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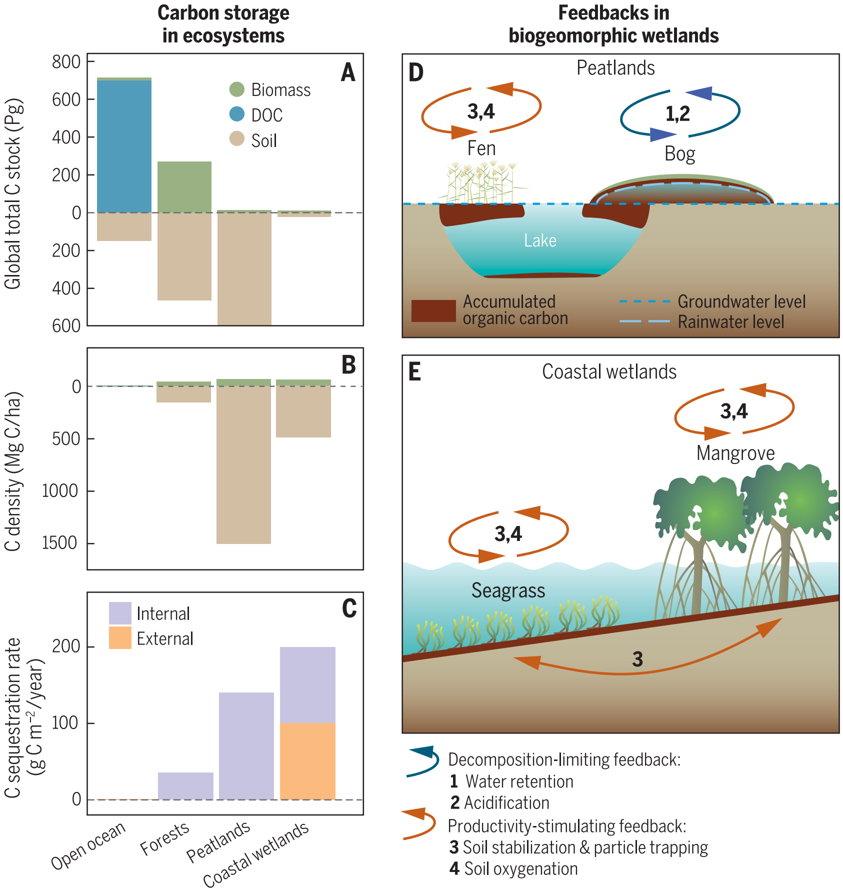
REVIEW SUMMARY

WETLAND ECOLOGY

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

Ralph J. M. Temmink*, Leon P. M. Lamers, Christine Angelini, Tjeerd J. Bouma, Christian Fritz, Johan van de Koppel, Robin Lexmond, Max Rietkerk, Brian R. Silliman, Hans Joosten, Tjisse van der Heide*

BACKGROUND: Evaluating effects of global warming from rising atmospheric carbon dioxide (CO_2) concentrations requires resolving the processes that drive Earth's carbon stocks and flows. Although biogeomorphic wetlands (peatlands, mangroves, salt marshes, and seagrass meadows) cover only 1% of 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 exceed 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.



Carbon storage in biogeomorphic wetlands. Organic carbon (**A**) stocks, (**B**) densities, and (**C**) sequestration rates 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** and **E**) Biogeomorphic feedbacks, indicated with 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 plants is amplified by productivity-stimulating feedbacks. Once the peat rises above the groundwater and is large enough to remain waterlogged by retaining rainwater, the resulting bog maintains being waterlogged and acidic, resulting in strong decomposition-limiting feedbacks. (E) Vegetated coastal ecosystems generate productivity-stimulating feedbacks that enhance local production and trapping of external organic matter.

ADVANCES: A key advancement in understanding wetland functioning has been the recognition of the role of reciprocal organism-landform interactions, "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 that dominates major carbon-storing wetlands generate self-facilitating feedbacks that shape the landscape and 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 because of 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 that are 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 work highlights that biogeomorphic wetlands serve as the world's biotic carbon hotspots, and that conservation and restoration of these hotspots offer an attractive contribution to mitigate global warming. Recent scientific findings show that restoration methods aimed at reestablishing biogeomorphic feedbacks can greatly increase establishment success and restoration yields, paving the way for large-scale restoration actions. Therefore, we argue that implementing such measures can facilitate humanity in its pursuit of targets set by the Paris Agreement and the United Nations Decade on Ecosystem Restoration. ■

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Temmink *et al.*, *Science* **376**, 594 (2022) 6 May 2022 **1 of 1**

REVIEW

WETLAND ECOLOGY

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

Ralph J. M. Temmink[1,2,3]*, Leon P. M. Lamers[3,4], Christine Angelini[5], Tjeerd J. Bouma[6,7,8,9], Christian Fritz[3,10], Johan van de Koppel[6,7], Robin Lexmond[11], Max Rietkerk[1], Brian R. Silliman[12], Hans Joosten[13], Tjisse van der Heide[2,7]*

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 (1% annually). Our findings highlight the urgency to stop through conservation ongoing losses and to reestablish landscape-forming feedbacks through restoration innovations that recover the role of biogeomorphic wetlands as the world's biotic carbon hotspots.

Global warming, resulting from rapidly rising atmospheric carbon dioxide (CO_2) concentrations since the Industrial Revolution, has increasingly drawn attention toward understanding and quantifying the processes that drive 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). Although wetlands cover just 2% of Earth's surface (5), they store more than 20% of global organic ecosystem carbon (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 as compared with those of 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 that underlie 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 through positive density-dependent relationships. Here, we focus on the major wetlands that are shaped by such vegetation-geomorphology feedbacks: (i) peatlands, where vegetation retains water by preventing lateral and vertical seepage, yielding landforms shaped by vertical and horizontal peat accretion (12), and (ii) 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 new 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, whereas 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 because of their large spatial extent, their area-specific carbon density (carbon stock per unit area) is smaller compared with that of biogeomorphic wetlands (Fig. 1B). Carbon density is highest in peatlands (1000 to 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 to 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 past 10 to 125 years are higher in tropical peatlands (200 g C m^{-2} $year^{-1}$) as compared with their boreal (100 g C m^{-2} $year^{-1}$) and temperate (120 g C m^{-2} $year^{-1}$) counterparts (Fig. 1C). Average salt marsh and mangrove sequestration rates (250 and 200 g C m^{-2} $year^{-1}$, respectively) may outpace or equal those of tropical peatlands, and seagrass meadows bury 150 g C m^{-2} $year^{-1}$, which is more than boreal and temperate but less than tropical peatlands (7, 19). For coastal ecosystems, 100 g C m^{-2} $year^{-1}$ originates from external (such as 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} $year^{-1}$ (Fig. 1C). Intact vegetated coastal wetlands and freshwater peatlands worldwide currently sequester 0.7 Pg C $year^{-1}$, 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

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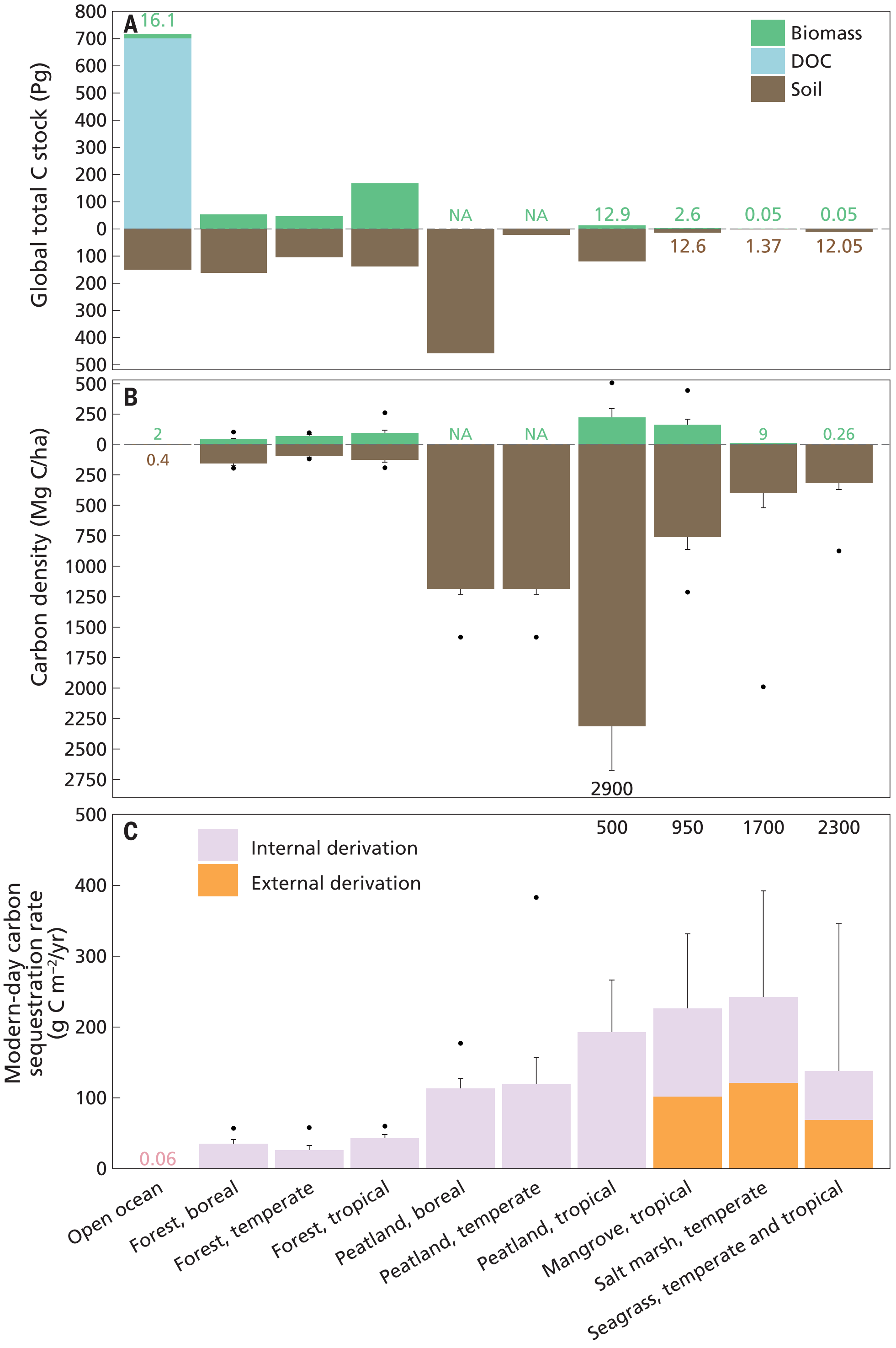

Fig. 1. Overview of the world's major carbon-storing ecosystems. (**A**) Global total carbon stocks. (**B**) Carbon densities. (**C**) Modern-day carbon sequestration rates. Oceans hold the largest stocks globally in the form of dissolved organic carbon (DOC; >97% of the carbon pool), whereas peatlands store the largest amounts of carbon per unit area. Coastal ecosystems generate the highest modern-day sequestration rates (mean rate over the past 10 to 125 years) by storing both locally and externally derived organic matter. This process, however, may become self-limiting when sediment elevation outpaces sea level rise, which is unlikely under current climate change. In addition, damage from stochastic disturbances such as storm-induced erosion can also limit long-term storage. Error bars in (B) and (C) indicate SD; black dots (or numbers when they fall outside the *y* axis) depict observed maxima. We could not calculate uncertainties for the ocean because these values were calculated from global estimates (*16*). Data were generally collected from recent synthesis studies per ecosystem type (*16*). Carbon sequestration rates are from periods ranging from 10 to 125 years (recent apparent rate of carbon accumulation, which are higher than long-term rates over ~10,000 years because of continued decomposition of accumulated matter) (*36*). References and methodological details are provided in table S1 (*16*). [Figure design: Ton A. W. Markus]

and carbon capture and storage processes (Fig. 2 and 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 slower, but because decomposition is more strongly limited, organic matter can accumulate in such wetland soils (Fig. 2).

Peatlands

Peatlands are effective organic carbon sinks in terms of long-term storage per unit area (Fig. 1B). Peatland landforms are shaped by landscape-scale interactions between plants, peat, and water (*12*). Their formation is typically initiated through one of two processes: (i) paludification and (ii) terrestrialization. Paludification is the process in which a change in the hydrological balance shifts a previously drier, vegetated, and inorganic soil terrestrial ecosystem toward a peat-accumulating, biogeomorphic wetland ecosystem (*24*). By contrast, terrestrialization occurs in aquatic

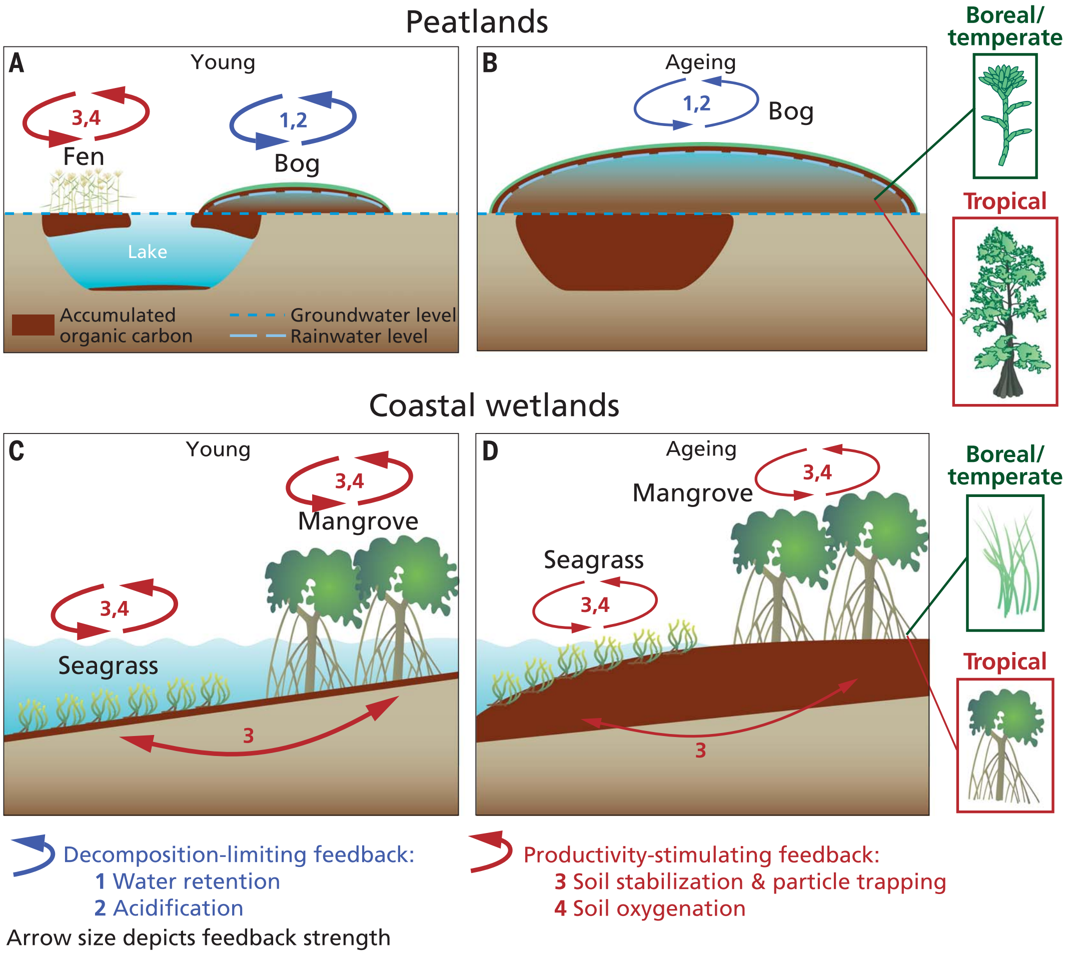

Fig. 2. Conceptual representation of the formation of carbon-storing biogeomorphic wetlands. Density-dependent processes underlying biogeomorphic feedbacks can be classified as productivity-stimulating or decomposition-limiting. (**A**) Peatland formation is initiated through either terrestrialization or paludification. Terrestrialization of aquatic systems by accumulation of organic matter from vascular plants is amplified by productivity-stimulating feedbacks in fens, whereas 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 water-logged 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 representation of all feedbacks. Boxes with vegetation indicate dominant vegetation type in boreal or temperate and tropical wetlands, respectively. [Figure design: Ton A. W. Markus. Symbols are from Integration and Application Network, IAN Image Library (https://ian.umces.edu/imagelibrary)]

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

Ecosystem	Climate zone	Global extent (million hectare)	Lost or degraded (%)	Annual loss rate (% year^{-1})	Global extent data source	Loss/degraded data source	Annual loss rate data source
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 to 3.0 [1.9]%	(92)	(63)	(74)
Salt marsh	Temperate	6	42%	1.0 to 2.0 [1.5]%	(93)	(61)	(74)
Seagrass meadow	Temperate and tropical	18 to 60 [39]	29%	0.4 to 2.6 [1.5]%	(94)	(62)	(74)

*Data includes polar and boreal peatlands. †Circa half of the boreal peatlands can be classified as permafrost peatlands (68). Their preindustrial extent was ~200 million ha, but because of human-induced climate warming, 15% of permafrost peatlands have been degraded at a loss rate of 0.9% since 1850, currently leaving 170 million ha. ‡Temperate peatlands are slowly increasing in extent owing to rewetting and restoration of degraded or drained peatlands (~300,000 ha in total).

systems, such as shallow lakes, when organic matter deposition outpaces its decomposition in the anoxic environment, resulting in the gradual in-filling of the water basin over time (25). As the waterbody accretes organic matter, it transitions into a "fen," a peatland under the influence of ground or surface water and often dominated by emergent fast-growing vascular plants such as grasses, rushes, and sedges (25). In fens, plant growth is supported by a productivity-stimulating positive feedback in which the vegetation's root mat traps and fixes the produced dead organic matter and maintains effective water storage through large pores and surface oscillation (26–28). Supported by oxygen released from the root mat, the labile organic matter decomposes rapidly, releasing nutrients that in turn stimulate plant growth (29, 30). The more recalcitrant fraction with the highest carbon percentage, however, remains and accumulates (31).

Once the peat surface rises above the groundwater, the system transitions into a bog in which decomposition-limiting feedbacks facilitate landscape formation (12). Bogs are fed primarily by rainwater, which is retained within the landform by both the vegetation—*Sphagnum* moss in cool region bogs, and trees in the tropics—and the accumulated peat layer (12). The plants, and their detrital remains, limit lateral and vertical drainage and regulate evaporation. As a result, soils remain persistently waterlogged, acidic, anoxic, and nutrient-poor; these conditions hamper the establishment of competitive species and stifle organic matter decomposition (12, 32–34).

The self-reinforcing biogeomorphic feedback between vegetation development, water retention, and peat accumulation yields a biogenic landscape that forms over a period of hundreds to thousands of years, with long-term peat and carbon accumulation rates of 1 to 3 mm year^{-1} and on average 18 g C m^{-2} year^{-1} [which is lower than modern sequestration rates due to continued decomposition (Fig. 1C)] (35, 36). Primary production is higher in tropical peatlands than boreal and temperate ones and is quantitatively different because of the production of lignin (37, 38), which allows for higher sequestration rates (Fig. 1C).

Coastal wetlands

Compared with peatlands, seagrass meadows, salt marshes, and mangrove forests are generally more productive and are driven by productivity-stimulating feedbacks (38, 39). Whereas peatlands generally have low inputs of external organic C, coastal wetlands commonly receive organic matter from the ocean and from rivers and thus sequester both externally and locally produced organic matter (20, 40). By attenuating currents and waves with their aboveground vegetation structures, coastal wetlands can trap large amounts of externally produced, suspended organic particles that end up buried in the root-stabilized anoxic soils (13, 41). The ratio of locally versus externally produced organic matter differs widely depending on wetland size, vegetation, and location (20, 42), with close proximity to productive coastal waters or rivers favoring allochthonous input (43, 44). Moreover, large wetlands with dense and stiff vegetation also tend to dissipate more hydrodynamic energy, favoring entrapment of incoming particles (45, 46). Externally produced organic material often appears to be much more recalcitrant than the internally produced fraction (47). This highlights that the filtering function of these wetlands may rival their local productivity in importance for carbon sequestration, because on average, almost 50% of all buried organic carbon originates from external sources, although this value varies with context (20–23) (Fig. 1C).

Regardless of its origin, the presence of organic matter in vegetated coastal wetlands creates a productivity-stimulating positive feedback. Decomposition of labile organic matter fueled by radial oxygen loss from plant roots (48) stimulates in situ plant production, while the more recalcitrant fraction is stored in the sediment layers (40, 49). In addition, soil stabilization and attenuation of hydrodynamic forces reduce losses from uprooting and erosion during storms, while the active trapping of particles from the water column also increases water clarity (13, 50), enhancing underwater light availability and favoring the growth of seagrass meadows (13). In salt marshes and mangroves, the trapping of particles increases the bed level, reducing inundation stress (51). Moreover, reciprocal facilitation between coastal vegetation and associated biota can further amplify carbon storage (52, 53). Last, an increasing number of studies highlight the importance of landscape-scale reciprocal interactions between coastal ecosystems. Specifically, seagrasses have been found to facilitate marsh and mangrove establishment through their attenuation of waves (54), and marshes and mangroves trap suspended particles to improve water clarify and facilitate adjacent seagrasses.

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

Human-induced breakdown of feedbacks: From carbon sink to source

Many biogeomorphic wetlands have been rapidly deteriorating and continue to decline in area at rates that range from 0.4 to 3.3% per year, with the exception of cooler-region, boreal peatlands that have remained stable (Table 1). Salt marshes have declined by 42%, and mangroves and seagrass meadows have lost 35 and 29% of their area over the past centuries, respectively (60–63). These losses are caused by habitat destruction from land-use change, overexploitation, eutrophication, salinization, trophic cascades, and climate change–related extreme events such as heat waves and increased storm magnitude and frequency (64, 65). In the future, sea level rise will likely result in major loss of coastal wetlands and their carbon stocks, particularly in areas where landward migration is hampered by human infrastructure—a phenomenon called "coastal squeeze" (66). Temperate and tropical peatlands have been degraded by 57 and 41% in their areal extent, respectively, mostly because of land-use changes, exploitation, and wildfires (60, 67). By contrast, boreal peatlands have not been rapidly declining in their overall extent (<5% loss). However, climate change–driven thawing of the permafrost, which encompasses about half of all boreal peatlands, has affected 15% of these coldest peatlands. The net effect of permafrost thaw on the climate remains unknown because permafrost thaw increases methane (CH_4) and CO_2 emissions from increased decomposition rates while simultaneously increasing productivity and carbon sequestration (68, 69).

At present, biogeomorphic wetlands worldwide experience average annual loss rates of around 1%, with associated yearly carbon losses amounting to 0.5 Pg C (Table 1), which would account for 5% of the current anthropogenic carbon emissions (11.5 Pg C) (4). In contrast to the immediate carbon losses from logging of forests, land-use changes in biogeomorphic wetlands do not necessarily result in the immediate removal of most carbon because the bulk of the carbon is stored in the soil (Fig. 1). Specifically, conversion of peatlands to agricultural land results in instant carbon loss owing to the removal of any aboveground biomass (70), but this is followed by a continued loss of soil organic carbon in the following century (Fig. 3) (71, 72). Loss of coastal wetland vegetation commonly results in rapid erosion and oxidation of carbon-rich soils because the vegetation no longer stabilizes the soil (73, 74). However, in regions where coastal wetlands are "reclaimed" under the protection of levees or dikes, erosion from currents and waves is obviously unimportant, causing accumulated organic matter to oxidize much more gradually (61).

Conservation and restoration of carbon hotspots

Our findings emphasize the importance of conserving and restoring biogeomorphic wetlands worldwide. Conservation measures are particularly rewarding in peatlands, where carbon densities are the highest and where carbon stocks lost by degradation take centuries to millennia to rebuild. Complementary to conservation, restoration of degraded biogeomorphic wetlands and their carbon storage and sink function should be a key element of our global carbon strategy. Restoration is likely to

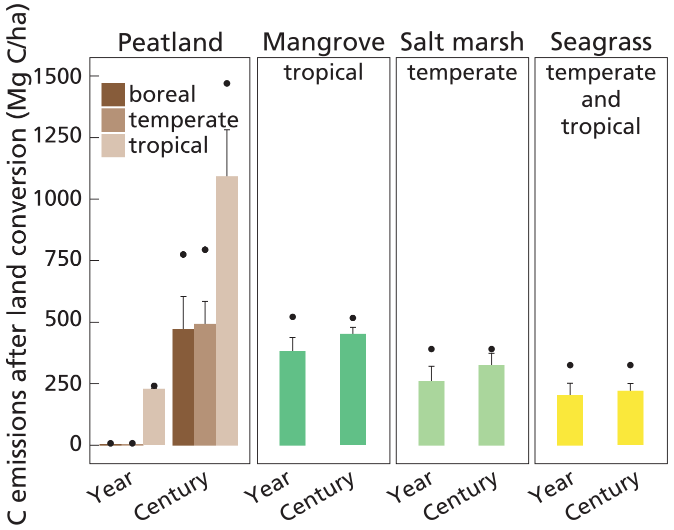

Fig. 3. Carbon emissions after land-use change in biogeomorphic wetlands. Land-use change and (subsequent) chemical and physical erosion result in rapid carbon losses in coastal systems. "Year" indicates 1 year loss. Although carbon losses in peatlands can also be high upon land-use change (for example, logging of tropical forests), they are typically lower but continue for centuries at a slower pace, resulting in higher overall carbon losses. "Century" indicates loss over 100 years. Error bars indicate SD; black dots indicate observed maxima. We assumed instantaneous emissions from biomass after land conversion. For coastal systems, loss of carbon after land conversion was assumed 25 to 100% after year 1 and 63 to 100% after 100 years (*74*), whereas for peatlands, we applied commonly used land-use emission factors to calculate long-term losses (*60*, *72*). References and methodological details are provided in table S2 (*16*). [Figure design: Ton A. W. Markus]

be most rewarding over shorter time scales in both high–carbon stock systems (where emissions can be avoided) and high-productivity systems (where fast sequestration takes place). Coastal wetlands can offer great potential for fast carbon accumulation by sequestering both externally and internally produced material on a time scale of years to decades (*75*). Although carbon sequestration rates of peatlands are slower than those in coastal systems, achieved gains from restoration can still be high because these measures reduce currently ongoing large emissions from these areas (*72*).

Because of the benefits for carbon storage and other ecosystem services, conservation practitioners and policy-makers increasingly consider restoration of biogeomorphic wetlands as a viable tool to counteract mounting losses (*76*, *77*). At present, however, restoration of these systems is often ineffective (generally <50% success) (*76*) and costly compared with restoration of other ecosystem types. For example, restoration costs of terrestrial ecosystems such as grasslands, woodlands, and temperate and tropical forests range from 500 to 5000 US $/ha (*77*), with restoration scales ranging from <1000 to >100,000 ha (*78*). By contrast, restoration of vegetated biogeomorphic wetlands most often occurs at spatial scales of 0.1 ha to tens of thousands of hectares, with costs ranging from 750 to 1,000,000 US$/ha (*76*, *79*). An important issue underlying these low success rates and high costs is that biogeomorphic feedbacks only work beyond a certain minimum vegetation patch size and density (*80*). Below these thresholds, unpredictable losses occur, while natural establishment is hampered (*13*, *81*). In such cases, a so-called "Window of Opportunity" may be required—a rare period of conditions that are particularly beneficial for vegetation establishment and allow vegetation to grow beyond the size or density threshold required for the biogeomorphic feedback to initiate and support longer-term survival (*82*).

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

Similar to coastal wetlands, peatland restoration has been most successful when recovering natural conditions through large, landscape-scale rewetting measures. This is particularly the case for peat bogs, where inserting dams to restore water retention in degraded bogs has been successful because it creates a window of opportunity for natural plant-hydrology feedbacks to reestablish (*87*). Sphagnum paludiculture, a new form of peat bog culturing, takes this approach one step further; after rewetting, peatmosses are actively introduced at a sufficient spatial scale to overcome establishment thresholds and allow their sustainable harvest (*88*). Similarly, paludiculture in fens focuses on large-scale reintroduction and sustainable harvest of rapidly growing helophytes, such as *Typha* sp., thus reestablishing productivity-stimulating feedbacks (*88*). Last, recent work revealed that peatland rewetting strategies in general can be improved by striking the best balance between stopping sustained CO_2 emissions from drainage and CH_4 release from rewetting by optimizing the water table height (*72*, *89*).

On the basis of this synthesis, we argue that stopping biogeomorphic wetland losses through conservation measures is of utmost importance. Moreover, recent technical advancements that focus on recovery of landscape-forming feedbacks have now paved the way for large-scale restoration that reverts biogeomorphic wetlands from sources back to sinks. Therefore, we argue that implementation of conservation measures combined with restoration actions can enhance the role of biogeomorphic wetlands as natural climate solutions, facilitating humanity to reach the targets set by the Paris Agreement and the United Nations Decade on Ecosystem Restoration.

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SUPPLEMENTARY MATERIALS

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Science

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

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Restoring wetlands for carbon
Wetlands disproportionately contribute to carbon sequestration globally. However, the ability of wetlands to store carbon depends on feedbacks between vegetation and geomorphology that allow wetlands to continue to develop over long time periods. When these feedbacks break down, wetlands can become carbon sources. Temmink *et al*. reviewed recent research on the role of plant-landform interactions in wetland carbon storage and the potential for restoration to restore these critical processes. —BEL

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