ecosystem responses to eCO_2 , the closing of which would improve our understanding of a key aspect of mangrove blue carbon cycling.

eCO₂ and Mangrove Carbon Cycling

Atmospheric CO₂ concentrations ultimately determine the material base for mangrove growth as carbon is extracted from CO₂ through photosynthesis. The largest carbon flux in a mangrove ecosystem is the CO₂ exchange among plants, soil, and the atmosphere (CO_2 flux in the vertical direction) (Fig. 1), with CH_4 maintaining a smaller footprint as a carbon source per se. A large proportion of CO₂ fixed in primary production is released into the atmosphere by canopy respiration, while the rest of the fixed carbon enters into the mangrove forest carbon cycle in the form of wood, roots (and their exudates), and foliage growth and decomposition [24]. Carbon in litterfall (foliage, small branches, and reproductive structures) is partly captured and fixed in the sediment but also decomposed or exported out of the mangrove ecosystem [25]. The export of carbon occurs via the lateral flux of detritus, dissolved inorganic carbon or organic carbon [26,27], and some of this carbon provides a permanent contribution to stored carbon within the ocean [28]. Soil and live belowground root respiration, as well as CH₄ emissions from surface sediments release a portion of carbon directly back to the atmosphere. Indeed, CH₄ emissions from mangroves, previously assumed to be negligible, are actually an important conduit for carbon loss when assessed by their influence on atmospheric warming [29], especially among mangroves with lower salinity as a permanent or seasonal condition. Under current climate conditions, the carbon budget of mangrove aboveground biomass has been well sorted [30,31]. However, carbon flux process at the soil-atmosphere interface is more complicated to capture for the purposes of modeling or assigning large-area flux values. Additionally, there are few long-term, ecosystemscale studies that have simulated the effects of eCO₂ on mangrove communities [32]. Because eCO_2 has the potential to influence carbon cycling and long-term storage, long-term and large-scale studies of the effects of eCO_2 on mangrove communities have great significance for projecting carbon fluxes under *e*CO₂ at large temporal and spatial scales.

Species	CO ₂ (ppm) ambient vs. elevated	Other Factors	RGR	BRGR	SLA	NPP	P _n	WUE	Reference
Avicennia germinans	400 vs. 800	Nitrogen	-3.7	-13.2	_	_	37.3	235.6	[15]
Avicennia germinans	365 vs. 720	Nitrogen	15.2	_	-4.8	_	_	_	[41]
Avicennia germinans	400 vs. 800	Salinity	_	_	3.6	_	16.9	172.7	[39]
Avicennia germinans	Instantaneous	_	_	_	_	-14	_	_	[19]
Avicennia marina	400 vs. 800	Flooding	95.5	44.8	44.6	_	58.5	98.8	[14], [18]
Conocarpus erectus	Instantaneous	_	-	—	-	-8	_	—	[19]
Kandelia obovata	400 vs. 700	_	15.4	153.3	—	_	_	_	[42]
Laguncularia racemosa	Instantaneous	_	-	-	—	-27	-	-	[19]
Rhizophora apiculata	340 vs. 700	Salinity, humidity	35.9	_	-6.2	_	40.5	14	[45]
Rhizophora apiculata	Instantaneous	_	_	_	—	-12	_	_	[19]
Rhizophora mangle	350 vs. 700	_	20.7	_	1.3	_	12.5	_	[33]
Rhizophora stylosa	340 vs. 700	Salinity, humidity	42.3	_	-0.3	_	46.2	52.2	[45]
Rhizophora stylosa	400 vs. 800	Flooding	47.5	3.5	7	-	58.5	59.6	[14], [18]

Table 2. The effects of elevated CO_2 on mangroves growth and carbon assimilation properties presented as the % change relative to values measured at ambient CO_2 concentrations (marked as ambient or low CO_2 concentrations).

RGR, relative growth rate; BRGR, belowground relative growth rate; SLA, specific leaf area; P_n , photosynthesis rate. WUE (water use efficiency) indicates no data. Instantaneous indicates a short exposure to a high CO_2 environment during measurement.

Above-ground carbon sequestration

The growth response of individual mangrove plants is related to increased photosynthetic rates (P_n) of leaves under eCO_2 . Mangroves also respond to eCO_2 by reducing stomatal conductance, stomatal density, and other physiological or morphological characteristics that could serve to reduce P_n [33,34]. Jacotot et al. [18] found that the P_n of *Avicennia marina* and *Rhizophora stylosa* seedlings increased by 59% and 75%, respectively, with eCO_2 up to a concentration of 800-ppm CO_2 . In fact, stimulated P_n is a general trend when measured under eCO_2 in mangroves, with increases ranging from 11% to 96% (Table 2).

For context, in herbaceous brackish wetlands, eCO_2 improved leaf P_n or reduced photorespiration, photoinhibition, and evapotranspiration [35,36] and enhanced plant growth [18]. However, after long-term manipulation of eCO_2 , photosynthesis-related genes and Rubisco activity may be down-regulated to adapt to higher CO_2 as has been observed in saltmarsh vegetation [37]. In terrestrial systems, eCO_2 can reduce transpiration of C_3 plants and improve leaf water use efficiency (WUE) [38].

In pot experiments, the WUE of mangroves increased by 17% to 213% with eCO_2 (Table 2), which was mainly caused by the increases in P_n [14,15]. This kind of leaf structural change substantially increases the WUE of leaves [39]. Indeed, from the available studies, it is likely that eCO_2 will moderately improve the salinity tolerance of mangroves through enhanced WUE.

 eCO_2 influences the carbon-to-nitrogen ratio (C:N ratio) in plant tissue [18]. The C:N ratio of terrestrial plants increased by approximately 15% in eCO_2 treatments [40], similar to observations in mangroves [41]. Jacotot et al. [18] showed that carbon fixation and the C:N ratio in roots and leaves increased remarkably with eCO_2 ; in this case, they are driven by low nitrogen content in plant tissues. The eCO_2 treatments also reduced leaf stomatal conductance, which limits transport of soil nitrogen to leaves in the transpiration stream [14]. In addition, phosphorus content in mangrove leaves decreased with eCO_2 [39]. This phenomenon was also linked to the decreased transpiration rates of leaves under eCO_2 . Declining transpiration rates and limited transport of phosphorus from roots to above-ground biomass are likely to have a important impact on the growth rate of mangroves in response to eCO_2 , especially in phosphorus-limited habitats [15].

Specific leaf area (SLA), the leaf area-to-weight ratio, is an indicator of CO2-induced changes in growth and photosynthetic activity [42-44]. Variations in SLA were observed in some mangrove species in the experimental eCO_2 treatments (Table 2). Increases in SLA have been attributed to increases in the concentration of nonstructural carbohydrates within leaves [18], while an increase in nonstructural carbohydrates reduces SLA in terrestrial species [44]. In most controlled experiments, mangrove SLA increased with eCO₂ [18,33,45]. However, there are also opposite results in some studies with the same species, which may be related to the different time scales of studies, where shorter time scales may not be sufficiently long for changes in the SLA since this characteristic would be manifested in new leaf growth under said conditions [45]. Using herbarium specimens from a 167-year record, Reef and Lovelock [46] found declining SLA over time as CO₂ concentrations have increased, inferring that primary productivity and growth of Avicennia marina (but not *Rhizophora stylosa*) have increased with eCO₂ in the atmosphere. However, change in SLA with eCO_2 probably does not occur where nutrients limit plant growth, as excess carbohydrates associated with increased photosynthesis were not transformed into plant tissue in terrestrial tree species growing under nutrient limitation [47].

Complicating our understanding of how eCO_2 affects mangroves are several bidirectional effects that have been documented for halophyte growth [33,41,48,49]. Laboratory data revealed that some mangrove species showed enhanced growth, while

Table 3. Studies conducted on mangrove responses to eCO ₂ conditio	n showing the location	, experimental setting,	interacted f	actors and
time scale.				

Species	Study sites	Methods	CO ₂ (ppm) ambient vs. elevated	Interacted factor	Time scale	Reference
Aegiceras cornicu- latum, Avicennia marina	Australia	Greenhouse	400 vs. 600	Salinity, competition	244 d	[22]
Rhizophora stylosa, Avicennia marina	New Caledonia	Greenhouse	400 vs. 800	Flooding period	365 d	[14], [18]
Avicennia germinans	United States	Greenhouse	380 vs. 700	Competition	308 d	[90]
Avicennia germinans	Panama	Greenhouse	400 vs. 800	Soil nutrient	132 d	[15]
Avicennia germinans	Panama	Greenhouse	280, 400, 800	Salinity	132 d	[39]
Rhizophora stylosa, Avicennia marina	Indo-western Pacific Region	Museum specimens	280-400	Latitude	167 year	[46]
Avicennia marina, Avicennia alba, Avicennia officinalis	Bangladesh	Field, chamber	373.5-378	No interacted factors	913 d	[105]
Avicennia germinans	United States	Greenhouse	365 vs. 720	Soil nitrogen content	500 d	[41]
Rhizophora mangle, Avicennia germi- nans, Laguncularia racemose, Conocarpus erectus	United States	Greenhouse, leaf chamber	340-360 361-485	No interacted factors	No data	[19]
Rhizophora apiculata, Rhizophora stylosa	Australia	Greenhouse	340 vs. 700	Salinity, humidity	98 d	[45]
Rhizophora mangle	United States	Greenhouse	350 vs. 700	No interacted factors	408 d	[33]

others declined or exhibited little or no change (Table 2). In mangrove seedlings, the growth rates increased by 15% to 96% under eCO₂ (Table 2). Jacotot et al. [18] found that the relative biomass growth rates of Avicennia marina and Rhizophora stylosa seedlings increased by 95% and 47%, respectively, under sustained CO₂ concentrations of 800 ppm. In contrast, for Avicennia germinans in one study, growth was inhibited while in other studies it was not (Table 2). In addition, Manea et al. [22] suggested that Aegiceras corniculatum seedlings were insensitive to eCO₂, and growth was even suppressed. Interspecific differences in mangrove response to eCO₂ may depend as strongly on species responses to various environmental stresses as they are to eCO_2 per se [45]; given the 70 mangrove species or putative hybrids present globally [50], species \times environment stress \times eCO₂ adjudication represents a large data gap. For example, R. stylosa increased growth at low humidity, while R. apiculata which occurs in the humid tropics did not [45].

Below-ground carbon sequestration

*e*CO₂ improves seedling productivity by promoting growth, which may lead to increased carbon sequestration in mangrove

ecosystems through below-ground adjustment, similar to aboveground adjustment [14,18]. Indeed, mangroves depend more strongly on root growth than litterfall to build vertical elevations and adjust to SLR [51], which in turn vectors root-based carbon belowground into long-term storage. Mangroves vary in their relative dependence on minerogenic versus biogenic processes as well [52], and this relative dependence feedbacks to carbon sequestration potential among mangrove types [53]. Some mangroves rely completely on root productivity to support vertical soil adjustment (e.g., [54]). The large root biomass and complex structure of mangrove roots not only maintain the plant community in soft sediments but also intercept allochthonous sediment for greater shoring [10].

Below-ground carbon sequestration in mangroves is divided into the production of roots and the burial of organic matter, which consists of autochthonous production, mainly from roots and litter, and the allochthonous supply of mineral sediment and carbon (Fig. 1). The mineral sediment supply is independent of eCO_2 , and the proportion of the overall below-ground carbon burial varies with the type of environmental setting of the mangrove ecosystem [53]. River- and tide-dominated



Fig.1. Elevated atmospheric CO₂ effects on mangrove blue carbon sequestration and mangroves lateral distribution. SLR is sea-level rise; R_h means heterotrophic respiration; R_a means autotrophic respiration; + and – represent positive and negative effect.

mangrove ecosystems receive large allochthonous inputs of sediment and carbon, while these inputs are insignificant in carbonate settings, where root growth is the major contributor to below-ground carbon storage [55,56]. There are few studies on changes in root biomass in response to eCO₂. Among these, eCO₂ significantly increased the length, biomass, and carbon content in mangrove roots, but this response in mangroves was less than that in other woody plants [15]. In saltmarsh mesocosms grown for 5 months in simulated eCO₂ (800 ppm) treatments, the soil surface elevation was raised approximately 2 mm by below-ground root expansion, while the soil surface elevation under the ambient CO₂ concentrations (400 ppm) decreased from shallow compaction [49]. Cherry et al. [57] also found that eCO₂ could increase the root biomass of saltmarshes, which caused a seasonal increase in soil surface elevation. With eCO₂, enhanced sequestration of organic carbon in mangrove soils is also expected.

eCO₂ alters the subsurface processes inherent to mangroves through eCO₂ effects on biomass growth and allocation and ecophysiological properties, such as root carbon concentrations and root density [58]. In response to eCO₂, mangroves have higher carbon concentrations in roots and stems associated with an enhanced C:N ratio [18]. This may increase carbon sequestration in mangrove soils as the C:N ratio of plant tissue was negatively correlated with the decomposition rate of soil organic matter [59–62]. Therefore, changes in the composition of mangrove tissues under elevated CO₂ may lower greenhouse gas emissions from soils and lateral carbon export to estuaries to improve the soil carbon storage capacity for mangrove ecosystems.

Further compelling is that microbial communities are abundant in the thin layer of the rhizosphere of all wetland plants. These microbial communities have important functions in mangrove ecosystems by controlling soil organic matter decomposition and other biogeochemical processes (such as phosphorus, organic acid, and iron carriers) and underpinning ecosystem sustainability [63-65]. However, in at least one study, eCO₂ was observed to have no significant impact on the rhizosphere bacterial community of Kandelia seedlings, but higher CO₂ had a clear impact on the structure of the archaeal community present within the soils, especially by influencing the presence of ammonia-oxidizing archaea [42], providing potential for eCO₂ priming of biogeochemical processes in mangrove soils. As carbon sources of rhizosphere microorganisms were manipulated, differences in their ability to use amino acids and carbohydrates led to changes in carbon metabolism [42].

Although eCO_2 is likely to have a positive effect on growth for some mangrove species (all woody mangrove plants at C₃), some of the models that project the future of mangroves using current atmospheric CO_2 concentrations have predicted that rising temperatures will lead to decreased productivity, and mangroves are expected to disappear in some regions with increasing global temperatures [66–68]. This apparent contradiction projects eCO_2 versus increasing atmospheric temperatures as a relatively new complication. In the last decade, approximately 10 studies reported results that eCO_2 significantly increased the P_n and relative growth rate (RGR) of mangrove seedlings (Table 2), which suggests that eCO_2 may influence mangrove productivity and their global distributions. Elevated temperature was not a covariable in any of these experimental designs (Table 2). Including long-term larger-scale experimental studies along with ecosystem carbon flux models can help to increase the accuracy of models projecting mangrove growth and carbon sequestration in the future.

The Combined Effects of eCO₂ with Multiple Environmental Factors

eCO₂ response to offset SLR effects

Global warming, as a consequence of eCO_2 , raises the sea level from thermal expansion of the oceans and the melting of polar ice, which may threaten mangrove ecosystems when mangrove sediment accretion and surface elevation are in large deficit with SLR [69] and/or landward migration of the mangrove ecosystems is prevented by steep morphological gradients, human settlements, seawalls, and dikes [17,32,70]. However, SLR is a special concern for coastal management in this respect. Therefore, the combined effects of eCO_2 and SLR have become a topic receiving the most attention when determining the response of mangroves to eCO_2 , keeping in mind that SLR was the prominent driver of mangrove carbon sequestration over the Holocene in some parts of the world [71].

eCO₂ directly promotes root growth and inhibits the decomposition of organic matter. This response can increase the surface elevation of wetlands to relieve the pressure of SLR if SLR is too high but may create a synergy if SLR is within the range of belowground adjustment, which has been demonstrated in saltmarshes [57,72]. The abundant structure of the above-ground roots can promote the interception or trapping of sediment and litter fall, further increasing soil volumes [73]. In mangroves, the promotion of sedimentation rates by above-ground roots and root zone expansion has a dual effect on mitigating the response to SLR [10]. Because of the positive influence of increasing allocation to belowground tissues and sediment trapping, the capacity of mangrove carbon sequestration will be generally enhanced under eCO₂, while this advantage will decrease with SLR if there is no accommodation space landward [71]. The combined effects of eCO_2 and SLR may contribute to mitigating climate change, if there is sufficient accommodation space for mangrove landward migration (Fig. 1), although some models suggest that this may not be the case [74].

However, only 20% of eCO_2 studies focusing on coastal wetlands included the simulation of SLR (Table 1). One way to overcome the deficiency of experimental data is to integrate the time series datasets from field studies. Based on field data, a SLR tolerance threshold for saltmarsh responses to eCO_2 was proposed. Langley et al. [72] built a threshold model of tolerance to eCO_2 and SLR for saltmarshes, which indicated that flood adaptation was generally larger than 3.9 mm year⁻¹ in combination with elevated CO_2 but will decreased by approximately 1 mm year⁻¹ when not considered in combination with elevated CO_2 . We need the similar models for mangroves to determine that they have the same phenomenon as saltmarshes.

The Sixth Assessment Report from Intergovernmental Panel on Climate Change (IPCC AR6) report (2021) presented 5 scenarios to predict global changes at the end of the 21st century. Here, we combined these models with a threshold model for

mangroves to survive with eCO_2 and SLR based on the assessment of mangrove thresholds presented by Saintilan et al. [69]. A modified conceptual diagram is shown in Fig. 2. The black line approximates the relationship between eCO₂ and SLR over the past 140 years. Among the SSPs, SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 were selected to represent 5 future climate scenarios. The eCO_2 effect on surface elevation gain is conservative compared with that measured in the field experiment [72], because of the uncertainties in extrapolating from short-term CO₂ effects on soil elevation change to actual mangrove elevation change in the field, which is influenced by subsidence, bioturbation, and other factors. When the rate of SLR under different scenarios exceeds the threshold of mangrove tolerance to SLR, as indicated by the green dashed line, mangroves will degrade or die, which is all projected to occur in our simple model (Fig. 2). Thus, mangrove ecosystems will be threatened by SLR and even disappear with eCO_2 in the future if mangroves cannot encroach inland. However, mangroves were unable to encroach inland due to human alteration of the landscape in many locations, such as where seawalls and dikes exist [75].

Increasing the allocation of biomass to root growth will accelerate soil elevation gain which can help mangroves resist SLR [10]. Species that have strong below-ground biomass growth under eCO_2 could also lead to mangrove colonization of newly available sediment that may arise because of SLR and other coastal processes (Fig. 1). eCO_2 can improve the RGR of mangroves (Table 2). The increment of RGR may also improve flooding tolerance of some species [14], which can help mangroves exposed to high levels of inundation, improving survival rates. In addition, eCO_2 may concentrate nonstructural carbohydrates in leaf tissues [76], which could slow the decomposition of litter incorporated within the soil promoting greater contributions of organic matter to soil surface elevation gains (Fig. 1).

The combined effects of eCO₂ and climatic factors

The different responses of mangrove species to eCO₂ may also affect how communities respond to environmental pressures associated with alternate climatic change factors. A variety of environmental factors, such as soil salinity, nitrogen availability, and tidal inundation interact with eCO₂ (Fig. 1). As halophytes, mangroves inhabit a moderate salinity environment, although salinity tolerance is variable by species. High salinity leads to a lower maximum growth rate for mangroves [77]. Global climate change is projected to strongly influence precipitation and evaporation, ultimately changing the salinity of estuarine and marine habitats and increasing the salinity pressure on mangroves in regions where rainfall is reduced [20]. Although photosynthetic nitrogen utilization of leaves increased significantly under the combined effect of eCO_2 and salinity, there was no significant increase in seedling growth by eCO₂ when mangroves grew under suboptimal salinity conditions (which salinity is not suitable for different mangrove species in their experiments) [45,46]. With the combined effect of salinity, eCO₂ had little influence on the RGR of mangroves at high salinity but enhanced the RGR at low salinity [45].

Global increases in CO_2 have also led to increases in both air and seawater temperatures. Future increases in surface seawater temperature can help to further stimulate individual tree development as well as mangrove habitat expansion (where they are temperature limited), as temperature affects seedling



Fig.2. Conceptual diagram of the mangrove tolerance threshold under elevated atmospheric CO_2 and sea-level rise under a range of SSPs (modified in [17,72]). The blue dotted line represents a threshold of fixed SLR at 6.1 mm year⁻¹ for global threshold that threatens many mangroves [69]. The green dashed line represents the surface elevation change (SEC) rate of mangrove ecosystems under the combined effect of eCO_2 and SLR, based on the data from controlled experimental studies [104]. The difference between the dotted line and the green dashed line indicates the potential influence of eCO_2 on mangrove resistance to SLR. SSP1-1.9: Holds warming to approximately 1.5 °C above 1850 to 1900 in 2100 after slight overshoot (median) and implied net zero. SSP1-2.6: Stays below 2.0 °C warming relative to 1850 to 1900 (median) with implied net zero emissions in the second half of the century. SSP2-4.5: The SSP2-4.5 scenario deviates mildly from a "no-additional climate-policy" reference scenario, resulting in a best-estimate warming around 2.7 °C by the end of the 21st century relative to 1850 to 1900. SSP3-7.0: A medium to high reference scenario resulting from no additional climate policy under the SSP3 socioeconomic development narrative. SSP3-7.0 has particularly high non-CO₂ emissions, including high aerosols emissions. SSP5-8.5: A high reference scenario with no additional climate policy. Emission levels as high as SSP5-8.5 are not obtained by integrated assessment models under any of the SSPs other than the fossil fueled SSP5 socioeconomic development pathway.

productivity with higher RGRs during warmer periods [78]. According to the often-used theoretical model of photosynthesis, eCO₂ influences the temperature response of photosynthesis [79,80], increases leaf P_n, and promotes plant water use and net primary productivity [81]. Increasing temperature and eCO₂ initially enhance microbial transformation rates of nitrogen and phosphorus in mangroves [13]. Under simultaneous warming and carbon "fertilization", mangroves may expand more rapidly poleward especially given that much of that mangrove expansion occurs in competition with, and at the expense of, C₄ plant species (e.g., Spartina) distributions [11]. C₄ species are biochemically less able to make use of eCO₂ through enhanced carbon fixation [72]. However, periods of high temperature in tropical regions have also been associated with mangrove dieback (e.g., in northern Australia, [82]). To date, it is unknown how eCO_2 will influence species responses to rising temperatures and associated declining leaf vapor pressure deficits in the tropics, but declines in productivity and species diversity may occur.

The interaction of eCO₂ and anthropogenic impacts

It is worth noting that the responsiveness of saltmarsh communities to eCO_2 is dependent on an ample nutrient supply [83]. The cycling of essential nutrients is also central to mangrove productivity. In the Anthropocene, the flow of nutrients, and other elements, beneficial or harmful to aquatic life into estuaries and the ocean has increased. Inflows enriched in nitrogen and phosphorus also present an opportunity for accelerated growth in mangroves, which are often nitrogen limited in coastal by increasing rates of photosynthesis [41]. Several studies have shown that the stimulatory effect of eCO_2 on plant growth is limited by nutrients [15,85]. Therefore, eCO_2 may have a positive biological impact on mangroves in areas with high nutrient availability. Previous experiments showed that the effects of eCO_2 on mangrove growth were greatly enhanced in the presence of additional nutrients [15]. Nutrient enrichment can also cause indirect effects on heterotrophic respiration by stimulating microbial activity, which might offset biomass gains with eCO_2 . With nutrient enrichment, allocation to root growth can be reduced and above-ground biomass increased, thus increasing the vulnerability of mangroves to climatic disturbances [86]. Hence, with nutrient enrichment, the positive gains in above-ground biomass may be countered by the lack of root development to maintain autochthonous inputs to soils.

intertidal zones [84]. Mangroves respond to nutrient enrichment

Over 70% of the studies we reviewed focused on mangrove responses to eCO_2 combined with the effects of salinity, nutrients, and competition, often with invasive species (Table 2). In addition to climate change, human activities are often the main cause of species invasion [87]. In order to protect coasts from erosion the saltmarsh cordgrass, *Spartina alterniflora*, has been introduced to China and has encroached into mangroves [88]. The photosynthetic ability of C₃ populations can be increased by elevated CO_2 , while C_4 populations rarely benefit from additional CO_2 [81,89]. Differences in the response of C₃ (such as mangroves) and C₄ (such as *Spartina alterniflora*) plants to eCO_2 may encourage further invasion by some C₄ non-native species. This situation could even influence carbon sequestration in the

intertidal zone, particularly under the combined effects of eCO_2 with SLR or enhanced soil nutrients [90]. Although eCO_2 is likely to be a key driver of woody plant growth, the complexity of interactions within mangrove environments leads to uncertainties for projecting mangrove growth responses to eCO_2 and other environmental factors in the future.

Global warming caused by eCO_2 has allowed mangroves to migrate to higher latitudes and encroach into saltmarshes in some temperate regions across continents [22,91]. Future increases in surface temperature can help to further stimulate tree development. eCO_2 can also influence the temperature response of photosynthesis in mangroves [79,80], increase the P_n of leaves [81], and affect plant water use and net primary productivity.

Development and Limitations of Research Methods

Many research efforts have been undertaken to discover how plants and ecosystems respond to eCO₂, both in natural and managed systems. In terrestrial ecosystems, the primary effects of eCO₂ on plants have come from studies on individual species grown in controlled environments or enclosure facilities [92–98]. Due to technical limitations in the late 20th century, the measurements were focused at the leaf level and were carried out in a leaf chamber with eCO_2 . These early experiments progressed to exposing potted plants in a small chamber/ greenhouse for short-term measurements as a way to study the physiological response of plants to eCO2. However, experiments to study the effects of eCO₂ on coastal wetlands rarely included the variation in conditions of tidal environments [49]. Studies on mangrove responses to eCO₂ have focused on the seedling/ sapling stages and have been conducted in microscale facilities (e.g., greenhouse or in situ growing chambers) while imposing some other environmental constraints [14,18,58,90]. These previous studies provided new knowledge on the mechanisms of carbon cycling at the individual plant level (Table 3). Controlled experiments were conducted on the seedlings/saplings in shortterm experiments (98 to 408 d) with limited species representation (e.g., species in Avicennia genus and Rhizophora genus) [14]. The influence of different interacting environmental factors commonly considered in experimental settings were salinity, nutrition, flooding, and species competition (Table 3). The indices measured included photosynthetic characteristics, WUE, nitrogen use efficiency, and growth. There have been few studies conducted at the ecosystem scale, although some studies have deduced the response of mangroves to eCO₂ since industrialization with herbarium specimens (Table 3).

The conclusions from these experiments form the basis of our knowledge on the physiological responses of mangroves to eCO_2 , yet potential limitations occur when using the enclosure systems to simulate eCO_2 . For example, enclosures with eCO_2 simulation may amplify the down-regulation of photosynthesis and production [99] and may, through environmental modification, produce a "chamber effect" that exceeds the effect of elevating CO_2 . Chambers tend to be limited in size and may have restricted capacity to follow trees and crops to maturity using robust experimental designs [100]. Furthermore, growing plants in pots may restrict the rooting volume and suppress plant responses to eCO_2 [49,101]. Mesocosms, which are defined here as large open-topped chambers, are relatively advanced research methods used to study ecosystem-scale responses to eCO_2 in recent years [49]. These facilities are favored by scientists because they weaken the "chamber effect" caused by small spaces while allowing for control over a variety of environmental factors.

Along the same lines, large-scale free-air CO_2 enrichment (FACE) experiments allow the exposure of mature plants to eCO_2 in natural and fully open-air conditions. FACE designs allow temporal and spatial control of CO_2 concentrations and have been used in crop and grass canopies and in homogeneous forests [102]. Limited data exist for long-term field manipulation with FACE in forested ecosystems [103] but none in mangroves. However, the impact of global climate change on the fate of mangroves is long-term, persistent, and important to understand. Trajectories of mangrove blue carbon storage in future climate scenarios with eCO_2 and SLR could be improved by development of methods suitable for large-scale and long-term field simulations of the effects of eCO_2 on mangroves that can be utilized to inform predictions of future productivity and distribution of mangrove ecosystems.

Outlook

eCO₂ are likely to play a major role in blue carbon cycling. However, the complex and variable climate conditions to which mangroves are exposed lead to uncertainty in trajectories of future carbon sequestration. As one of the world's carbon storage hotspots, mangroves offer a pathway for efficient blue carbon storage and can play a role in carbon mitigation and adaptation strategies. Despite such uncertainties associated with the effects of eCO_2 on mangroves, especially due to the species-specific differences and long-term effects for mangroves above-ground/ below-ground biomass, current knowledge indicates that many responses of mangroves to eCO2 can be positive in terms of carbon sequestration. Under eCO₂, the litter biomass can increase and/or heterotrophic respiration and below-ground decay can decrease to support below-ground carbon burial. In contrast, the increase in autotrophic respiration and CH₄ emissions with eCO2 may decrease future blue carbon accumulation potential (Fig. 1). However, many scientific questions remain to be addressed, and future research on the effect of eCO_2 could include:

- 1. Establish more experiments to understand the influence of eCO_2 on below-ground biological processes, particularly including processes that lead to non- CO_2 greenhouse gas emissions. More fundamental research investigating interspecific differences of mangrove below-ground processes in their responses to eCO_2 could aid in reducing uncertainty in the impacts of eCO_2 on mangrove ecosystems.
- 2. Increase knowledge of the combined effects of *e*CO₂ and other local environmental factors (e.g., hydrology, flooding, nutrient enrichment, and species competition) could reduce uncertainty in the impacts of *e*CO₂ with varying anthropogenic and climate stressors.
- 3. Increase the number of case studies on the impacts of eCO_2 on mangroves and on ecological processes using combined simulation experiments and field observations. This could enable greater confidence in global-scale models that predict the size of mangrove ecosystem carbon sinks in the future.
- 4. Invest in mesocosm-scale simulation experiments on the effects of *e*CO₂, which could provide datasets for the prediction of mangrove seedling/sapling response in

the future. Investment in long-term eCO_2 simulation experiments can help to reduce the uncertainty and improve the accuracy of prediction at an ecosystem scale. Additionally, long-term field observations that monitor carbon fluxes, e.g., eddy covariance and permanent plots, can help to calibrate predictive models. The accurate assessment of the carbon sequestration capacities and the potentials for future sequestration in mangroves under eCO_2 scenarios can provide fundamental information for modeling.

5. Strengthen science-policy linkages to develop the critical next steps in leveraging mangrove forest management for climate change mitigation efforts.

Multidisciplinary research teams and development of innovative research methods can address the scientific directions recommended above. This research can integrate fundamental knowledge while broadening the community of practice of blue carbon science, which can contribute to management and new economic pathways to support carbon neutral strategies.

Acknowledgments

Funding: The National Natural Science Foundation of China (42076176 and U22A20584), the Natural Science Foundation of Fujian Province of China (2020J01048), the Fundamental Research Funds for the Central Universities of China (20720210075), and the Scientific and Technological Plant Projects in Xiamen (3502Z2026020) supported L.C. The U.S. Geological Survey Climate R&D Program provided support to K.W.K. The DSI/NRF Research Chair in Shallow Water Ecosystems (UID 84375) supported J.B.A. **Competing interests:** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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