

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

45 **Enhanced abstract**

46 **Background:** Evaluating effects of global warming from rising atmospheric carbon dioxide  
47 (CO<sub>2</sub>) concentrations requires resolving the processes driving Earth's carbon stocks and flows.  
48 Although biogeomorphic wetlands (peatlands, mangroves, salt marshes, and seagrass  
49 meadows) cover only 1% of the Earth's surface, they store 20% of the global organic  
50 ecosystem carbon. This disproportionate share is fueled by high carbon sequestration rates  
51 per unit area and effective storage capacity, which greatly exceeds those of oceanic and  
52 forest ecosystems. We highlight that feedbacks between geomorphology and landscape-  
53 building wetland vegetation underlie these critical qualities, and that disruption of these  
54 biogeomorphic feedbacks can switch these systems from carbon sinks into sources.

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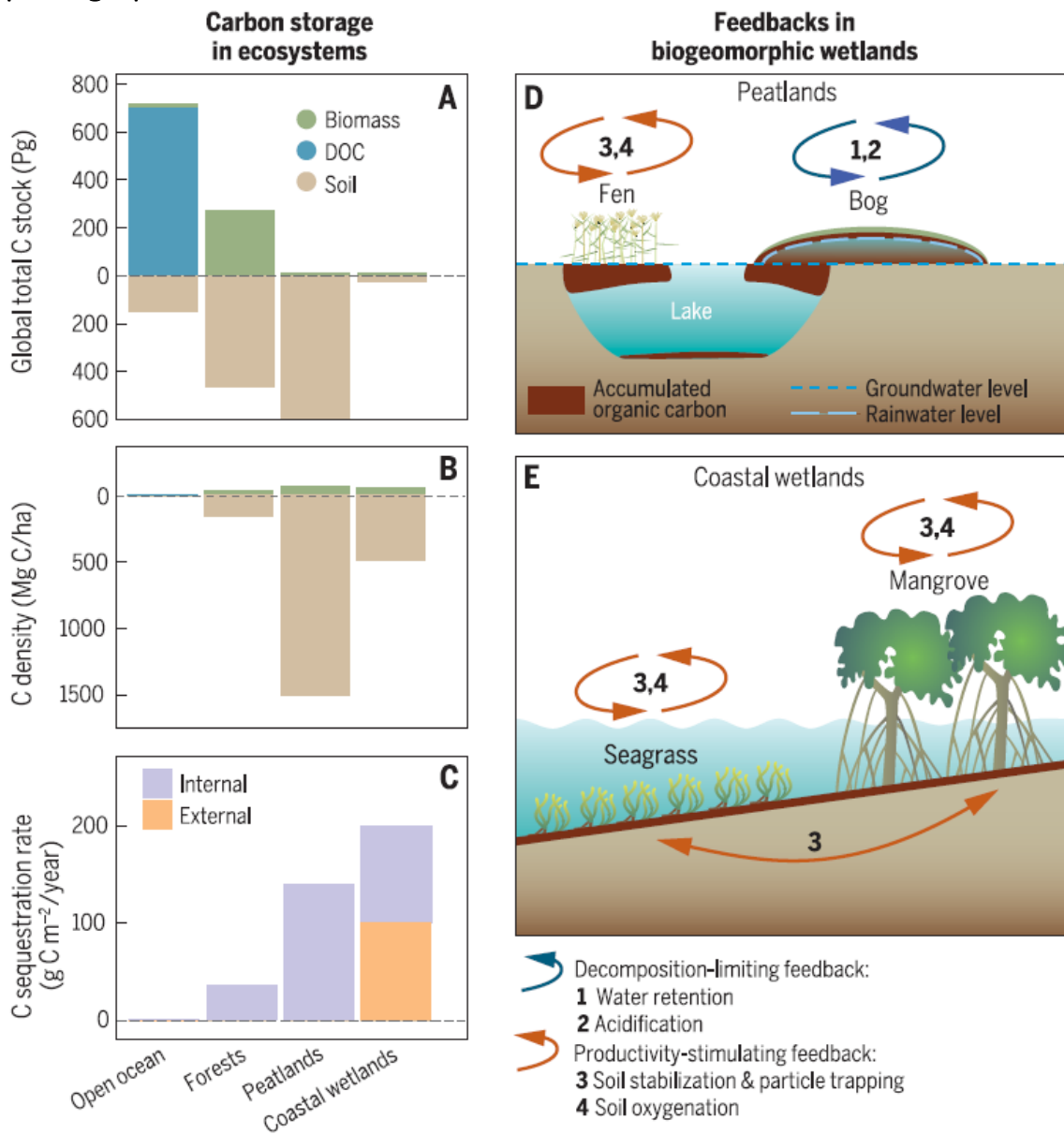
56 **Advances:** A key advancement in understanding wetland functioning has been the recognition  
57 of the role of reciprocal organism-landform interactions, so-called biogeomorphic feedbacks.  
58 Biogeomorphic feedbacks entail self-reinforcing interactions between biota and  
59 geomorphology, by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

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

71

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

77 Caption graphical abstract



78  
 79 **Carbon storage in biogeomorphic wetlands.** Organic carbon stocks (A), densities (B), and  
 80 carbon sequestration rates (C) in the world's major carbon-storing ecosystems. Oceans hold  
 81 the largest stock, peatlands (boreal, temperate and tropical aggregated) store the largest  
 82 amount per unit area, and coastal ecosystems (mangroves, salt marshes and seagrasses  
 83 aggregated) support the highest sequestration rates. (D-E) Biogeomorphic feedbacks,  
 84 depicted by arrows, can be classified as productivity-stimulating or decomposition-limiting.  
 85 Productivity-stimulating feedbacks increase resource availability and thus stimulate  
 86 vegetation growth and organic matter production. Although production is lower in wetlands  
 87 with decomposition-limiting feedbacks, decomposition is more strongly limited, resulting in  
 88 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

95 **Abstract**

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

106

107 **Keywords:** feedbacks, climate change, positive interactions, restoration, conservation,  
108 peat(formation), wetlands

109

## 110 Introduction

111 Global warming, resulting from rapidly rising atmospheric carbon dioxide (CO<sub>2</sub>)  
112 concentrations since the Industrial Revolution, has increasingly drawn attention towards  
113 understanding and quantifying the processes driving Earth's carbon stocks and flows (1, 2).  
114 Burial of organic matter remains the largest carbon sequestering process on the planet,  
115 rivaled only by the ocean's inorganic carbon solubility pump (3, 4). While wetlands cover just  
116 2% of the Earth's surface (5), they store more than 20% of global organic ecosystem carbon  
117 (i.e. all live and dead organic matter from terrestrial, freshwater and oceanic systems  
118 combined) (4, 6). Moreover, wetland carbon sequestration rates can be orders of magnitude  
119 higher compared to terrestrial and oceanic ecosystems (7). Recent work has addressed the  
120 importance of wetlands as natural climate solutions and the cost-effectiveness of their  
121 restoration (8, 9). However, restoring carbon storage functions requires an understanding of  
122 the mechanisms underlying their large carbon stocks and high sequestration rates.

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

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

## 142 Comparing organic carbon stocks and sequestration rates between ecosystems

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

152 Recent sequestration rates of internally and externally produced organic carbon per  
153 unit area over the last 10-125 years are higher in tropical peatlands (200 g C m<sup>-2</sup> yr<sup>-1</sup>)  
154 compared to their boreal (100 g C m<sup>-2</sup> yr<sup>-1</sup>) and temperate (120 g C m<sup>-2</sup> yr<sup>-1</sup>) counterparts (**Fig.**  
155 **1C**). Average salt marsh and mangrove sequestration rates (250 and 200 g C m<sup>-2</sup> yr<sup>-1</sup>,  
156 respectively), may outpace or equal those of tropical peatlands, while seagrass meadows bury  
157 150 g C m<sup>-2</sup> yr<sup>-1</sup>, which is more than boreal and temperate, but less than tropical peatlands (7,  
158 19). For coastal ecosystems, 100 g C m<sup>-2</sup> yr<sup>-1</sup> originates from external (e.g., riverine and  
159 marine) sources, which gets trapped and buried (20–23). All of these vegetated wetland rates  
160 are higher than those of terrestrial forests and oceans, where net sequestration rates are  
161 below 50 g C m<sup>-2</sup> yr<sup>-1</sup> (**Fig 1C**). Intact vegetated coastal wetlands and freshwater peatlands  
162 worldwide currently sequester 0.7 Pg C per year, equaling 6% of the total annual global  
163 anthropogenic carbon emissions (which were estimated in 2019 to be 11.5 Pg C) (4).

164

## 165 Biogeomorphic feedbacks shape wetland carbon storage hotspots

166 In 45% of all wetlands worldwide, biogeomorphic feedbacks shape landscape formation and  
167 carbon capture and storage processes (**Fig. 2, Table 1**) (5). Two overarching types of  
168 feedbacks control the ability of biogeomorphic wetlands to capture and store carbon. In  
169 wetlands driven by 'productivity-stimulating' feedbacks, landscape formation and carbon  
170 storage are enhanced by feedback processes that increase resource availability and thus  
171 stimulate vegetation growth and organic matter production. In wetlands shaped by  
172 '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<sup>-1</sup> and on average 18 g C m<sup>-2</sup> yr<sup>-1</sup> (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<sup>-1</sup>, while in  
246 mangroves and seagrasses rates can be as high as 21 and 10 mm yr<sup>-1</sup>, 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<sup>-1</sup>) (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<sub>4</sub>) and CO<sub>2</sub> 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

## 286 **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).

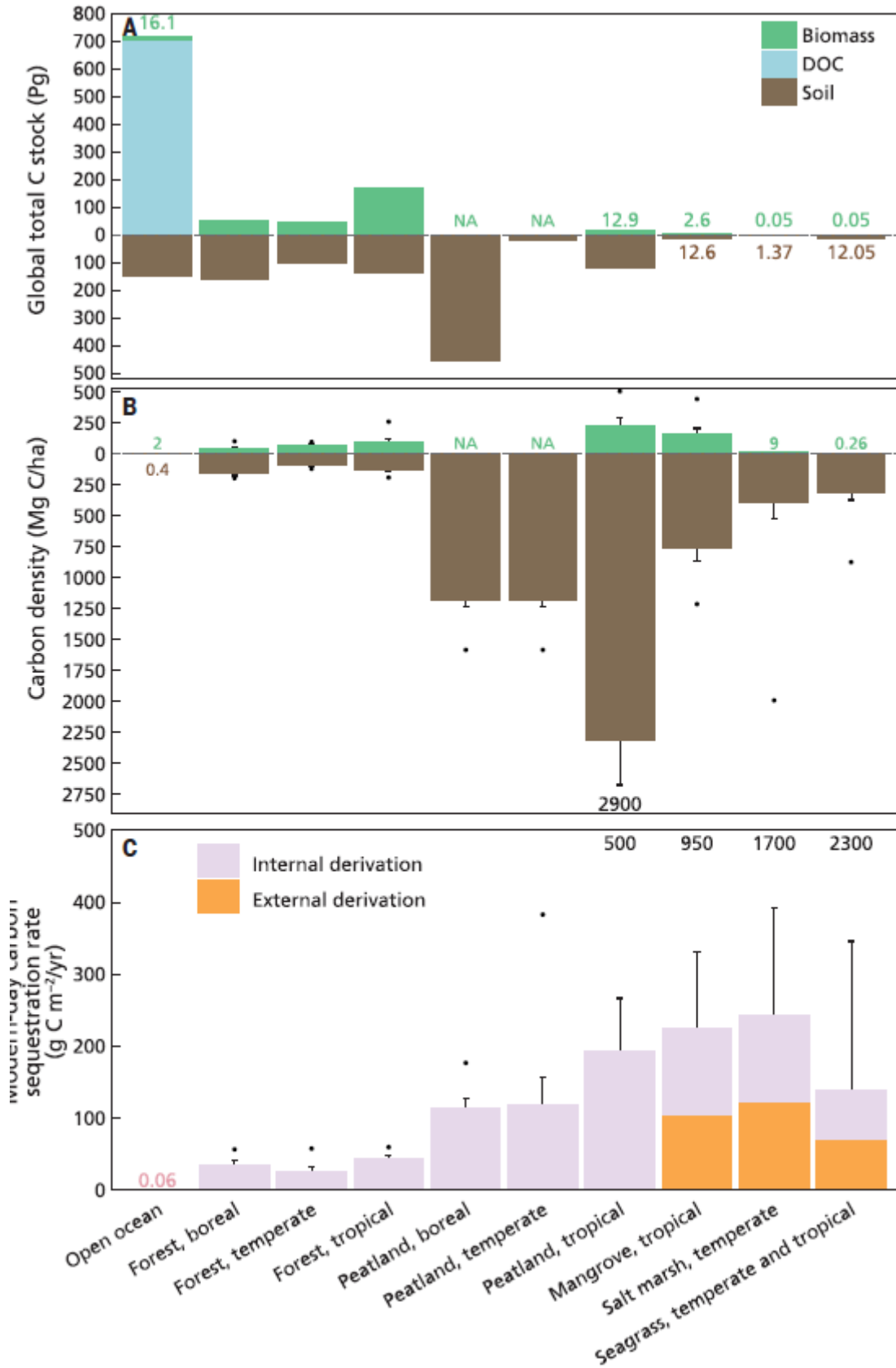
329           Similar to coastal wetlands, peatland restoration has been most successful when  
330 recovering natural conditions by large, landscape-scale rewetting measures. This is  
331 particularly the case for peat bogs, where inserting dams to restore water retention in

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<sub>2</sub> emissions from drainage and CH<sub>4</sub> 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.

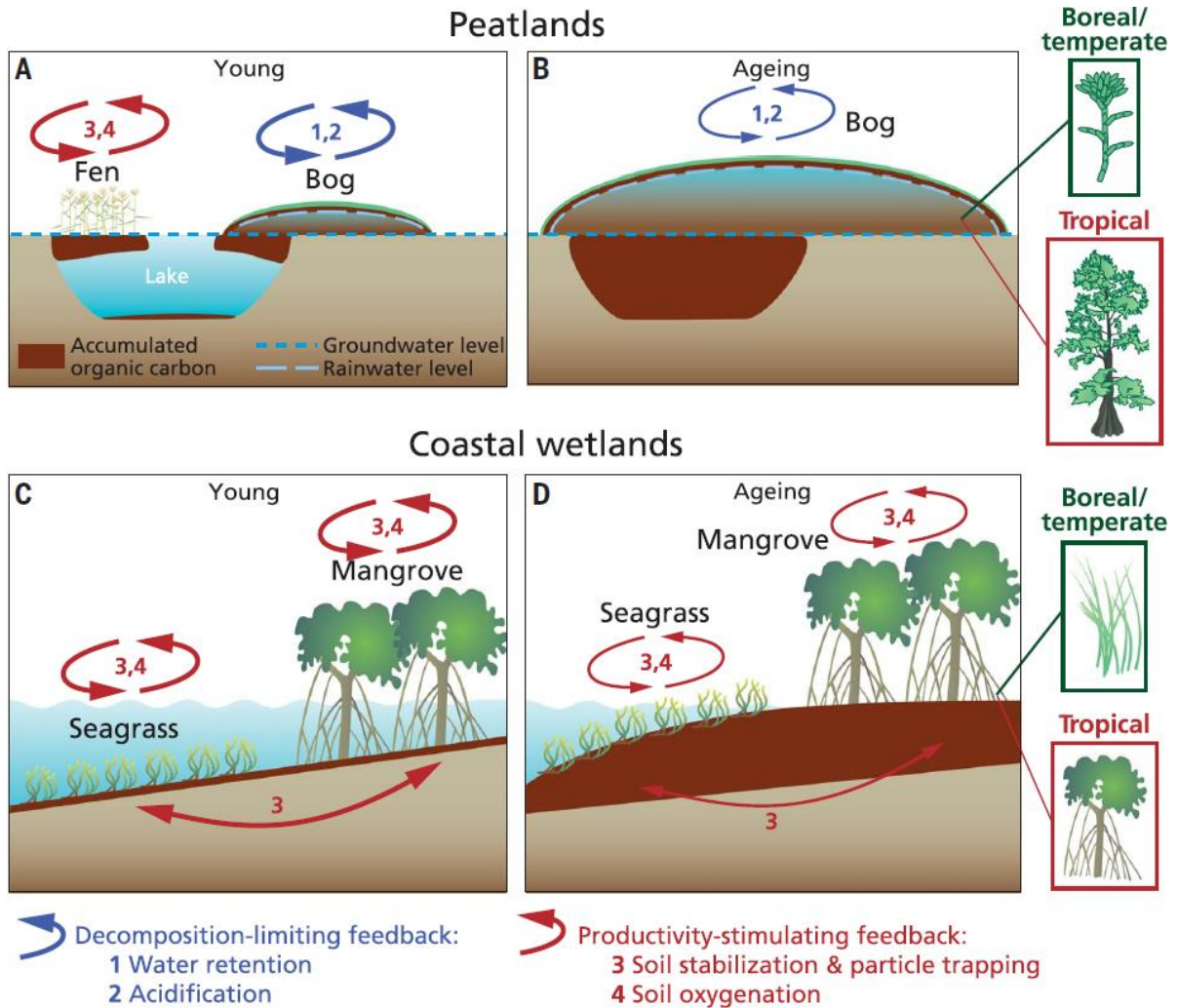
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351 Figures captions and Tables



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).





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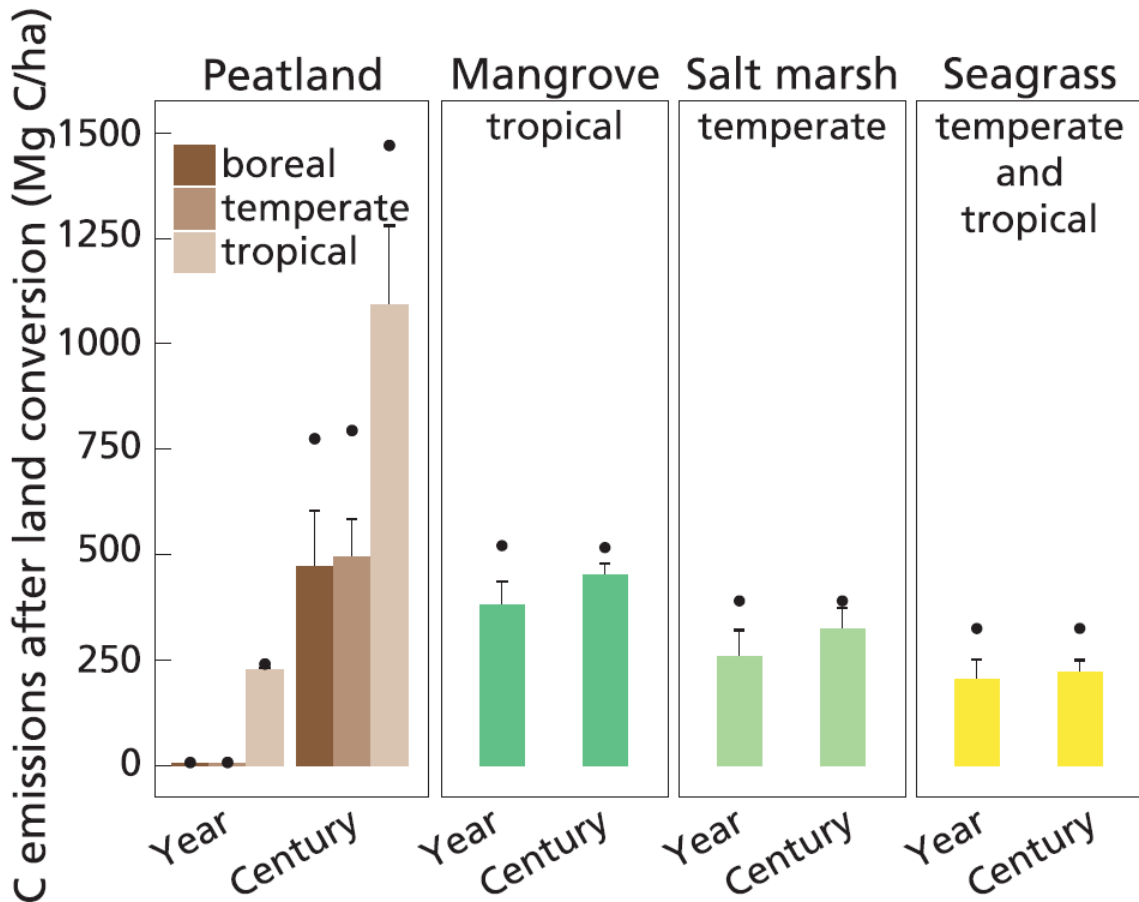
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**Fig. 2. Conceptual representation of the formation of carbon-storing biogeomorphic wetlands.** Density-dependent processes underlying biogeomorphic feedbacks can be classified as productivity-stimulating or decomposition-limiting. (A) Peatland formation 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.



385  
 386 **Fig. 3. Carbon emissions after land-use change in biogeomorphic wetlands.** Land-use change  
 387 and (subsequent) chemical and physical erosion result in rapid carbon losses in coastal  
 388 systems (labeled 'Year'; one year loss). Although carbon losses in peatlands can also be high  
 389 upon land-use change (e.g., logging of tropical forests), they are typically lower, but continue  
 390 for centuries at a slower pace (labeled 'Century'; loss over 100 years), resulting in higher  
 391 overall carbon losses. Error bars depict standard deviation of the mean (SD); black dots depict  
 392 observed maxima. We assumed instantaneous emissions from biomass after land conversion.  
 393 For coastal systems, loss of carbon after land conversion was assumed 25-100% after year 1  
 394 and 63-100% after 100 years (74), while for peatlands we applied commonly used land-use  
 395 emission factors to calculate long-term losses (60, 72). See **Table S2** for references and  
 396 methodological details (16).

397  
 398 **Table 1.** Global extent (million hectare) of (near) natural biogeomorphic wetlands, lost or  
 399 degraded (%) and the annual rate of human-induced losses (% yr<sup>-1</sup>). The range shows  
 400 minimum to maximum and the central value (square brackets).

Ecosystem	Climate zone	Global	Lost	or	Annual	Ref.	Ref. loss /	Ref.
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		<b>extent (million hectare)</b>	<b>degraded (%)</b>	<b>loss rate (% yr<sup>-1</sup>)</b>	<b>Global extent</b>	<b>degraded</b>	<b>Annual loss rate (% yr<sup>-1</sup>)</b>
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).

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**Data and materials availability:** Data underlying analyses presented in this study are deposited in the DANS-repository at <http-link will be added upon acceptance>. (95)



## Supplementary Materials for

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

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### **This PDF file includes:**

Materials and Methods  
Tables S1 to S2



## 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  $^{137}\text{Cs}$  and  $^{210}\text{Pb}$  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
<i>Panel A: Total C stocks*</i>			
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 <sub>3</sub> 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
<i>Panel B: C density*</i>			
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 <sub>3</sub> 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	(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
Peatland, temperate			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 <i>n</i> .  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 an overestimation, because of the high values found in Mediterranean <i>P. oceanica</i> meadows (101). Mean was directly obtained from (101).	C density	The SD was calculated from the reported CI and <i>n</i> .
<b>Panel C: C sequestration rates**</b>			
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 <sub>3</sub> sediments, as well as dissolved organic and inorganic C in the water column. In our study, we only included the organic sinks 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	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.
Forest, temperate			
Forest, tropical			

	(e.g., after mud or lava flow or land-use change).		
Peatland, boreal	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 <sup>137</sup> Cs peak fallout (30 to 50-year timescale), using half-life time of the radioactive <sup>210</sup> Pb (~100-year timescale) or <sup>14</sup> C.	Sequestration rate	The mean and SD were calculated from the included data.
Peatland, temperate			
Peatland, tropical			
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 <sup>137</sup> Cs peak fallout (30 to 50-year timescale) or using half-life time of the radioactive <sup>210</sup> 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 <sup>137</sup> Cs peak fallout (30 to 50-year timescale) or using half-life time of the radioactive <sup>210</sup> 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 <sup>137</sup> Cs peak fallout (30 to 50-year timescale) or using half-life time of the radioactive <sup>210</sup> 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 is 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.**

<b>Ecosystem</b>	<b>Sources and data description</b>	<b>Metric reported</b>	<b>Calculations</b>
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 <sub>4</sub> and N <sub>2</sub> O, 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 <sub>4</sub> and N <sub>2</sub> O, 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.