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1 Recovering wetland biogeomorphic feedbacks to restore the world's biotic

2 carbon hotspots

3

4 **Short title:** Recovering biogeomorphic feedbacks

5

6 **One-sentence summary:** Recovering landscape-building vegetation-geomorphology

7 feedbacks can restore degraded wetlands as biotic carbon hotspots

8

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44

Enhanced abstract

Background: Evaluating effects of global warming from rising atmospheric carbon dioxide (CO_2) concentrations requires resolving the processes driving Earth's carbon stocks and flows. Although biogeomorphic wetlands (peatlands, mangroves, salt marshes, and seagrass meadows) cover only 1% of the Earth's surface, they store 20% of the global organic ecosystem carbon. This disproportionate share is fueled by high carbon sequestration rates per unit area and effective storage capacity, which greatly exceeds those of oceanic and forest ecosystems. We highlight that feedbacks between geomorphology and landscape-building wetland vegetation underlie these critical qualities, and that disruption of these biogeomorphic feedbacks can switch these systems from carbon sinks into sources.

Advances: A key advancement in understanding wetland functioning has been the recognition of the role of reciprocal organism-landform interactions, so-called biogeomorphic feedbacks. Biogeomorphic feedbacks entail self-reinforcing interactions between biota and geomorphology, by which organisms – often vegetation – engineer landforms to their own benefit following a positive density-dependent relationship. Vegetation dominating major carbon-storing wetlands generate self-facilitating feedbacks that shape the landscape, amplify carbon sequestration and storage. As a result, per unit area, wetland carbon stocks and sequestration rates greatly exceed those of terrestrial forests and oceans, ecosystems that worldwide harbor large stocks due to their large areal extent.

Worldwide biogeomorphic wetlands experience human-induced average annual loss rates of around 1%. We estimate that associated carbon losses amount to 0.5 Pg C per year, levels equivalent to 5% of the estimated overall anthropogenic carbon emissions. Because carbon emissions from degraded wetlands are often sustained for centuries until all organic matter has been decomposed, conserving and restoring biogeomorphic wetlands must be part of global climate solutions.

Outlook: Our findings highlight that biogeomorphic wetlands serve as the world's biotic carbon hotspots, and that their conservation and restoration offers an attractive contribution to mitigate global warming. Recent findings show that restoration aimed at re-establishing biogeomorphic feedbacks can greatly increase restoration yields, and can facilitate humanity in its pursuit of targets set by the Paris Agreement and UN Decade on Ecosystem Restoration.

77   Caption graphical abstract
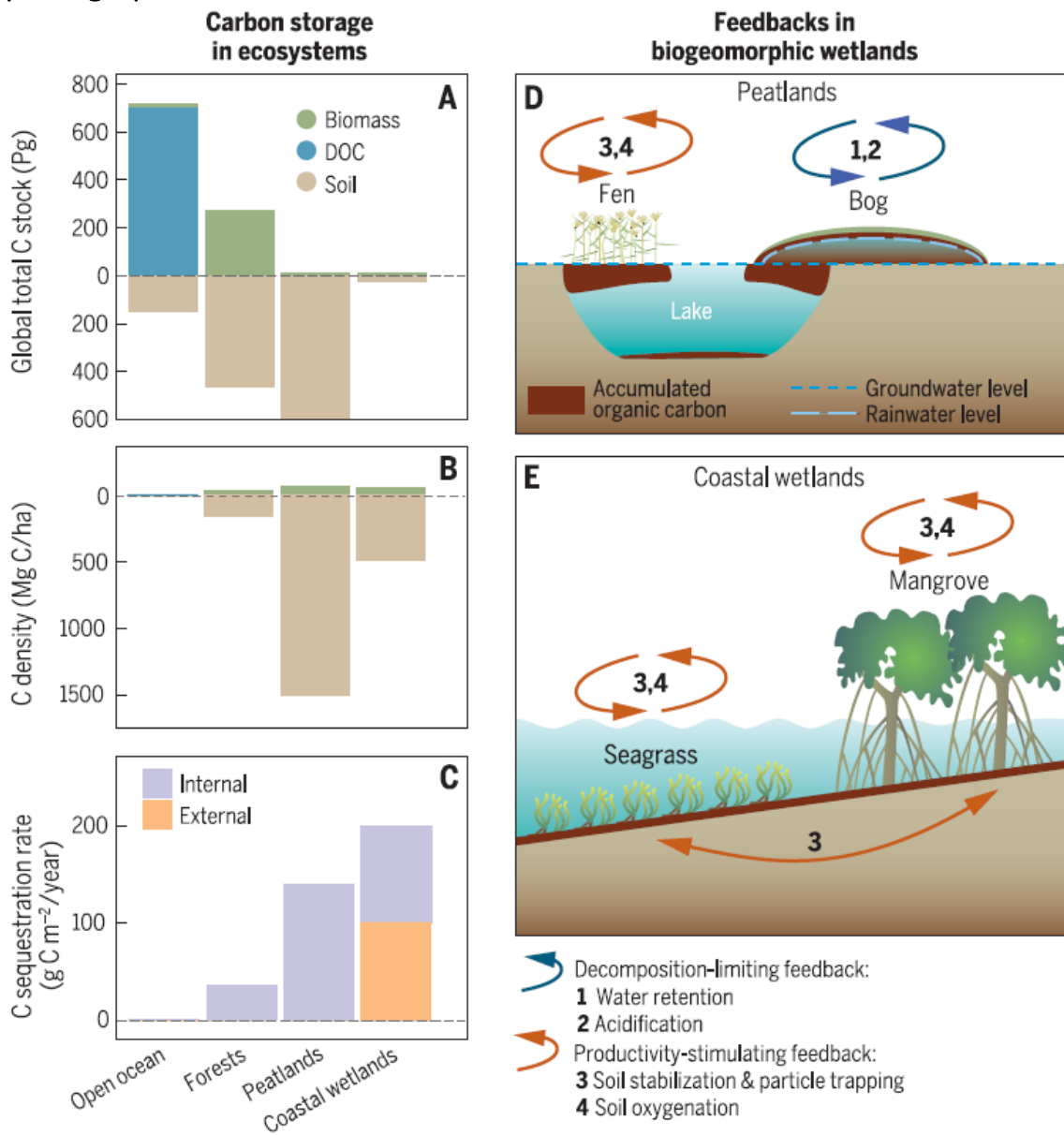
Carbon storage in biogeomorphic wetlands. Organic carbon stocks **(A)**, densities **(B)**, and carbon sequestration rates **(C)** in the world's major carbon-storing ecosystems. Oceans hold the largest stock, peatlands (boreal, temperate and tropical aggregated) store the largest amount per unit area, and coastal ecosystems (mangroves, salt marshes and seagrasses aggregated) support the highest sequestration rates. **(D-E)** Biogeomorphic feedbacks, depicted by arrows, can be classified as productivity-stimulating or decomposition-limiting. Productivity-stimulating feedbacks increase resource availability and thus stimulate vegetation growth and organic matter production. Although production is lower in wetlands with decomposition-limiting feedbacks, decomposition is more strongly limited, resulting in net accumulation of organic matter. **(D)** In fens, organic matter accumulation from vascular

89   plants is amplified by productivity-stimulating feedbacks. Once the peat rises above the

90   groundwater, and is large enough to remain waterlogged by retaining rainwater, the resulting

91   bog maintains waterlogged and acidic, resulting in strong decomposition-limiting feedbacks.

92   **(E)** Vegetated coastal ecosystems generate productivity-stimulating feedbacks that enhance

93   local production and trapping of external organic matter.

94

Abstract

Biogeomorphic wetlands cover 1% of Earth's surface, but store 20% of ecosystem organic carbon. This disproportional share is fueled by high carbon sequestration rates and effective storage in peatlands, mangroves, salt marshes, and seagrass meadows, which greatly exceed those of oceanic and forest ecosystems. Here, we review how feedbacks between geomorphology and landscape-building vegetation underlie these qualities, and how feedback disruption can switch wetlands from carbon sinks into sources. Currently, human activities are driving rapid declines in the area of major carbon-storing wetlands (i.e., 1% annually). Our findings highlight the urgency to stop ongoing losses via conservation, and to re-establish landscape-forming feedbacks through restoration innovations that recover the role of biogeomorphic wetlands as the world's biotic carbon hotspots.

Introduction

Global warming, resulting from rapidly rising atmospheric carbon dioxide (CO_2) concentrations since the Industrial Revolution, has increasingly drawn attention towards understanding and quantifying the processes driving Earth's carbon stocks and flows (*1, 2*). Burial of organic matter remains the largest carbon sequestering process on the planet, rivaled only by the ocean's inorganic carbon solubility pump (*3, 4*). While wetlands cover just 2% of the Earth's surface (*5*), they store more than 20% of global organic ecosystem carbon (i.e. all live and dead organic matter from terrestrial, freshwater and oceanic systems combined) (*4, 6*). Moreover, wetland carbon sequestration rates can be orders of magnitude higher compared to terrestrial and oceanic ecosystems (*7*). Recent work has addressed the importance of wetlands as natural climate solutions and the cost-effectiveness of their restoration (*8, 9*). However, restoring carbon storage functions requires an understanding of the mechanisms underlying their large carbon stocks and high sequestration rates.

An important advancement in understanding wetland functioning has been the recognition of the key role of reciprocal organism-landform interactions, so-called biogeomorphic feedbacks (*10, 11*). Biogeomorphic feedbacks entail self-reinforcing interactions between biota and geomorphology, by which organisms – often vegetation – engineer landforms via positive density-dependent relationships. Here, we focus on the major wetlands that are shaped by such vegetation-geomorphology feedbacks: 1) peatlands where vegetation retains water by preventing lateral and vertical seepage, yielding landforms shaped by vertical and horizontal peat accretion (*12*), and 2) coastal wetlands including seagrass meadows (*13*), salt marshes (*10*), and mangroves (*14*) where vegetation traps suspended particles from the water and stabilizes underlying soils to form elevated landscape features. Although it has been known for two centuries that vegetation-driven feedbacks shape 'biogeomorphic wetlands' (*15*), the role of these feedbacks in controlling carbon sequestration and storage have received insufficient attention.

In this review, we first compare the carbon stocks and sequestration rates of the three major carbon-storing ecosystems – oceans, forest, and wetlands – after which we highlight how vegetation-geomorphology feedbacks shape wetland landscapes and their role as global carbon hotspots. We summarize how anthropogenic disruption transforms these carbon sinks and stocks into sources and highlight how implementing novel restoration designs aimed at jumpstarting and sustaining biogeomorphic feedbacks may improve carbon sequestration.

Comparing organic carbon stocks and sequestration rates between ecosystems

Our literature-based compilation highlights that the major carbon-storing wetlands store the bulk of their organic carbon as soil organic matter, while oceans and forests hold most of their carbon in the water layer and living biomass, respectively (**Fig 1A**) (*16*). Although oceans and forests hold massive amounts of organic carbon due to their large spatial extent, their area-specific carbon density (carbon stock per unit area) is smaller compared to biogeomorphic wetlands (**Fig. 1B**). Carbon density is highest in peatlands (1000-2000 Mg C ha^{-1}), followed by mangroves (900 Mg C ha^{-1}), salt marshes (400 Mg C ha^{-1}) and seagrass meadows (330 Mg C ha^{-1}). Carbon density is lower in terrestrial forests (150-230 Mg C ha^{-1}) and much lower in the oceans (2.4 Mg C ha^{-1}) (*17, 18*).

Recent sequestration rates of internally and externally produced organic carbon per unit area over the last 10-125 years are higher in tropical peatlands (200 g C m^{-2} yr^{-1}) compared to their boreal (100 g C m^{-2} yr^{-1}) and temperate (120 g C m^{-2} yr^{-1}) counterparts (**Fig. 1C**). Average salt marsh and mangrove sequestration rates (250 and 200 g C m^{-2} yr^{-1}, respectively), may outpace or equal those of tropical peatlands, while seagrass meadows bury 150 g C m^{-2} yr^{-1}, which is more than boreal and temperate, but less than tropical peatlands (*7, 19*). For coastal ecosystems, 100 g C m^{-2} yr^{-1} originates from external (e.g., riverine and marine) sources, which gets trapped and buried (*20–23*). All of these vegetated wetland rates are higher than those of terrestrial forests and oceans, where net sequestration rates are below 50 g C m^{-2} yr^{-1} (**Fig 1C**). Intact vegetated coastal wetlands and freshwater peatlands worldwide currently sequester 0.7 Pg C per year, equaling 6% of the total annual global anthropogenic carbon emissions (which were estimated in 2019 to be 11.5 Pg C) (*4*).

Biogeomorphic feedbacks shape wetland carbon storage hotspots

In 45% of all wetlands worldwide, biogeomorphic feedbacks shape landscape formation and carbon capture and storage processes (**Fig. 2, Table 1**) (*5*). Two overarching types of feedbacks control the ability of biogeomorphic wetlands to capture and store carbon. In wetlands driven by 'productivity-stimulating' feedbacks, landscape formation and carbon storage are enhanced by feedback processes that increase resource availability and thus stimulate vegetation growth and organic matter production. In wetlands shaped by 'decomposition-limiting' feedbacks and consequent nutrient immobilization, production is

173 slower, but because decomposition is more strongly limited, organic matter can accumulate

174 in such wetland soils (**Fig. 2**).

175

176 *Peatlands*

177 Peatlands are effective organic carbon sinks in terms of long-term storage per unit area (**Fig.**

178 **1B**). Peatland landforms are shaped by landscape-scale interactions between plants, peat and

179 water (*12*). Their formation is typically initiated via one of two processes: 1) paludification and

180 2) terrestrialization. Paludification is the process in which a change in the hydrological balance

181 shifts a previously drier, vegetated, and inorganic soil terrestrial ecosystem towards a peat-

182 accumulating, biogeomorphic wetland ecosystem (*24*). Terrestrialization, in contrast, occurs

183 in aquatic systems, such as shallow lakes, when organic matter deposition outpaces its

184 decomposition in the anoxic environment, resulting in the gradual in-filling of the water basin

185 over time (*25*). As the waterbody accretes organic matter, it transitions into a 'fen': a

186 peatland under the influence of ground or surface water, often dominated by emergent fast-

187 growing vascular plants such as grasses, rushes and sedges (*25*). In fens, plant growth is

188 supported by a productivity-stimulating positive feedback in which the vegetation's root mat

189 traps and fixes the produced dead organic matter and maintaining effective water storage

190 through large pores and surface oscillation (*26–28*). Supported by oxygen released from the

191 root mat, the labile organic matter decomposes rapidly, releasing nutrients that in turn

192 stimulate plant growth (*29, 30*). The more recalcitrant fraction with the highest carbon

193 percentage, however, remains and accumulates (*31*).

194   Once the peat surface rises above the groundwater, the system transitions into a bog

195 in which decomposition-limiting feedbacks facilitate landscape formation (*12*). Bogs are fed

196 primarily by rainwater, which is retained within the landform by both the vegetation –

197 *Sphagnum* moss in cool region bogs, and trees in the tropics – and the accumulated peat

198 layer (*12*). The plants, and their detrital remains, limit lateral and vertical drainage and

199 regulate evaporation. As a result, soils remain persistently waterlogged, acidic, anoxic,

200 nutrient-poor; these conditions hamper the establishment of competitive species, and stifle

201 organic matter decomposition (*12, 32–34*).

202   The self-reinforcing biogeomorphic feedback between vegetation development, water

203 retention and peat accumulation yields a biogenic landscape that forms over a period of

204 hundreds to thousands of years, with long-term peat and carbon accumulation rates of 1-3

205 mm yr^{-1} and on average 18 g C m^{-2} yr^{-1} (which is lower than modern sequestration rates due

206 to continued decomposition, **Fig 1C**) (*35, 36*). Primary production is higher in tropical

207 peatlands than boreal and temperate ones, and is quantitatively different because of the

208 production of lignin (*37, 38*), which allows for higher sequestration rates (**Fig. 1C**).

209

210 *Coastal wetlands*

211 Compared to peatlands, seagrass meadows, salt marshes and mangrove forests are generally

212 more productive, and are driven by productivity-stimulating feedbacks (*38, 39*). While

213 peatlands generally have low inputs of external organic C, coastal wetlands commonly receive

214 organic matter from the ocean and from rivers, and thus sequester both externally and locally

215 produced organic matter (*20, 40*). By attenuating currents and waves with their aboveground

216 vegetation structures, coastal wetlands can trap large amounts of externally produced,

217 suspended organic particles that end up buried in the root-stabilized anoxic soils (*13, 41*). The

218 ratio of locally versus externally produced organic matter differs widely depending on

219 wetland size, vegetation and location (*20, 42*), with close proximity to productive coastal

220 waters or rivers favoring allochthonous input (*43, 44*). Moreover, large wetlands with dense

221 and stiff vegetation also tend to dissipate more hydrodynamic energy, thereby favoring

222 entrapment of incoming particles (*45, 46*). Externally produced organic material often

223 appears to be much more recalcitrant than the internally produced fraction (*47*). This

224 highlights that the filtering function of these wetlands may rival their local productivity in

225 importance for carbon sequestration as on average almost 50% of all buried organic carbon

226 originates from external sources, although this value varies with context (*20–23*) (**Fig 1C**).

227   Regardless of its origin, the presence of organic matter in vegetated coastal wetlands

228 creates a productivity-stimulating positive feedback. Decomposition of labile organic matter

229 fueled by radial oxygen loss from plant roots (*48*) stimulates *in situ* plant production, while

230 the more recalcitrant fraction is stored in the sediment layers (*40, 49*). In addition, soil

231 stabilization and attenuation of hydrodynamic forces reduce losses from uprooting and

232 erosion during storms, while the active trapping of particles from the water column also

233 increases water clarity (*13, 50*), enhancing underwater light availability and favoring the

234 growth of seagrass meadows (*13*). In salt marshes and mangroves, the trapping of particles

235 increases the bed-level, thereby reducing inundation stress (*51*). Moreover, reciprocal

236 facilitation between coastal vegetation and associated biota can further amplify carbon

237 storage (*52*, *53*). Finally, an increasing number of studies highlight the importance of
238 landscape-scale reciprocal interactions between coastal ecosystems. Specifically, seagrasses
239 have been found to facilitate marsh and mangrove establishment through their attenuation
240 of waves (*54*), while marshes and mangroves trap suspended particles to improve water
241 clarify and facilitate adjacent seagrasses.

242 These multiple, and in many cases cross-ecosystem, productivity-stimulating
243 biogeomorphic feedbacks result in highly productive wetland complexes, with soils that
244 rapidly accrete, both vertically and laterally, over time in the initial phase of development
245 (*55*). In salt marshes, sediment accretion rates can reach up to 25 mm yr^{-1}, while in
246 mangroves and seagrasses rates can be as high as 21 and 10 mm yr^{-1}, respectively (*56*). As
247 these ecosystems age and develop, their sediment accumulation rates may keep pace with or
248 even exceed sea level rise (current relative sea level rise: 0-10 mm yr^{-1}) (*57*, *58*). When
249 sediment accretion rates exceed relative sea level rise, local carbon accumulation levels out
250 as the increasing surface elevation decreases water saturation (i.e., higher decomposition)
251 and flooding frequency (i.e., lower organic matter import) (*57*, *59*).

252
253 ## Human-induced breakdown of feedbacks: from carbon sink to source

254 Many biogeomorphic wetlands have been rapidly deteriorating and continue to decline in
255 area at rates ranging from 0.4 to 3.3% per year, with the exception of cooler-region, boreal
256 peatlands that have remained stable (**Table 1**). Salt marshes have declined by 42%, while
257 mangroves and seagrass meadows have lost 35 and 29% of their area over the last centuries,
258 respectively (*60–63*). These losses are caused by habitat destruction from land use change,
259 overexploitation, eutrophication, salinization, trophic cascades and climate change-related
260 extreme events such as heat waves and increased storm magnitude and frequency (*64*, *65*). In
261 the future, sea level rise will likely result in major loss of coastal wetlands and their carbon
262 stocks, particularly in areas where landward migration is hampered by human infrastructure –
263 a phenomenon called 'coastal squeeze' (*66*). Temperate and tropical peatlands have been
264 degraded by 57% and 41% in their areal extent, respectively, mostly due to land use changes,
265 exploitation, and wildfires (*60*, *67*). By contrast, boreal peatlands have not been rapidly
266 declining in their overall extent (<5% loss). However, climate change-driven thawing of the
267 permafrost, which encompasses about half of all boreal peatlands, has affected 15% of these
268 coldest peatlands. The net effect of permafrost thaw on the climate remains unknown,

269   because on the one hand permafrost thaw increases methane (CH_4) and CO_2 emissions from

270   increased decomposition rates, while simultaneously increasing productivity and carbon

271   sequestration (*68*, *69*).

272   At present, biogeomorphic wetlands worldwide experience average annual loss rates

273   of around 1% with associated yearly carbon losses amounting to 0.5 Pg C (**Table 1**), which

274   would account for 5% of the current anthropogenic carbon emissions (11.5 Pg C) (*4*). In

275   contrast to the immediate carbon losses from logging of forests, land-use changes in

276   biogeomorphic wetlands do not necessarily result in the immediate removal of most carbon,

277   as the bulk of the carbon is stored in the soil (**Fig. 1**). Specifically, conversion of peatlands to

278   agricultural land results in instant carbon loss due to the removal of any aboveground

279   biomass (*70*), but this is followed by a continued loss of soil organic carbon in the following

280   century (*71*, *72*) (**Fig. 3**). Loss of coastal wetland vegetation commonly results in rapid erosion

281   and oxidation of carbon rich soils, as the vegetation no longer stabilizes the soil (*73*, *74*).

282   However, in regions where coastal wetlands are 'reclaimed' under the protection of levees or

283   dikes, erosion from currents and waves is obviously unimportant, causing accumulated

284   organic matter to oxidize much more gradually (*61*).

285

Conservation and restoration of carbon hotspots

287   Our findings emphasize the importance of conserving and restoring biogeomorphic wetlands

288   worldwide. Conservation measures are particularly rewarding in peatlands where carbon

289   densities are the highest, and where carbon stocks lost by degradation take centuries to

290   millennia to rebuild. Complementary to conservation, restoration of degraded biogeomorphic

291   wetlands and their carbon storage and sink function should be a key element of our global

292   carbon strategy. Restoration is likely to be most rewarding over shorter timescales in both

293   high carbon stock systems (i.e., where emissions can be avoided) and high productivity

294   systems (i.e., where fast sequestration takes place). Coastal wetlands can offer great potential

295   for fast carbon accumulation by sequestering both externally and internally produced

296   material on a timescale of years to decades (*75*). Although carbon sequestration rates of

297   peatlands are slower than those in coastal systems, achieved gains from restoration can still

298   be high because these measures reduce currently ongoing large emissions from these areas

299   (*72*).

300   Because of the benefits for carbon storage and other ecosystem services,
301   conservation practitioners and policy makers increasingly consider restoration of
302   biogeomorphic wetlands as a viable tool to counteract mounting losses (*76, 77*). At present,
303   however, restoration of these systems is often ineffective (generally <50% success) (*76*), and
304   costly compared to other ecosystem types. For example, restoration costs of terrestrial
305   ecosystems such as grasslands, woodlands, temperate and tropical forests range from 500 to
306   5,000 US$/ha (*77*), with restoration scales ranging from <1000 to >100.000 ha (*78*). By
307   contrast, restoration of vegetated biogeomorphic wetlands most often occurs at spatial scales
308   of 0.1 to 10,000s ha with costs ranging from 750 to 1,000,000 US$/ha (*76, 79*). An important
309   issue underlying these low success rates and high costs is that biogeomorphic feedbacks only
310   work beyond a certain minimum vegetation patch size and density (*80*). Below these
311   thresholds, unpredictable losses occur, while natural establishment is hampered (*13, 81*). In
312   such cases, a so-called 'Window of Opportunity' may be required – a rare period of conditions
313   that are particularly beneficial for vegetation establishment and allow vegetation to grow
314   beyond the size or density threshold required for the biogeomorphic feedback to initiate and
315   support longer-term survival (*82*).

316   Despite the importance of facilitation by biogeomorphic feedbacks in wetlands, classic
317   restoration approaches have been strongly influenced by agriculture and forestry science,
318   which typically plant in dispersed spatial configuration with the aim of minimizing competition
319   (*83*). Recent advancements now emphasize the importance of facilitation over competition in
320   these systems. In coastal wetlands, restoration experiments demonstrate that large-scale
321   approaches favor facilitative interactions and are therefore typically more successful (*84*).
322   Similarly, facilitation can be harnessed at smaller scales by planting in clumps rather than
323   applying plantation-style dispersed designs, a change that was found to double restoration
324   yields (*83*). Moreover, the same can be achieved when individual small seagrass or marsh
325   grass plants are transplanted within biodegradable structures that temporarily mimic
326   facilitating effects of larger patches, such as suppression of waves and sediment mobility (*46,*
327   *85*). Finally, depending on the system, it may also be possible to artificially create a Window
328   of Opportunity with engineering measures to allow natural re-establishment (*86*).

329   Similar to coastal wetlands, peatland restoration has been most successful when
330   recovering natural conditions by large, landscape-scale rewetting measures. This is
331   particularly the case for peat bogs, where inserting dams to restore water retention in

332 degraded bogs has been successful as it creates a Window of Opportunity for natural plant-

333 hydrology feedbacks to re-establish (*87*). Sphagnum paludiculture, a new form of peat bog

334 culturing, takes this approach one step further as after rewetting, peatmosses are actively

335 introduced at a sufficient spatial scale to overcome establishment thresholds and allow their

336 sustainable harvest (*88*). Similarly, paludiculture in fens focuses on large-scale reintroduction

337 and sustainable harvest of rapidly growing helophytes, such as *Typha* sp., thus re-establishing

338 productivity-stimulating feedbacks (*88*). Finally, recent work revealed that peatland rewetting

339 strategies in general can be improved by striking the best balance between stopping

340 sustained CO_2 emissions from drainage and CH_4 release from rewetting by optimizing the

341 water table height (*72*, *89*).

342 Based on this synthesis, we argue that stopping biogeomorphic wetland losses via

343 conservation measures is of utmost importance. Moreover, recent technical advancements

344 that focus on recovery of landscape-forming feedbacks have now paved the way for large-

345 scale restoration that revert biogeomorphic wetlands from sources back to sinks. Therefore,

346 we argue that implementation of conservation measures combined with restoration actions

347 can enhance the role of biogeomorphic wetlands as natural climate solutions, facilitating

348 humanity to reach the targets set by the Paris Agreement and the UN Decade on Ecosystem

349 Restoration.

350

Figures captions and Tables
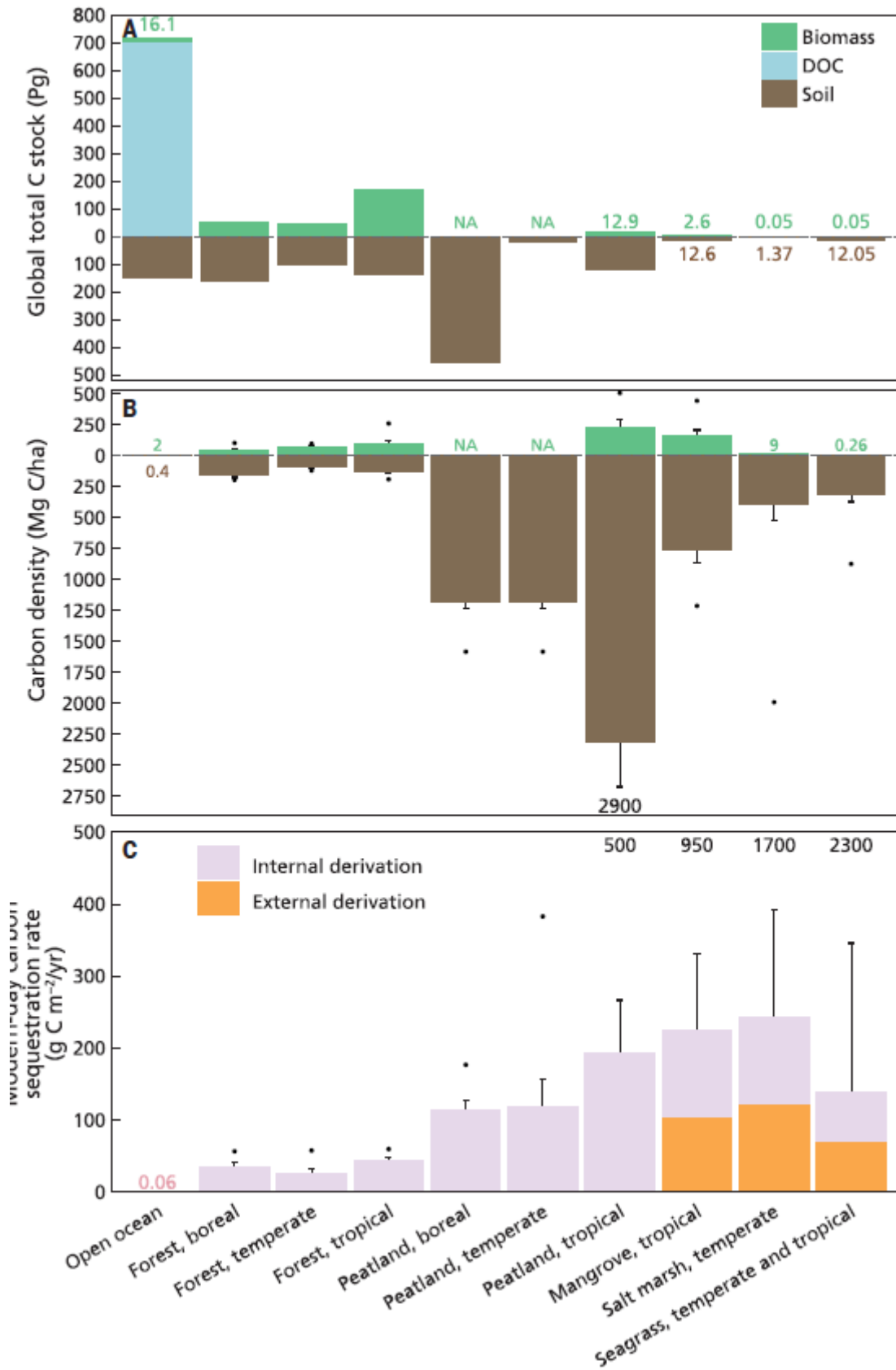
353   **Fig. 1. Overview of organic carbon stocks (A), densities (B) and modern-day carbon**
354   **sequestration rates (C) in the world's major carbon-storing ecosystems.** Ocean's hold the
355   largest stocks globally in the form of dissolved organic carbon (DOC, >97% of the carbon
356   pool), while peatlands store the largest amounts of carbon per unit area. Coastal ecosystems
357   generate the highest modern-day sequestration rates (mean rate over the last 10-125 years)
358   by storing both locally and externally derived organic matter. This process, however, may
359   become self-limiting when sediment elevation outpaces sea level rise, which is unlikely under
360   current climate change. In addition, damage from stochastic disturbances like e.g., storm-
361   induced erosion can also limit long-term storage. Error bars in panels B and C depict standard
362   deviation of the mean (SD); black dots (or numbers when they fall outside the y-axis) depict
363   observed maxima. Note that we could not calculate uncertainties for the ocean, because
364   these values were calculated from global estimates (*16*). Data were generally collected from
365   recent synthesis studies per ecosystem type (*16*). Carbon sequestration rates from periods
366   ranging from 10 to 125 years (recent apparent rate of carbon accumulation, which are higher
367   than long-term rates over *c.* 10k years due to continued decomposition of accumulated
368   matter) (*36*). See **Table S1** for references and methodological details (*16*).
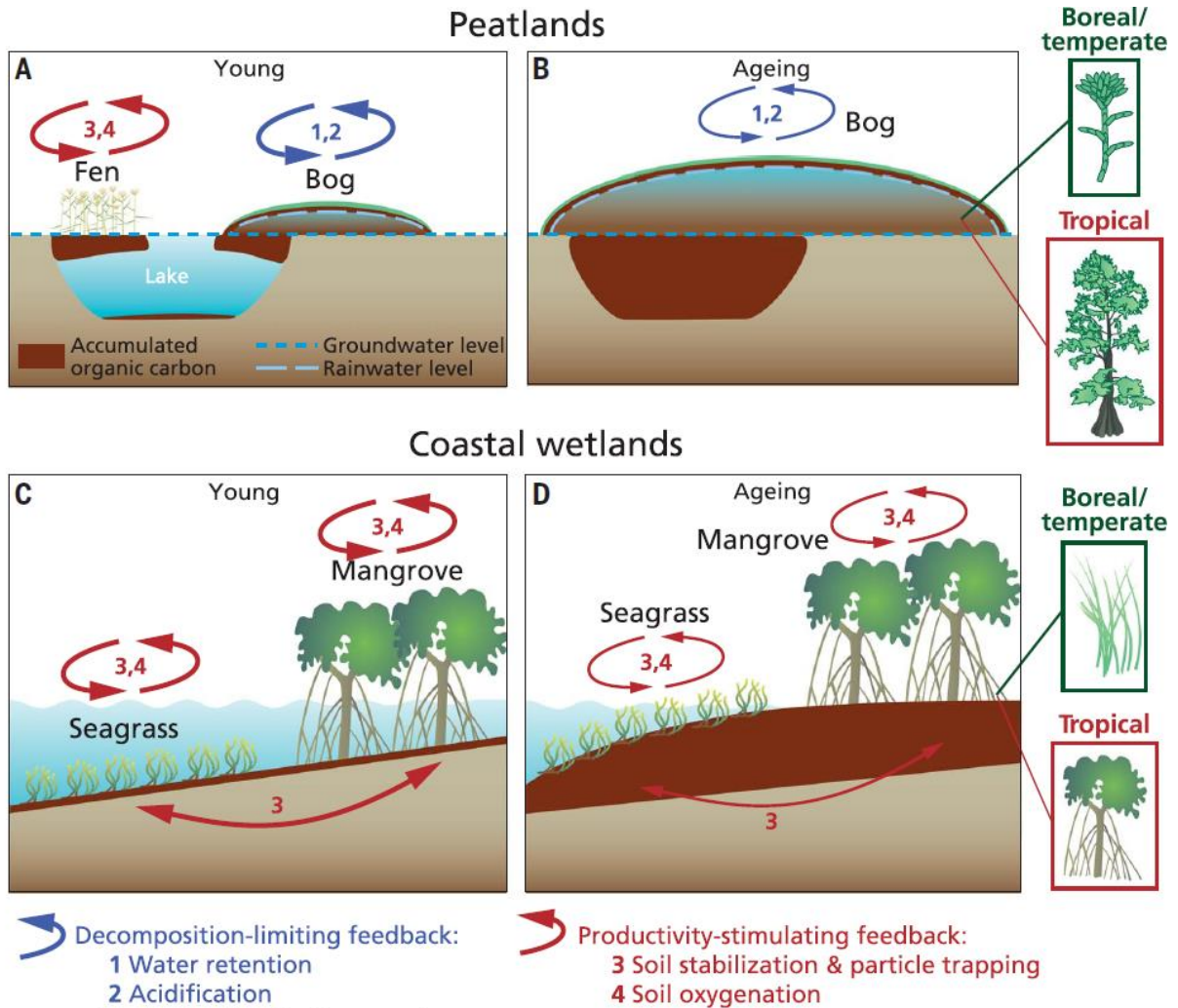
Fig. 2. Conceptual representation of the formation of carbon-storing biogeomorphic wetlands. Density-dependent processes underlying biogeomorphic feedbacks can be classified as productivity-stimulating or decomposition-limiting. (A) Peatland formation is initiated via either terrestrialization or paludification. Terrestrialization of aquatic systems by accumulation of organic matter from vascular plants is amplified by productivity-stimulating feedbacks in fens, while paludification initiates directly over mineral soil. (B) Once the peat surface rises above the groundwater level, and the peat is large enough to remain waterlogged by retaining rainwater, the resulting bog maintains waterlogged and acidic conditions, resulting in strong decomposition-limiting feedbacks. (C) Vegetated coastal ecosystems (seagrass meadows, mangroves and salt marshes) generate productivity-stimulating feedbacks that stimulate local production and substrate building. (D) This process can become self-limiting as the system ages, because increasing sediment elevation limits further development when this process outpaces sea level rise. This is not a comprehensive

383   representation of all feedbacks. Boxes with vegetation represent dominant vegetation type in

384   boreal/temperate and tropical wetlands, respectively.

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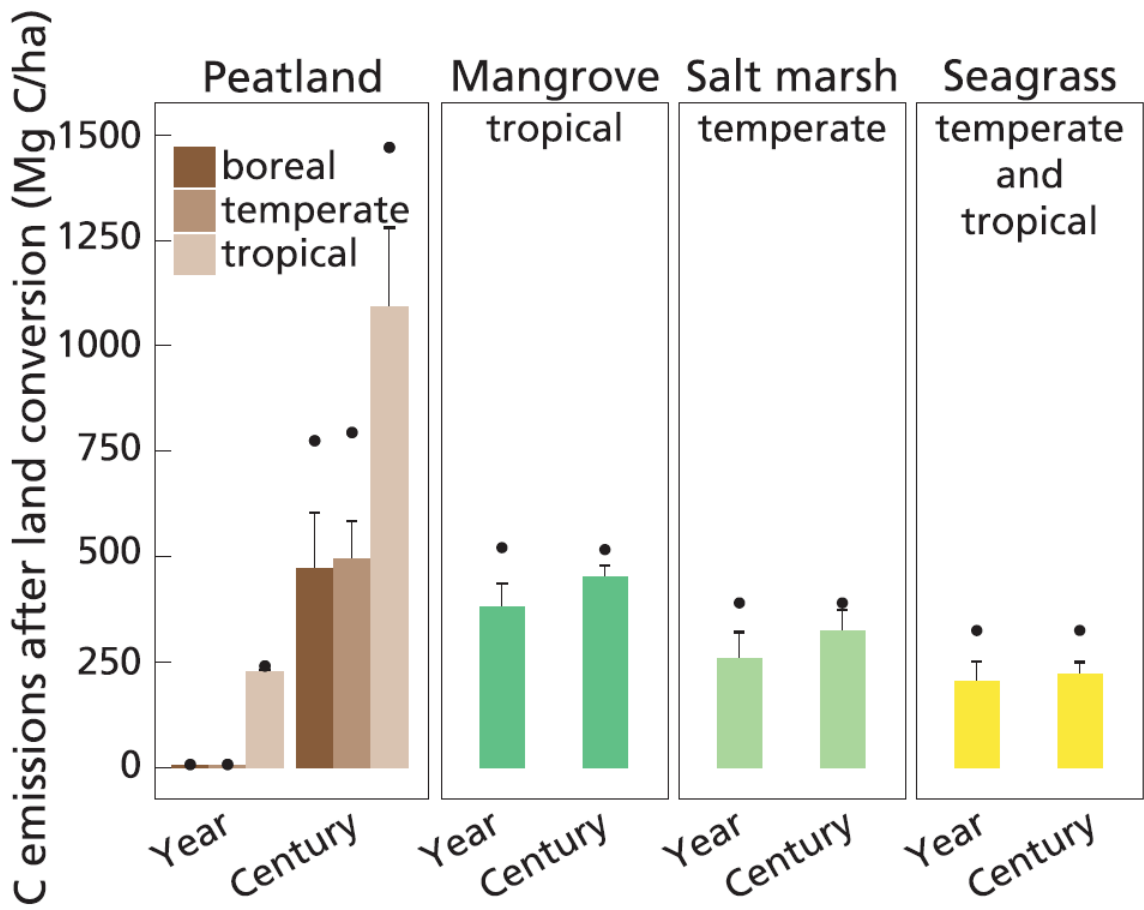
Fig. 3. Carbon emissions after land-use change in biogeomorphic wetlands. Land-use change and (subsequent) chemical and physical erosion result in rapid carbon losses in coastal systems (labeled 'Year'; one year loss). Although carbon losses in peatlands can also be high upon land-use change (e.g., logging of tropical forests), they are typically lower, but continue for centuries at a slower pace (labeled 'Century'; loss over 100 years), resulting in higher overall carbon losses. Error bars depict standard deviation of the mean (SD); black dots depict observed maxima. We assumed instantaneous emissions from biomass after land conversion. For coastal systems, loss of carbon after land conversion was assumed 25-100% after year 1 and 63-100% after 100 years (74), while for peatlands we applied commonly used land-use emission factors to calculate long-term losses (60, 72). See Table S2 for references and methodological details (16).

Table 1. Global extent (million hectare) of (near) natural biogeomorphic wetlands, lost or degraded (%) and the annual rate of human-induced losses (% yr^{-1}). The range shows minimum to maximum and the central value (square brackets).

Ecosystem	Climate zone	Global	Lost or	Annual	Ref.	Ref. loss /	Ref.

		extent (million hectare)	degraded (%)	loss rate (% yr^{-1})	Global extent	degraded	Annual loss rate (% yr^{-1})
Peatland	Boreal[*]	386 (170[**])	4% (15%[**])	0% (0.9%[**])	(60)	(60)	(90)
Peatland	Temperate	19	57%	0%[***]	(60)	(60)	(90)
Peatland	Tropical	59	41%	3.3 %	(60)	(60)	(91)
Mangrove	Tropical	17	35%	0.7 – 3.0 [1.9] %	(92)	(63)	(74)
Salt marsh	Temperate	6	42%	1.0 – 2.0 [1.5] %	(93)	(61)	(74)
Seagrass meadow	Temperate and tropical	18-60 [39]	29%	0.4 – 2.6 [1.5] %	(94)	(62)	(74)

401 [*]Includes polar and boreal peatlands; [**]Circa half of the boreal peatlands can be classified as permafrost peatlands (68). Their

402 pre-industrial extent was circa 200 million ha, but due to human-induced climate warming, 15% of permafrost peatlands have

403 been degraded at a loss rate of 0.9% since 1850, currently leaving 170 million ha; [***]Temperate peatlands are slowly

404 increasing in extent due to rewetting/restoration of degraded/drained peatlands (*c.* 300.000 ha in total).

References and notes

1. H. D. Matthews, N. P. Gillett, P. A. Stott, K. Zickfeld, The proportionality of global warming to cumulative carbon emissions. *Nature*. **459**, 829–832 (2009).

2. M. R. Allen *et al.*, Warming caused by cumulative carbon emissions towards the trillionth tonne. *Nature*. **458**, 1163–1166 (2009).

3. P. Ciais *et al.*, The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. *Chang. IPCC Clim.* **18**, 465–570 (2013).

4. P. Friedlingstein *et al.*, Global carbon budget 2020. *Earth Syst. Sci. Data*. **12**, 3269–3340 (2020).

5. N. C. Davidson, E. Fluet-Chouinard, C. M. Finlayson, Global extent and distribution of wetlands: trends and issues. *Mar. Freshw. Res.* **69**, 620–627 (2018).

6. Y. M. Bar-On, R. Phillips, R. Milo, The biomass distribution on Earth. *Proc. Natl. Acad. Sci.* **115**, 6506–6511 (2018).

7. E. McLeod *et al.*, A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. *Front. Ecol. Environ.* **9**, 552–560 (2011).

8. B. W. Griscom *et al.*, Natural climate solutions. *Proc. Natl. Acad. Sci.* **114**, 11645–11650 (2017).

9. P. Taillardat, B. S. Thompson, M. Garneau, K. Trottier, D. A. Friess, Climate change mitigation potential of wetlands and the cost-effectiveness of their restoration. *Interface Focus*. **10**, 20190129 (2020).

10. C. Schwarz *et al.*, Self-organization of a biogeomorphic landscape controlled by plant life-history traits. *Nat. Geosci.* **11**, 672–677 (2018).

11. C. Wang, S. Temmerman, Does biogeomorphic feedback lead to abrupt shifts between alternative landscape states?: An empirical study on intertidal flats and marshes. *J. Geophys. Res. Earth Surf.* **118**, 229–240 (2013).

12. H. Rydin, J. K. Jeglum, *The Biology of Peatlands* (Oxford University Press, 2013).

13. P. S. Maxwell *et al.*, *Biol. Rev.*, in press, doi:10.1111/brv.12294.

14. E. B. Barbier *et al.*, The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* **81**, 169–193 (2011).

15. J. H. C. Dau, Ansicht einiger der größeren und kleineren Moore Holsteins und

Schleswigs, nebst daraus abgeleitete Betrachtungen (Overview of some of the larger and smaller peatlands of Holstein and Schleswig with some considerations derived from them). *Schleswig-Holstein-Lauenburgsche Prov.* **10**, 73–82 (1821).

16. Materials and methods are available as supplementary materials on Science Online.

17. S. Emerson, J. I. Hedges, Processes controlling the organic carbon content of open ocean sediments. *Paleoceanography*. **3**, 621–634 (1988).

18. K. MacDicken *et al.*, *Global forest resources assessment 2015: how are the world's forests changing?* (The Food and Agriculture Organization, 2016), vol. Second Edi.

19. X. Ouyang, S. Y. Lee, Updated estimates of carbon accumulation rates in coastal marsh sediments. *Biogeosciences*, 5057 (2014).

20. J. J. Middelburg, J. Nieuwenhuize, R. K. Lubberts, O. van de Plassche, Organic Carbon Isotope Systematics of Coastal Marshes. *Estuar. Coast. Shelf Sci.* **45**, 681–687 (1997).

21. H. Kennedy *et al.*, Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochem. Cycles*. **24** (2010), doi:10.1029/2010GB003848.

22. P. Mueller *et al.*, Assessing the long-term carbon-sequestration potential of the semi-natural salt marshes in the European Wadden Sea. *Ecosphere*. **10**, e02556 (2019).

23. S. D. Sasmito *et al.*, Organic carbon burial and sources in soils of coastal mudflat and mangrove ecosystems. *Catena*. **187**, 104414 (2020).

24. H. Joosten, D. Clarke, *Wise use of mires and peatlands - background and principles including a framework for decision-making* (International Mire Conservation Group and International Peat Society, 2002).

25. L. P. M. Lamers *et al.*, Ecological restoration of rich fens in Europe and North America: from trial and error to an evidence-based approach. *Biol. Rev.* **90**, 182–203 (2015).

26. J. Schoelynck *et al.*, The trapping of organic matter within plant patches in the channels of the Okavango Delta: a matter of quality. *Aquat. Sci.* **79**, 661–674 (2017).

27. S. F. Stofberg, J. van Engelen, J.-P. M. Witte, S. E. van der Zee, Effects of root mat buoyancy and heterogeneity on floating fen hydrology. *Ecohydrology*. **9**, 1222–1234 (2016).

28. C. Fritz, D. I. Campbell, L. A. Schipper, Oscillating peat surface levels in a restiad peatland, New Zealand—magnitude and spatiotemporal variability. *Hydrol. Process.* **22**, 3264–3274 (2008).

29. D. J. Greenwood, The effect of oxygen concentration on the decomposition of organic

materials in soil. *Plant Soil*. **14**, 360–376 (1961).

30. L. P. M. Lamers *et al.*, Microbial transformations of nitrogen, sulfur, and iron dictate vegetation composition in wetlands: a review. *Front. Microbiol.* **3**, 156 (2012).

31. P. Rovira, V. R. Vallejo, Labile and recalcitrant pools of carbon and nitrogen in organic matter decomposing at different depths in soil: an acid hydrolysis approach. *Geoderma*. **107**, 109–141 (2002).

32. N. Van Breemen, How Sphagnum bogs down other plants. *Trends Ecol. Evol.* **10**, 270–275 (1995).

33. R. S. Clymo, The origin of acidity in Sphagnum bogs. *Bryologist*. **67**, 427–431 (1964).

34. E. Gorham, S. J. Eisenreich, J. Ford, M. V Santelmann, in *Chemical processes in lakes* (John Wiley and Sons, 1985), pp. 339–362.

35. Z. Yu, J. Loisel, D. P. Brosseau, D. W. Beilman, S. J. Hunt, Global peatland dynamics since the Last Glacial Maximum. *Geophys. Res. Lett.* **37** (2010).

36. D. M. Young *et al.*, Misinterpreting carbon accumulation rates in records from near-surface peat. *Sci. Rep.* **9**, 1–8 (2019).

37. A. Prager, A. Barthelmes, H. Joosten, A touch of tropics in temperate mires: on Alder carrs and carbon cycles. *Peatlands Int.* **2**, 26–29 (2006).

38. I. Aselmann, P. J. Crutzen, Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. *J. Atmos. Chem.* **8**, 307–358 (1989).

39. C. M. Duarte, J. Cebrián, The fate of marine autotrophic production. *Limnol. Oceanogr.* **41**, 1758–1766 (1996).

40. S. T. Chew, J. B. Gallagher, Accounting for black carbon lowers estimates of blue carbon storage services. *Sci. Rep.* **8**, 2553 (2018).

41. D. C. Donato *et al.*, Mangroves among the most carbon-rich forests in the tropics. *Nat. Geosci.* **4**, 293 (2011).

42. J. L. Breithaupt, J. M. Smoak, T. J. Smith III, C. J. Sanders, A. Hoare, Organic carbon burial rates in mangrove sediments: Strengthening the global budget. *Global Biogeochem. Cycles*. **26** (2012).

43. S. Bouillon *et al.*, Mangrove production and carbon sinks: A revision of global budget estimates. *Global Biogeochem. Cycles*. **22** (2008), doi:10.1029/2007GB003052.

44. S. Bouillon, R. M. Connolly, in *Ecological connectivity among tropical coastal*

ecosystems (Springer, 2009), pp. 45–70.

45. T. J. Bouma *et al.*, Trade-offs related to ecosystem engineering: a case study on stiffness of emerging macrophytes. *Ecology*. **86**, 2187–2199 (2005).

46. R. J. M. Temmink *et al.*, Mimicry of emergent traits amplifies coastal restoration success. *Nat. Commun.* **11**, 1–9 (2020).

47. M. Van de Broek *et al.*, Long-term organic carbon sequestration in tidal marsh sediments is dominated by old-aged allochthonous inputs in a macrotidal estuary. *Glob. Chang. Biol.* **24**, 2498–2512 (2018).

48. K. Koop-Jakobsen, F. Wenzhöfer, The Dynamics of Plant-Mediated Sediment Oxygenation in Spartina anglica Rhizospheres—a Planar Optode Study. *Estuaries and Coasts*. **38**, 951–963 (2015).

49. M. E. Gonneea, A. Paytan, J. A. Herrera-Silveira, Tracing organic matter sources and carbon burial in mangrove sediments over the past 160 years. *Estuar. Coast. Shelf Sci.* **61**, 211–227 (2004).

50. R. K. James *et al.*, Maintaining tropical beaches with seagrass and algae: a promising alternative to engineering solutions. *Bioscience*. **69**, 136–142 (2019).

51. G. S. Fivash *et al.*, Elevated micro-topography boosts growth rates in Salicornia procumbens by amplifying a tidally-driven oxygen pump: implications for natural recruitment and restoration. *Ann. Bot.* (2019), doi:10.1093/aob/mcz137.

52. T. B. Atwood *et al.*, Predators help protect carbon stocks in blue carbon ecosystems. *Nat. Clim. Chang.* **5**, 1038–1045 (2015).

53. L. Ren, K. Jensen, P. Porada, P. Mueller, Biota-mediated carbon cycling—A synthesis of biotic-interaction controls on blue carbon. *Ecol. Lett.* **n/a** (2022), doi:https://doi.org/10.1111/ele.13940.

54. L. G. Gillis *et al.*, Potential for landscape-scale positive interactions among tropical marine ecosystems. *Mar. Ecol. Prog. Ser.* **503**, 289–303 (2014).

55. C. J. T. Ladd, M. F. Duggan-Edwards, T. J. Bouma, J. F. Pages, M. W. Skov, Sediment supply explains long-term and large-scale patterns in salt marsh lateral expansion and erosion. *Geophys. Res. Lett.* **46**, 11178–11187 (2019).

56. C. M. Duarte, I. J. Losada, I. E. Hendriks, I. Mazarrasa, N. Marbà, The role of coastal plant communities for climate change mitigation and adaptation. *Nat. Clim. Chang.* **3**, 961–968 (2013).

57.   M. L. Kirwan, J. P. Megonigal, Tidal wetland stability in the face of human impacts and sea-level rise. *Nature*. **504**, 53–60 (2013).

58.   M. L. Kirwan, S. Temmerman, E. E. Skeehan, G. R. Guntenspergen, S. Fagherazzi, Overestimation of marsh vulnerability to sea level rise. *Nat. Clim. Chang.* **6**, 253–260 (2016).

59.   A. Jacotot, C. Marchand, B. E. Rosenheim, E. W. Domack, M. Allenbach, Mangrove sediment carbon stocks along an elevation gradient: Influence of the late Holocene marine regression (New Caledonia). *Mar. Geol.* **404**, 60–70 (2018).

60.   J. Leifeld, L. Menichetti, The underappreciated potential of peatlands in global climate change mitigation strategies /704/47/4113 /704/106/47 article. *Nat. Commun.* **9**, 1071 (2018).

61.   K. B. Gedan, B. R. Silliman, M. D. Bertness, Centuries of Human-Driven Change in Salt Marsh Ecosystems. *Ann. Rev. Mar. Sci.* **1**, 117–141 (2009).

62.   M. Waycott *et al.*, Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci.* **106**, 12377–12381 (2009).

63.   M. A. E. Millennium Ecosystem Assessment, thesis, Island Press, Washington, DC (2005).

64.   R. J. Orth *et al.*, A Global Crisis for Seagrass Ecosystems. *Bioscience*. **56**, 987–996 (2006).

65.   M. F. Adame *et al.*, Future carbon emissions from global mangrove forest loss. *bioRxiv* (2020).

66.   C. E. Lovelock, R. Reef, Variable impacts of climate change on blue carbon. *One Earth*. **3**, 195–211 (2020).

67.   M. R. Turetsky *et al.*, Global vulnerability of peatlands to fire and carbon loss. *Nat. Geosci.* **8**, 11–14 (2015).

68.   G. Hugelius *et al.*, Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. *Proc. Natl. Acad. Sci.* **117**, 20438–20446 (2020).

69.   M. R. Turetsky *et al.*, Carbon release through abrupt permafrost thaw. *Nat. Geosci.* **13**, 138–143 (2020).

70.   K. Hergoualc'h, L. V Verchot, Stocks and fluxes of carbon associated with land use change in Southeast Asian tropical peatlands: A review. *Global Biogeochem. Cycles*. **25** (2011), doi:10.1029/2009gb003718.

71. B. Tiemeyer *et al.*, High emissions of greenhouse gases from grasslands on peat and other organic soils. *Glob. Chang. Biol.* **22**, 4134–4149 (2016).

72. A. Günther *et al.*, Prompt rewetting of drained peatlands reduces climate warming despite methane emissions. *Nat. Commun.* **11**, 1644 (2020).

73. Z. Wang *et al.*, Human-induced erosion has offset one-third of carbon emissions from land cover change. *Nat. Clim. Chang.* **7**, 345–349 (2017).

74. L. Pendleton *et al.*, Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS One*. **7** (2012).

75. P. I. Macreadie *et al.*, Blue carbon as a natural climate solution. *Nat. Rev. Earth Environ.*, 1–14 (2021).

76. E. Bayraktarov *et al.*, The cost and feasibility of marine coastal restoration. *Ecol. Appl.* **26**, 1055–1074 (2016).

77. R. S. De Groot *et al.*, Benefits of Investing in Ecosystem Restoration. *Conserv. Biol.* **27**, 1286–1293 (2013).

78. E. Romijn *et al.*, Land restoration in Latin America and the Caribbean: an overview of recent, ongoing and planned restoration initiatives and their potential for climate change mitigation. *Forests*. **10**, 510 (2019).

79. R. Andersen *et al.*, An overview of the progress and challenges of peatland restoration in Western Europe. *Restor. Ecol.* **25**, 271–282 (2017).

80. T. J. Bouma *et al.*, Density-dependent linkage of scale-dependent feedbacks: a flume study on the intertidal macrophyte Spartina anglica. *Oikos*. **118**, 260–268 (2009).

81. M. Scheffer, S. Carpenter, J. A. Foley, C. Folke, B. Walker, Catastrophic shifts in ecosystems. *Nature*. **413**, 591–596 (2001).

82. T. J. Bouma *et al.*, Identifying knowledge gaps hampering application of intertidal habitats in coastal protection: Opportunities & steps to take. *Coast. Eng.* **87**, 147–157 (2014).

83. B. R. Silliman *et al.*, Facilitation shifts paradigms and can amplify coastal restoration efforts. *Proc. Natl. Acad. Sci.* **112**, 14295–14300 (2015).

84. M. M. van Katwijk *et al.*, Global analysis of seagrass restoration: the importance of large-scale planting. *J. Appl. Ecol.* **53**, 567–578 (2016).

85. T. van der Heide *et al.*, Coastal restoration success via emergent trait-mimicry is context dependent. *Biol. Conserv.* **264**, 109373 (2021).

86. G. S. Fivash *et al.*, Restoration of biogeomorphic systems by creating Windows of Opportunity to support natural establishment processes. *Ecol. Appl.*, e2333 (2021).

87. N. Kettridge *et al.*, Moderate drop in water table increases peatland vulnerability to post-fire regime shift. *Sci. Rep.* **5**, 1–4 (2015).

88. W. Wichtmann, C. Schröder, H. Joosten, *Paludiculture-productive use of wet peatlands* (Schweizerbart Science Publishers, Stuttgart, 2016).

89. C. D. Evans *et al.*, Overriding water table control on managed peatland greenhouse gas emissions. *Nature*, 1–7 (2021).

90. H. Joosten, The Global Peatland CO2 Picture: peatland status and drainage related emissions in all countries of the world. *Glob. Peatl. CO2 Pict. Peatl. status Drain. Relat. Emiss. all Ctries. world.* (2009).

91. H. Joosten, M. Tapio-Biström, S. Tol, *Peatlands - guidance for climate change mitigation through conservation, rehabilitation and sustainable use* (Rome, the Food and Agriculture Organization of the United Nations and Wetlands International, 2012).

92. J. Sanderman *et al.*, A global map of mangrove forest soil carbon at 30 m spatial resolution. *Environ. Res. Lett.* (2018).

93. C. J. Mcowen *et al.*, A global map of saltmarshes. *Biodivers. data J.* (2017).

94. E. P. Green, F. T. Short, T. Frederick, *World atlas of seagrasses* (Univ of California Press, 2003).

95. T. Temmink, R.J.M., Lamers, L.P.M., Angelini, C., Bouma, T.J., Fritz, C., van de Koppel, J., Lexmond, R., Rietkerk, M., Silliman, B.R., Joosten, H., van der Heide, Data from: Recovering wetland biogeomorphic feedbacks to restore the world's biotic carbon hotspots. *Zenodo* (2022) (available at doi: 10.5281/zenodo.6411400).

96. R. A. Houghton, Balancing the global carbon budget. *Annu. Rev. Earth Planet. Sci.* **35**, 313–347 (2007).

97. R. Dommain, J. Couwenberg, H. Joosten, Development and carbon sequestration of tropical peat domes in south-east Asia: links to post-glacial sea-level changes and Holocene climate variability. *Quat. Sci. Rev.* **30**, 999–1010 (2011).

98. I. P. on C. C. (IPCC), *2013 supplement to the 2006 IPCC guidelines for national greenhouse gas inventories: Wetlands* (2014).

99. L. P. Gouvêa *et al.*, Golden carbon of Sargassum forests revealed as an opportunity for

climate change mitigation. *Sci. Total Environ.*, 138745 (2020).

100. H. Joosten, 19 Current Soil Carbon Loss and Land Degradation Globally: Where are the Hotspots and Why There? *Soil Carbon Sci. Manag. Policy Mult. Benefits*. **71**, 224 (2014).

101. J. W. Fourqurean *et al.*, Seagrass ecosystems as a globally significant carbon stock. *Nat. Geosci.* **5**, 505 (2012).

102. M. A. Charette, W. H. F. Smith, The volume of Earth's ocean. *Oceanography*. **23**, 112–114 (2010).

103. J. Loisel *et al.*, A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *the Holocene*. **24**, 1028–1042 (2014).

104. E. Gorham, Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecol. Appl.* **1**, 182–195 (1991).

105. G. C. Dargie *et al.*, Age, extent and carbon storage of the central Congo Basin peatland complex. *Nature*. **advance on** (2017), doi:10.1038/nature21048http://www.nature.com/nature/journal/vaop/ncurrent/abs/nature21048.html#supplementary-information.

106. S. E. Page, J. O. Rieley, C. J. Banks, Global and regional importance of the tropical peatland carbon pool. *Glob. Chang. Biol.* **17**, 798–818 (2011).

107. F. Zehetner, Does organic carbon sequestration in volcanic soils offset volcanic CO2 emissions? *Quat. Sci. Rev.* **29**, 1313–1316 (2010).

108. W. M. Post, K. C. Kwon, Soil carbon sequestration and land-use change: processes and potential. *Glob. Chang. Biol.* **6**, 317–327 (2000).

109. Y. Yang *et al.*, Increased topsoil carbon stock across China's forests. *Glob. Chang. Biol.* **20**, 2687–2696 (2014).

110. J. Turunen, N. T. Roulet, T. R. Moore, P. J. H. Richard, Nitrogen deposition and increased carbon accumulation in ombrotrophic peatlands in eastern Canada. *Global Biogeochem. Cycles*. **18** (2004).

111. J. Loisel, Z. Yu, Recent acceleration of carbon accumulation in a boreal peatland, south central Alaska. *J. Geophys. Res. Biogeosciences*. **118**, 41–53 (2013).

112. G. Primeau, M. Garneau, Carbon accumulation in peatlands along a boreal to subarctic transect in eastern Canada. *The Holocene*, 0959683620988031 (2021).

113. H. Zhang *et al.*, Decreased carbon accumulation feedback driven by climate-induced

drying of two southern boreal bogs over recent centuries. *Glob. Chang. Biol.* **26**, 2435–2448 (2020).

114. C. Craft, C. Washburn, A. Parker, in *Wastewater treatment, plant dynamics and management in constructed and natural wetlands* (Springer, 2008), pp. 23–31.

115. J. A. Villa, W. J. Mitsch, Carbon sequestration in different wetland plant communities in the Big Cypress Swamp region of southwest Florida. *Int. J. Biodivers. Sci. Ecosyst. Serv. Manag.* **11**, 17–28 (2015).

116. M. F. Billett *et al.*, Carbon balance of UK peatlands: current state of knowledge and future research challenges. *Clim. Res.* **45**, 13–29 (2010).

117. K. Bao *et al.*, Carbon accumulation in temperate wetlands of Sanjiang Plain, Northeast China. *Soil Sci. Soc. Am. J.* **75**, 2386–2397 (2011).

118. K. Bao, X. Yu, L. Jia, G. Wang, Recent carbon accumulation in Changbai Mountain peatlands, northeast China. *Mt. Res. Dev.* **30**, 33–41 (2010).

119. C. Zaccone *et al.*, Highly anomalous accumulation rates of C and N recorded by a relic, free-floating peatland in Central Italy. *Sci. Rep.* **7**, 1–10 (2017).

120. M. Wang *et al.*, Higher recent peat C accumulation than that during the Holocene on the Zoige Plateau. *Quat. Sci. Rev.* **114**, 116–125 (2015).

121. K. Bao, G. Wang, W. Xing, J. Shen, Accumulation of organic carbon over the past 200 years in alpine peatlands, northeast China. *Environ. Earth Sci.* **73**, 7489–7503 (2015).

122. C. A. León, G. Oliván, Recent rates of carbon and nitrogen accumulation in peatlands of Isla Grande de Chiloé-Chile. *Rev. Chil. Hist. Nat.* **87**, 1–7 (2014).

123. M. S. Bunsen, J. Loisel, Carbon storage dynamics in peatlands: Comparing recent-and long-term accumulation histories in southern Patagonia. *Glob. Chang. Biol.* **26**, 5778–5795 (2020).

124. S. Van Bellen *et al.*, Late-Holocene climate dynamics recorded in the peat bogs of Tierra del Fuego, South America. *The Holocene*. **26**, 489–501 (2016).

125. B. Bernal, W. J. Mitsch, Carbon sequestration in freshwater wetlands in Costa Rica and Botswana. *Biogeochemistry*. **115**, 77–93 (2013).

126. S. Suzuki, T. Ishida, T. Nagano, S. Waijaroen, Influences of deforestation on carbon balance in a natural tropical peat swamp forest in Thailand. *Environ. Control Biol.* **37**, 115–128 (1999).

127. S. E. Page *et al.*, A record of Late Pleistocene and Holocene carbon accumulation and

climate change from an equatorial peat bog (Kalimantan, Indonesia): implications for past, present and future carbon dynamics. *J. Quat. Sci.* **19**, 625–635 (2004).

128. L. F. Lourençato *et al.*, Carbon accumulation rates recorded in the last 150 years in tropical high mountain peatlands of the Atlantic Rainforest, SE-Brazil. *Sci. Total Environ.* **579**, 439–446 (2017).

129. S. Page, R. Wust, C. Banks, Past and present carbon accumulation and loss in Southeast Asian peatlands. *Pages News*. **18**, 25–26 (2010).

130. K. A. Hapsari *et al.*, Environmental dynamics and carbon accumulation rate of a tropical peatland in Central Sumatra, Indonesia. *Quat. Sci. Rev.* **169**, 173–187 (2017).

131. Y. Xiong, B. Liao, F. Wang, Mangrove vegetation enhances soil carbon storage primarily through in situ inputs rather than increasing allochthonous sediments. *Mar. Pollut. Bull.* **131**, 378–385 (2018).

132. N. Garcias-Bonet *et al.*, Carbon and Nitrogen Concentrations, Stocks, and Isotopic Compositions in Red Sea Seagrass and Mangrove Sediments . *Front. Mar. Sci.* . **6** (2019), p. 267.

133. C. E. Stringer, C. C. Trettin, S. J. Zarnoch, Soil properties of mangroves in contrasting geomorphic settings within the Zambezi River Delta, Mozambique. *Wetl. Ecol. Manag.* **24**, 139–152 (2016).

134. J. Zhou, Y. Wu, Q. Kang, J. Zhang, Spatial variations of carbon, nitrogen, phosphorous and sulfur in the salt marsh sediments of the Yangtze Estuary in China. *Estuar. Coast. Shelf Sci.* **71**, 47–59 (2007).

135. B. R. Tanner *et al.*, Comparison of bulk and compound-specific $\delta 13C$ analyses and determination of carbon sources to salt marsh sediments using n-alkane distributions (Maine, USA). *Estuar. Coast. Shelf Sci.* **86**, 283–291 (2010).

136. N. Saintilan, K. Rogers, D. Mazumder, C. Woodroffe, Allochthonous and autochthonous contributions to carbon accumulation and carbon store in southeastern Australian coastal wetlands. *Estuar. Coast. Shelf Sci.* **128**, 84–92 (2013).

137. T. Gebrehiwet, C. M. Koretsky, R. V Krishnamurthy, Influence of Spartina and Juncus on saltmarsh sediments. III. Organic geochemistry. *Chem. Geol.* **255**, 114–119 (2008).

138. H. T. S. Boschker, J. F. C. De Brouwer, T. E. Cappenberg, The contribution of macrophyte-derived organic matter to microbial biomass in salt-marsh sediments: Stable carbon isotope analysis of microbial biomarkers. *Limnol. Oceanogr.* **44**, 309–

319 (1999).

139. C. M. Duarte *et al.*, Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochem. Cycles*. **24** (2010), doi:10.1029/2010GB003793.

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Supplementary Materials for

Recovering wetland biogeomorphic feedbacks to restore the world's biotic carbon hotspots

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Materials and Methods

In this review, we start by evaluating the carbon stocks and sequestration rates of the world's major carbon-storing ecosystems as generally reported in literature (*96*). These are (1) oceans, (2) forests, and (3) wetlands (*4, 8, 75*). Next, we focus on the importance and functioning of so-called 'biogeomorphic wetlands' that have the highest carbon stocks per unit area. Wetlands are defined as areas where water covers the soil, or is present either at or near the surface of the soil all year or for varying periods of time during the year. The landscape of biogeomorphic wetlands is built by biogeomorphic feedbacks defined as self-reinforcing interactions between biota and geomorphology. This means that organisms – often vegetation – engineer landforms to their own benefit following positive density-dependent relationships. Moreover, we focus on biogeomorphic wetlands with a relatively large spatial extent (**Table 1, S1**). Ecosystems that meet the above definitions are peatlands, mangroves, salt marshes and seagrass meadows. Combined these ecosystems encompass 45% of all wetlands worldwide (**Table 1,** based on total wetland extent and the extent of biogeomorphic wetlands) (*5*). Similar to forests, we have segregated peatlands following main climate zones (boreal, temperate and tropical), but for reasons of simplicity and data availability chose to not split peatlands into further subcategories (e.g., raised bog, blanket bog, rich fen, poor fen). Similarly, we have not segregated various types of mangroves, salt marshes and seagrass meadows.

Data acquisition

To obtain data on global carbon stocks, density, sequestration, and spatial extent, we used relevant references obtained from Google Scholar and Web of Science. In addition, we also checked reference lists of papers found for additional sources. Only data on organic carbon were included, implying that inorganic carbon sinks such as carbonate sediments and reef structures were excluded. See **Table S1-S2** for an overview of the used sources per biogeomorphic wetland type.

Sequestration Rate Calculations

We chose to include modern sequestration rates (10-125 years) based on ^{137}Cs and ^{210}Pb rather than historic ones (at timescales of *c.* 10k years (*36, 97*)). Although these proxies cannot account for decomposition of older peat layers (*36*), they most accurately reflect current climate change mitigation potential, and enable direct comparisons between ecosystem types. Consequently, extrapolation of our estimates to longer timescales would result in an overestimation, because part of the organic matter stored in this upper layer continues to decompose (*36, 97*). However, averaging carbon sequestration rates over longer timescales would cause significant deviations from the actual current rates, because historic fluctuations in climatic and environmental conditions greatly affect sequestration rates (*17, 36, 97, 98*). See **Table S1** for sources and ecosystem specific information.

Carbon Emission Calculations

To calculate the effect of land-use and land-use changes on carbon emissions from different ecosystems on different timescales, we assumed that upon deforestation all carbon in standing aboveground biomass is instantaneously lost (e.g., tropical peatlands and mangroves) and that carbon in other living biomass was negligible. For peatlands, we assumed sustained carbon emissions for (at least) 100 years due to ongoing decomposition of the soil organic matter (*98*). Following Pendleton et al. (*74*), we further assumed that all coastal ecosystems lose 25-100% of their susceptible carbon in the top meter of soil upon land-use change. See **Table S2** for used sources and details on calculations.

Table S1. Sources and calculations underlying Figure 1.

Ecosystem	Sources and data description	Metric reported	Calculations
	Panel A: Total C stocks[*]		
Open ocean	Schematics of the global C cycle with annual fluxes and C reservoirs (biota, dissolved organic C and soil organic C). (*3*, *17*) differentiated between soil organic C and $CaCO_3$ sediments, as well as dissolved organic and inorganic C in the water column. In our study, we only included the organic sinks in including ocean biomass (*99*).	Stocks	NA
Forest, boreal Forest, temperate Forest, tropical	Database compiled by (*18*) from standardized Country Reports as part of the Global Forest Resources Assessments 2015. Aboveground C includes trees, stem stumps, branches, bark, seeds and foliage. Soil organic C, summarized by (*100*), was measured to a depth of 1 m.	Stocks	NA
Peatland, boreal Peatland, temperate	Database compiled by (*60*) for temperate and boreal peat soils. Best estimates from updated global peatland area, peat deposits until mineral subsoil, bulk density and its C content. C in biomass was assumed to be negligible.	Stocks	NA
Peatland, tropical	Soil C data were obtained as stocks from (*60*) (see above). Aboveground C data were derived from C density from (*70*) and areal extent data reported by (*60*).	Stocks Areal extent C density	Aboveground C was calculated by multiplying aboveground C density by areal extent.
Mangroves, tropical	Soil organic C was compiled by (*92*). Median sampling depth was 1 m, but ranged from 0.05 to 3 m. (*92*) calculated total soil C for 1 and 2 m soil depth (6.4 and 12.6 Pg C, respectively). We used the C estimate for 2 m soil depth. Aboveground C was compiled by (*41*).	Stocks	NA
Salt marsh, temperate	(*19*) compiled C density of the soil, (*74*) compiled aboveground C, and (*93*) compiled the areal extent. Soil C density was based on bulk density and C content for near-surface C (< 1 m).	Areal extent C density	C stock in either soil or biomass was calculated by multiplying C density by areal extent.
Seagrass meadow, temperate and tropical	Soil organic C and biomass was compiled by (*101*). Global estimates of soil organic C for top meter (4.2 to 8.4 Pg C) and deeper cores (9.8 to 19.9 Pg C) are based on dry bulk density and its C content.	Stocks	NA
	*Panel B: C density**		
Open ocean	Schematics of the global C cycle with annual fluxes and C reservoirs (biota, dissolved organic C and soil organic C). (*3*, *17*) differentiated between soil organic C and $CaCO_3$ sediments, as well as dissolved organic and inorganic C in the water column. In our study, we only included the organic sinks in including ocean biomass (*99*). Areal extent from (*102*). Note that we could not calculate uncertainties for the ocean, because these values were calculated from global estimates.	Stocks Areal extent	C density in soils or biomass was calculated by dividing global stocks by areal extent.
Forest, boreal Forest, temperate Forest, tropical	Database compiled by (*18*) from standardized Country Reports as part of the Global Forest Resources Assessments 2015. Aboveground C includes trees, stem stumps, branches, bark, seeds and foliage. Soil organic C, summarized by (*100*), was measured to a depth of 1 m.	Stocks Areal extent C density	Aboveground C density was calculated for each climate type by dividing country stocks by areal extent. The mean and SD were then calculated. Mean soil C density and SD were calculated for each climate type with data on different forest types.

Peatland, boreal Peatland, temperate	(*103*) compiled peat properties including means and SDs of peat bulk density and peat C percentage, and (*104*) compiled peat depths, both for temperate and boreal peatlands. C in biomass was assumed to be negligible.	C content Bulk density Peat thickness	Aboveground C: NA Soil C density was calculated for both climate zones with region-specific data with the formula from (*103*, *104*): peat depth × bulk density × C percentage. Maximum soil C density was calculated with the above formula using maximum C content.
Peatland, tropical	(*70*) compiled aboveground C density, which includes living trees as well as litter and dead wood. Mean was directly obtained from (*70*). (*105*) compiled peat properties of tropical lowland African (Cuvette Centrale, Central Congo Basin), Asian (Central Kalimantan, Borneo) and American (Pastaza-Marañón Basin, western Amazonia) peatlands, including means and SDs with peat depth, peat bulk density and peat C percentage. We used the Asian region as a model for high-density peatlands to estimate the maximum, as the average peat thickness here is 4.7 m. (*106*).	C density C content Bulk density Peat thickness	Aboveground C: NA The SD for C in aboveground biomass was calculated with the reported SE and *n*. Soil C density was calculated for the three main tropical peat regions with the formula from (*103*, *104*): peat depth × bulk density × C percentage. We calculated the mean and SD from the obtained outputs. Maximum soil C density was calculated with the above formula using the average peat thickness of Asian peatlands.
Mangroves, tropical	Aboveground C: (*41*) compiled aboveground live C densities of mangrove forests including standing tree and dead wood using standard biometric techniques. Mean and SD originate from (*41*). Soil C: (*92*) compiled country-specific C densities and compiled a global map of mangrove forest soil carbon. We used the C stock data of 2 m depth to calculate C density (*92*).	C density Stocks Areal extent	Aboveground C: NA Soil C density was calculated by dividing the C stock by areal extent. We used the country statistics to calculate the SD.
Salt marsh, temperate	(*19*) compiled C density of the soil and (*74*) compiled C in aboveground biomass. (*19*) calculated soil C density for the top one meter with bulk density and C content.	C density	The mean and SD were calculated from the data.
Seagrass meadow, temperate and tropical	(*101*) compiled soil (< 1 m) and biomass C densities. Note that the mean value of soil C may be and overestimation, because of the high values found in Mediterranean *P. oceanica* meadows (*101*). Mean was directly obtained from (*101*).	C density	The SD was calculated from the reported CI and *n*.
	Panel C: C sequestration rates[**]		
Open ocean	Schematics of the global C cycle with annual fluxes and C reservoirs (biota, dissolved organic C and soil organic C). (*3*, *17*) differentiated between soil organic C and $CaCO_3$ sediments, as well as dissolved organic and inorganic C in the water column. In our study, we only included the organic sinks in including ocean biomass (*99*). Areal extent from (*102*). Note that we could not calculate uncertainties.	Fluxes Areal extent	The sequestration rate was calculated by dividing global fluxes with areal extent.
Forest, boreal Forest, temperate Forest, tropical	Studies that quantified C sequestration in newly established forests for the boreal (*107*), and temperate and tropical regions (*107–109*). We included sites that had an age of 25-125 years to account for land-conversion or early succession	Sequestration rate	The mean and SD were calculated from the selected data.

	(e.g., after mud or lava flow or land-use change).		
Peatland, boreal Peatland, temperate Peatland, tropical	Studies that used variable periods to quantify C sequestration, ranging from 10 to ~100 years, for boreal (*110–113*), temperate (*114–124*) and tropical (*36, 125–130*) peatlands. Studies predominantly dated the soil using ^{137}Cs peak fallout (30 to 50-year timescale), using half-life time of the radioactive [210]Pb (~100-year timescale) or [14]C.	Sequestration rate	The mean and SD were calculated from the included data.
Mangroves, tropical	Modern-day sequestration rates from (*7*) and allochthonous burial from (*7, 23, 131–133*). Studies used variable periods to quantify C sequestration, which ranged from 1 to ~100 years. Studies predominantly dated the sediment using ^{137}Cs peak fallout (30 to 50-year timescale) or using half-life time of the radioactive [210]Pb (~100-year timescale). These methods cannot distinguish between allochthonous and autochthonous produced organic C.**	Sequestration rate	The mean and SD were calculated from the included sequestration rate data. The mean percentage of allochthonous burial was calculated from the included data. We then multiplied this percentage by modern-day sequestration rates.
Salt marsh, temperate	Modern-day sequestration rates from (*19*) and allochthonous burial from (*19, 20, 22, 47, 134–138*). Studies used variable periods to quantify C sequestration, which ranged from 1 to ~100 years. Studied predominantly dated the sediment using ^{137}Cs peak fallout (30 to 50-year timescale) or using half-life time of the radioactive [210]Pb (~100-year timescale). These methods cannot distinguish between allochthonous and autochthonous produced organic C.**	Sequestration rate	The mean and SD were calculated from the selected sequestration rate data. The mean percentage of allochthonous burial was calculated from the included data. We then multiplied this percentage by modern-day sequestration rates.
Seagrass meadow, temperate and tropical	Modern-day sequestration rates from (*7*) and allochthonous burial from (*7, 21*). Studies used variable periods to quantify C sequestration, which ranged from 1 to ~100 years. Studied predominantly dated the sediment using ^{137}Cs peak fallout (30 to 50-year timescale) or using half-life time of the radioactive [210]Pb (~100-year timescale). These methods cannot distinguish between allochthonous and autochthonous produced organic C.** Maximum sequestration rate was obtained from (*139*).	Sequestration rate	The mean and SD were calculated from the included sequestration rate data. The mean percentage of allochthonous burial was calculated from the included data. We then multiplied this percentage by modern-day sequestration rates.

*Soil organic carbon stock and density in forests may be overestimated, because a considerable extent of tropical and boreal forests have thick peat soils and are thus also peatlands, which may lead to them also being included under "peatlands". We used various soil depths to quantify organic C stocks, because the depth distribution of C differs per ecosystem (peat deposits can be several meters thick, while carbon in salt marshes and seagrasses in concentrated in the top meter).

**Carbon sequestration rates in coastal systems concern both locally produced and buried organic matter, as well as imported, externally produced organic matter that has been trapped and buried by these ecosystems.

Table S2. Sources and calculations underlying Figure 3.

Ecosystem	Sources and data description	Metric reported	Calculations
Peatland, boreal (Peatland, temperate	Annual emission factors (EF) of peatlands with various land uses (*72*). C in biomass assumed to be negligible. This is a conservative estimate, because drained peatlands also emit CH_4 and N_2O, and are more susceptible to fires.	Emission factor	Year: EF multiplied by 1 Century: EF multiplied by 100. We calculated the mean and SD from the obtained outputs.
Peatland, tropical	Annual emission factors (EF) of peatlands with various land uses (*72*) plus instant emissions from C stored in tropical forest biomass (*70*) (see Table S1, panel B). This is a conservative estimate, because drained peatlands also emit CH_4 and N_2O, and are more susceptible to fires.	Emission factor C density	Year: EF multiplied by 1 plus biomass C. Century: EF multiplied by 100 plus biomass C. We calculated the mean and SD from the obtained outputs.
Mangroves, tropical	We used the mean soil C density of the top 1 m of soil as susceptible C (*74*) and biomass C density (see Table S1, panel B). Following (*74*), we assumed 25–100% loss of C upon land-use change with 25% (minimum), 63% (median) and 100% (maximum) C loss after one year, and 63% and 100% C loss after one century.	C density C losses	Year: lost percentage multiplied by C density plus biomass C. Century: lost percentage multiplied by C density plus aboveground biomass C. We calculated the mean and SD from the obtained outputs.
Salt marsh, temperate Seagrass meadow, temperate and tropical	We used the mean soil C density of the top 1 m of soil as susceptible C (*74*) (see Table S1, panel B). C in biomass assumed to be negligible. Following (*74*), we assumed 25–100% loss of C upon land-use change with 25% (minimum), 63% (median) and 100% (maximum) C loss after one year, and 63% and 100% C loss after one century.	C density C losses	Year: lost percentage multiplied by C density. Century: lost percentage multiplied by C density. We calculated the mean and SD from the obtained outputs.