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Ecological resilience of restored peatlands to climate change

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Degradation of peatlands through land-use change and drainage is currently responsible for 5-10% of global annual anthropogenic carbon dioxide emissions. Therefore, restoring disturbed and degraded peatlands is an emerging priority in efforts to mitigate climate change. While restoration can revive multiple ecosystem functions, including carbon storage, the resilience of restored peatlands to climate change and other disturbances remains poorly understood. Here, we review the recent literature on the response of degraded and restored peatlands to fire, drought and flood. We find that degraded sites can generally be restored in a way that allows for net carbon sequestration. However, biodiversity, hydrological regime, and peat soil structure are not always fully restored, even after a decade of restoration efforts, potentially weakening ecosystem resilience to future disturbances. As the recovery of degraded peatlands is fundamental to achieving net-zero goals and biodiversity targets, sound science and monitoring efforts are needed to further inform restoration investments and priorities.

Peatland ecosystems are wetlands consisting of partially decomposed plant remnants and organic matter that accumulate over millennia to form carbon-rich soils, called peat, that can reach several meters in thickness. These ecosystems are waterlogged, meaning that their soils are permanently wet; this feature drastically slows down soil decomposition. Altogether, peat-accumulating wetlands only cover 3% of the global land area. They are predominantly found across the northern mid- and high-latitude regions (~45–70°), though they can also be regionally abundant in the tropics and sub-tropics (~0–30°). Globally, the peatland soil carbon stock has been estimated at ~600 ± 100 gigatonnes[1]. Climate change and anthropogenic pressures can lead to rapid losses of these long-term soil carbon stores and tip some peatlands into net sources of carbon to the atmosphere[2–4]. Other key peatland ecosystem services, such as water storage and biodiversity, are also being lost worldwide[5,6]. A recent expert assessment suggested that the carbon balance of peatlands globally may switch from sink to source in the near future (years 2020–2100)[7]. This is mainly because of tropical peatland emissions caused by fire, drought, and land-use change combined with emissions from permafrost thaw that will likely surpass the carbon gain expected from enhanced plant productivity in the northern high latitudes.

Ongoing global restoration efforts are targeting degraded peatlands[8,9], as these ecosystems are recognized as efficient nature-based climate solutions[10–12]. Global estimates of the greenhouse gas saving potential of restoring peatlands negatively affected by land-use change is similar to the most optimistic estimates of the sequestration potential of all agricultural soils[13]. However, the resilience of restored peatlands to climate change and other disturbances remains poorly understood. Here, we describe the main ecohydrological factors that make most undisturbed peatlands effective long-term carbon stores. Using two case studies from the boreal and temperate regions, we discuss whether current restoration efforts can effectively revive key

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ecohydrological features and enhance the resilience of managed peatlands. Improved restoration efforts will require new methods and knowledge of peatland systems and, until we can overcome the difficulties in fully restoring all ecosystem functions, we must endeavor to avoid additional losses of pristine peatlands.

Peatland resilience

Ecosystem resilience refers to the ability of an ecosystem to maintain ecological structure and related functioning[14,15] following disturbance or change, either through resistance or adaptation[16]. For the most part, intact peatlands have been resilient to natural disturbances, maintaining carbon and water storage functions over long time periods, from decades to millennia[17]. This is largely attributable to a number of physical features and ecohydrological feedbacks[18] that ensure peatlands remain hydrologically stable and waterlogged. Waterlogging creates anoxic conditions, which drastically slow down the microbial decomposition of plant litter and organic matter. In cold regions, low soil temperatures aid peat formation by further slowing down peat decay[19]. Whereas in the tropics, decomposition is slowed down by organic matter recalcitrance as well as high soil moisture condition[18]. In addition to waterlogged conditions, a relatively stable water table is important to limit decomposition and maintain the ecological habitat of peat-forming species, such as *Sphagnum* moss[20].

Degraded ecosystems may deteriorate and meet a critical threshold, where small changes in the environment can lead to large changes in ecosystem condition, function, and state. Human interventions—particularly those that induce water table draw-downs such as draining—may push an ecosystem across such a threshold. For instance, peat drainage leads to peat oxidation (i.e., intensified soil decomposition due to dry, aerobic conditions that promote microbial activity) and carbon dioxide (CO_2) emissions, themselves leading to subsidence (i.e., elevation loss) and/or to changes in plant communities that could completely change the carbon and water balance of the peatland. Importantly, human-driven land-use changes in peatland ecosystems are superimposed on a changing climate which, on its own, can also destabilize some peatlands[21]. Extreme weather events, fires, droughts, and floods can all lead to non-linear changes in peatland state.

Biodiversity, surface microtopography, and peat formation all contribute to the unique hydrological properties that result in peatland resilience. In the sections below, we describe how these features may become degraded, and the implications for ecosystem resilience and subsequent restoration priorities. Note that our focus is on extratropical peatlands (boreal and temperate), although some of the peatland features described therein may also be true for tropical peatlands.

Peat structure. The process of peat formation is the result of long-term accumulation of organic-rich, partly decomposed plant material forming a soil matrix that slows down water movement across peatland basins. Near the surface, the peat matrix is much looser and less decomposed than the deeper peat[22]; this upper portion of the soil profile can hold excess water. Indeed, water can be quickly stored in the near-surface peats following precipitation events; water is then slowly released from the deeper peats during dry periods[23,24]. Likewise, any excess water (think of inundation following snowmelt or a large rain event) can be rapidly discharged from the near-surface peat to nearby streams, thus helping the maintenance of an adequate water table by preventing long-term water exceedance after such events. In contrast, during a drought, water table levels drop, but near-surface water movement is also reduced, leading to some water retention. This process is accompanied by surface peat contraction caused by surface drying, which further slows water flow[25]. Together, these processes help peatlands slow water movement and maintain high water levels, which keep the ecosystem wet/anoxic and allow continuation of peat accumulation and carbon storage. This self-regulation feedback between peat accumulation and water table depth is one of the key features that makes peatlands resilient to ecohydroclimatic changes[26,27].

When a peatland is permanently drained and converted, decomposition increases, leading to higher bulk density (i.e., denser soils) and decreased porosity. These conditions reduce subsurface flow losses, which slows down peatland drying (in some cases, surface flows may temporarily increase). Over decades, however, continuous dewatering of peat may lead to desiccation, soil instability, stronger water table fluctuations, and erosion, resulting in an increase in rapid runoff during and following precipitation events, and loss of regulating capacity[28,29]. In addition, prolonged or intense drying can lead to peat cracks that cause subsurface flows to increase. This loss of hydrological stability has been linked with net carbon, water, and biodiversity losses. This is because peat desiccation leads to oxic conditions that promote soil decomposition. The plant communities also change under these new hydrological conditions.

Modern measurements and paleoecological reconstructions suggest that there are hydrological thresholds beyond which a peatland's ability to store carbon is compromised[30–32]. In boreal and temperate peatlands, for example, water depths ~20 cm below the surface (or ~10 cm above the surface) may lead to a negative carbon balance[4]. This optimum water table level for carbon sequestration for extratropical peatlands applies to both pristine and degraded sites[4]. Degradation can, in summary, lead to irreversible changes in peat structure (compaction, cracking) that decrease the stability of the ecosystem.

Plant and microbial diversity. In general, greater biodiversity has been shown to enhance ecosystem resilience[33]. In peatlands in particular, many plant functional types and specialized micro-organisms have developed physiological and metabolic adaptations to low oxygen availability, cold temperature, acidity, and oligotrophy[34–36]. Some plant genera are also considered ecosystem engineers—species that modify their environment to suit their own needs. One such example is *Sphagnum*, which is known to hold up about 20 times its dry weight in water, allowing it to persist during dry periods; it also acidifies its environment and makes it difficult for other plants to colonize the site[37]. *Sphagnum* has the ability to recover from any residual fragments and spread by spores over long distances, making it a good candidate for site colonization or recovery[38]. Brown moss and true moss species can also be abundant in peatlands; they often carpet sites, with different species associated with specific hydrological and trophic gradients. Altogether, mosses (and *Sphagnum*) provide water retention and peat-building capacities to a large number of mid- and high-latitude peatlands[39,40]. Towering (or creeping) over them are many vascular peatland plants. Such plants often possess tissues that are rich in lignin-like compounds and phenolics, making them recalcitrant to decay and thus important building blocks in the process of peat formation[41]. The root systems of some vascular plants can also make up a significant portion of the peat matrix; this is because roots—especially those that reach the permanently saturated portion of the peat profile—are less susceptible to decay due to lack of oxygen at depth.

Plant diversity tends to decrease following drainage. It can be particularly difficult for mosses (including *Sphagnum*) to recolonize a drained site, in part because of the hydrological changes combined with a loss of the original soil characteristics[42]. For example, due to widespread drainage of fens across Europe, many fen species are considered endangered[43]. By comparing 320 rewetted fen sites with 243 near-natural sites of similar origin from the major fen peatland regions of Europe, Kreyling et al.[44] found that rewetting drained fens induces the establishment of tall, graminoid wetland plants, with no trend back to their former biodiversity and ecosystem functioning for at least several decades in more than half of the sites. These novel ecosystem assemblages have implications beyond biodiversity, as plant species composition affects carbon cycling via litter quality, root exudates, and production and consumption of carbon in the rhizosphere, which impact gaseous emissions. Brown mosses are largely absent from rewetted peatlands dominated by graminoids. As for soil microbiota, there remains a lack of process-based understanding of how this aspect of soil health impacts the resilience associated with land use[45]. It was suggested that degraded sites can experience decreases in substrate availability and microbial activity and/or diversity[46]. Interestingly, peat mining and restoration did not consistently affect bacterial or archaeal community composition at six sites in eastern Canada[47]. In summary, vegetation and microbial diversity likely decrease after drainage, although we lack sufficient understanding of the effects of peatland degradation on the microbial biota, and this decreases the ability of the affected peatland to cope with stressors (e.g., climate change).

Surface microtopography. In *Sphagnum*-dominated peatlands, vegetation assemblages with different wetness tolerances develop into microforms within a single peatland, including wet hollows, intermediate lawns, and dry hummocks. As surface water conditions change over time, the relative proportions of these microforms also change[48,49]. During wet events, hollows might expand to allow for additional water storage. Conversely, during drier periods, hummocks might increase their coverage as these microforms are capable of holding on to water more effectively. While these vegetation mosaics are usually seen as stabilizing properties, they can also promote perturbations. This is particularly the case in continental settings, where the expansion of dry hummocks can amplify dry conditions, as the vascular plants are able to pump water from the adjacent hollows[50]. For instance, the expansion of ericaceous shrubs on hummocks during prolonged drier periods is associated with an increase of polyphenol content which, when combined with the growth of fungi (under drying conditions), feeds back positively on ericaceous shrubs by facilitating the symbiotic acquisition of dissolved organic nitrogen, in turn increasing organic matter decomposition[51]. Eventually, shrub and tree encroachment can lead to peatlands shifting toward alternative stable states such as forest ecosystems[32,52]. In other words, mosaics of vegetation assemblages can increase peatland resilience to hydrological changes, allowing the peatland to adapt to a broad range of conditions, though some ecological thresholds may exist[22,50,52].

In general, drainage leads to more similar water table depths across the ecosystem, which hinders the creation of resilient ecological niches[53]. A lesser variety of microforms tends to lead to lower biodiversity and, oftentimes, to a dominance of vascular plants[54–57]. The reinforcing mechanisms between plant diversity, water table variability, and peat formation are thus lost. In turn, this loss of spatial heterogeneity may lead to increases in both inundation and desiccation events, themselves further limiting species richness. A lesser variety of microforms also reduces the buffering capacity of a peatland to absorb hydrological changes. For these reasons, degraded systems may be more susceptible to become sources of CO_2 emissions (due to increased mineralization) when the water table drops, and sources of methane during times of inundation[58,59]. In addition, CO_2 emissions may, in some instances, increase in drained sites as nitrogen becomes more available in degraded surface peat[59]. This means the carbon sink function and stability are heavily compromised at degraded sites (Fig. 1).

Recovering peatland ecological resilience. Restoration efforts are primarily aimed at returning waterlogged conditions and peatland biodiversity to revive the peatland carbon and water cycles (Fig. 1). For both fens and bogs, the effectiveness of peatland restoration has been documented and assessed regarding the carbon storage function[60–63], characteristic vegetation[64–69], and typical hydrological conditions[70,71]. In the following sections, we present successful case studies of heavily degraded peatland sites that were restored, and where net carbon sequestration has been measured. We also present evidence that biodiversity, hydrological regime, and peat structure may not be fully restored or maintained, or may take decades to return (if at all), which is why the resilience of restored peatlands is put into question[72]. Still, it has been argued that restoration actions provide some resilience when compared to degraded sites[73].

Canadian peat bog restoration. Over 20 years of restoration experiments and monitoring have been underway across Canadian peat bogs that have been drained and mined for peat moss[74–77]. Using the Moss Layer Transfer Technique, scientists and practitioners have demonstrated that, in some cases, a *Sphagnum* cover can be re-established in as fast as four growing seasons. This technique includes the reintroduction of *Sphagnum* mosses—particularly the subgenus Acutifolia—which has been shown to have the greatest potential to re-establish peatland resilience due to its moisture retention capacity[78]. *Sphagnum* Acutifolia were also shown to more rapidly reinstate the carbon accumulation function of restored peatland ecosystems[61]. Multiple studies have indicated clear restoration benefits, including the return to a moss cover, high and stable water table conditions, net carbon sequestration, and resistance to wildfire[61,67,71]. With regards to the latter, a restored site located in southeastern Canada burned ~10 years following its restoration. The site was restored in 2005–2006[65]; seven years following the restoration, the site exhibited *Sphagnum* and *Polytrichum* covers of 29% and 26% respectively, which is deemed a desirable outcome[79]. In August 2014, an accidental fire burned nine hectares of the restored site; seven hectares remained intact, allowing for comparison between burnt and intact areas. Lawn-adapted species *Sphagnum* Acutifolia and *Eriophorum* sedges lost less biomass than their wetter hollow counterparts, which were dominated by *Sphagnum* Cuspidata and *Scirpus* sedges[73]. With that said, all sites—including the hollows—rapidly recovered. Overall, while plant diversity was not fully reestablished, this case study suggests that the return of plant functional diversity and associated microtopographic features allowed for the reinstatement of a peat-accumulating system with some resilience to short-term climate fluctuations and wildfire.

Scottish blanket bog restoration. Peatlands in Scotland have been affected by peat mining and grazing, but more importantly, they were heavily drained for conifer planting through government incentives since the early 1980s. The conservation status of Scottish bogs has been described as 'unfavorably declining', and 70% of all peatlands in Scotland are degraded[80]. Not only did planting affect peat carbon storage, but bird populations in adjacent pristine bogs were also impacted, leading to a decline in wader bird populations[35]. This planting trend was halted in the late 1980s when the government ended its financial incentives, but by then ~190,000 hectares of UK bogs had been drained and planted with trees[81]. Since the 1990s, different restoration

Fig. 1 Future scenarios of human impacts on extratropical peatlands. a Draining and mining. Peatlands are typically drained by digging ditches. Dried-out peat layers become susceptible to rapid decay and can be mined for peat blocks, which can be used to generate energy when burned, and peat moss and *Sphagnum* peat can be used for compost and as a growing media for horticulture. Drained peat surfaces can also be converted into large-scale agricultural fields or for cattle grazing. **b** Restoration. Peatland restoration and rewetting typically involve drainage blocking and recolonization of the site with native plant species. Together this can lead to restoring net peat accumulation, carbon storage, and increased biodiversity. Artist: Patrick Campbell.

projects have been implemented. For example, peatland action supported by the Scottish government has, since 2012, restored over 25,000 hectares of blanket bogs in Scotland. For example, 14 years of restoration monitoring in the Flow Country, a vast expanse of blanket bog in the North of Scotland, shows a recovery of moisture conditions but full recovery of vegetation has only happened in the wetter areas of the bog and not on the drier patches[82]. This agrees with other studies that found plant recovery from erosion can be predicted from the micro-local hydrological and climatic characteristics of a peatland's surface topography[83]. New remote sensing monitoring tools, such as InSAR, have successfully been applied to monitor peatland status of restored Scottish blanket bogs[84]; results from these studies also raise questions as to what is the optimum restoration target, mainly in terms of vegetation, as some areas of bogs are naturally "stiffer" (i.e., the amplitude of vertical motion is small) and not conducive for *Sphagnum* cover. Additionally, although recovery was almost complete in the chemistry of surface water and deep pore-water after 17 years in a restored blanket bog site, shallow pore-water recovery was slower[85]. This suggests that, in some cases, more than 17 years are required for complete recovery of water chemistry to bog conditions, in particular for water table depth, nitrogen species, and pH, because of the legacy effects of drainage and afforestation[85]. Overall, the restoration of Scottish bogs has returned the carbon sink function in these ecosystems[86]. Currently, 63% of blanket bog, 60% of raised bog, and 72% of fen, marsh, and swamp features on designated sites are in 'favorable condition'[80]. However, peat surface microtopography and plant functional diversity have not been fully re-established, which brings into question the future resilience of these systems to a changing climate, particularly when it comes to their ability to cope with fluctuations in water table variability, including floods and droughts.

Assessing the success of restoration efforts

These examples highlight a few important points. First, successful peatland restoration should be linked to a net increase in water regulation capacity because of rapid new peat formation that will increase peatland surface elevation and provide new, albeit temporary, water storage space. However, considerable differences in the capacity of different restored peatlands to regulate water movement are expected, mostly due to their past history. For instance, peat properties may be significantly altered so as to lose their ability to hold on to water in the same way as undisturbed peat. Second, a restored peatland might still be a net carbon source to the atmosphere because the restored vegetation may have lower NPP and/or a different, less recalcitrant litter quality, thereby limiting carbon input. Indeed, while rewetting has been shown to reduce CO_2 emissions by inhibiting peat mineralization[87,88], the impact of novel vegetation assemblages on the total greenhouse gas budget of a peatland remains uncertain[44]. Likewise, a restored, functioning peatland with living and growing biomass, and recently accumulated peat, can still undergo significant "old" peat decomposition due to site history, which could lead to a net carbon loss to the atmosphere[89,90]. Third, in the case of *Sphagnum*-dominated systems, if restoration fails to re-establish the hummock-hollow microtopography that contributes to hydrological self-regulation, the ecosystem is left vulnerable to changing ecohydrological conditions.

Duration and intensity of drainage, as well as the amount of time it took to restore a degraded site, have effects on key properties that may impact the success of restoration. For instance, we know that some sites that have undergone intensified, prolonged drainage have not been successfully restored for at least several decades, namely due to increases in nutrient availability and irreversible changes in peat hydraulic variables[91]. This

Box 1 | 26th Conference of the Parties (COP26) climate summit highlights with regards to peatland management

The 26th Conference of the Parties (COP26) climate summit in Glasgow (November 2021) included a number of pledges and promises related to the way the world's land is managed. Of interest is the "Glasgow Leaders' Declaration on Forests and Land Use", which was signed by more than 140 countries, and promises to "wor[k] collectively to halt and reverse forest loss and land degradation by 2030". By limiting further degradation of ecosystems, this Declaration should be beneficial for peatlands. In addition, many countries (including Chile, Peru, Indonesia, and the Democratic Republic of the Congo) included peatlands in their national pledges under the Paris Agreement—known as Nationally Determined Contributions—for the first time. Another outcome is that the extraction of peat and electricity generation from peat are now seen as unaligned with the Paris goals, meaning that multilateral development banks may change how investments are made with regards to these practices. Overall, much work still needs to be done to facilitate the protection and restoration of peatlands worldwide, but it is encouraging to see their importance recognized in the international policy arena.

does not mean that those sites cannot be restored; rather, it may take a long period of time to achieve success. Likewise, new methods could be developed to help ensure restoration success, such as topsoil removal in the case of heavily damaged systems[92]. A point worth mentioning is the dearth of old restored sites that could be used to know how, when, or if resilience returns. We also know that changes to peat properties persist after restoration[93]; peat may develop a lower specific yield during drainage and this may remain after rewetting; a low specific yield is associated with greater fluctuations in water tables, which may prevent some functions returning fully. Landscape-scale hydrological management may also be needed to help restore high and stable water table levels. In coastal Finland, fen restoration is more likely to be successful if the whole catchment is managed rather than small-scale projects, as regional water drawdowns have impacted local restoration efforts[94]. Overall, rewetting may slow down carbon losses to the atmosphere, but restoration of biodiversity and soil processes may take decades or longer after rewetting[44].

Climate warming may be changing the current geographic extent of peatlands[95]. While pristine sites can persist, to some extent, outside their bioclimatic envelope due to built-in negative ecohydrological feedbacks[96], restoration may be unsuccessful if the ecological state targeted to inform plant diversity has become less relevant[97,98]. Perhaps more importantly, degraded and restored sites may be more sensitive to extreme weather events than pristine ones; an ecosystem unable to regulate against flood or drought may be easier to push through a threshold beyond which ecosystem properties can be lost. In this case, climate change can be seen as a potentially additive pressure on a system that was already damaged by land use. For instance, a restored peatland that undergoes drought conditions (and/or a fire) may not be structurally equipped to sustain its water and carbon regulating functions. It is known that fires can burn more easily through drained and degraded peatlands due to their lack of hydrological stability[99]; those sites also represent smoldering hotspots[100]. Overall, it is expected that climate change will have more profound impacts on peatland carbon balance in restored sites due to changes in ecosystem and process-based attributes that no longer confer the same degree of ecological resilience[72].

Outlook

Compliance with the Paris Agreement implies carbon neutrality by 2050–2070[101], meaning that we must avoid additional loss of peatlands, ensure their sustainable use, and restore/rewet ~500,000 km^2 of drained peatlands[44] (Box 1). Assessing the restoration capacity and economic efficiency of peatland restoration must thus urgently take place[102]. This includes detailing a clear strategy for restoration, identifying explicit restoration goals (such as biodiversity or functional biodiversity targets, hydrological stability, and peat accumulation/carbon sequestration) and associated monitoring needs, and of course ensuring that ecosystem processes are well known. The latter is particularly important, with keeping in mind that non-linear, threshold-like responses of peatlands to environmental and land-use changes need to be further discussed and understood.

While restoration may not return a degraded site to a state where all ecosystem services are recovered, a lot of evidence exists in support for peatland restoration, as discussed in this compilation. In particular, prompt rewetting of drained peatlands can quickly reduce carbon losses and/or lead to net carbon accumulation[88,103], even if it may not fully restore "natural" conditions, even within decades, particularly in severely disturbed and long-drained peatlands. Hydrological stability must be returned to degraded peatlands to increase chances of successful ecosystem recovery; this is particularly the case under climate change and increases in weather extremes[72].

As all peatland ecosystem services and functions cannot easily be restored, the protection of intact peatlands should also be prioritized. While most policy instruments such as carbon offsetting are not well suited to protect large intact carbon-rich sites[104], this situation is changing, with the growing interest in nature-based climate solutions, which brings to light the role of peatlands and other carbon-rich ecosystems in mitigating climate change.

Overall, taking action to monitor, assess, and restore peatland ecosystems is a point of urgency to meet global climate mitigation targets. The UN Decade of Ecosystem Restoration—starting just now—is also the critical period for achieving peat restoration targets. Further work is required to quantify the effectiveness of peatland restoration as mitigation and adaptation measures to climate change; we also need to help support biodiversity in these ecosystems. In particular, it is critical to ask whether restoration measures will continue to be viable for a range of plausible future climate scenarios, and if they will maintain or increase the provision of ecosystem services on which local people depend, including water, food, and materials, now and under future climates[105]. To help achieve these goals, we call for more research on the resilience of restored peatlands. Long-term monitoring of restoration projects is critically needed so that response to disturbance (e.g., drought, flooding, etc.) can be observed and resilience be assessed. New restoration methods should also be developed, tested, and implemented as soon as possible (see Huth et al.[92] for an example). This is particularly important in many parts of the world where challenges brought about by the level of site degradation, financial costs, and the difficulty to successfully attain the levels of functional biodiversity and hydrological stability needed to jump-start the ecosystem remain large impediments to restoration projects. Local community endorsement and support are also needed for the long-term sustainability of restoration interventions[106]. We thus need international and interdisciplinary collaboration to ensure the effective implementation and long-term sustainability of restoration interventions worldwide.

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J.L. and A.G.-S. conceived, designed, and wrote the article together. J.L. and A.G.-S. have approved this submitted version.

Competing interests

The authors declare no competing interests.

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