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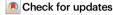
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# Increased but not pristine soil organic carbon stocks in restored ecosystems

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Ecosystem restoration can contribute to climate change mitigation, as recovering ecosystems sequester atmospheric  $CO_2$  in biomass and soils. It is, however, unclear how much soil organic carbon (SOC) stocks recover across different restored ecosystems. Here, we show SOC recovery in different contexts globally by consolidating 41 meta-analyses into a second-order meta-analysis. We find that restoration projects have, since their inception, led to significant SOC increases compared to the degraded state in 12 out of 16 ecosystem-previous land-use combinations, with mean SOC increases thus far that range from 25% (grasslands; 10-39%, 95% CI) to 79% (shrublands; 38-120% CI). Yet, we observe a SOC deficit in restored ecosystems compared to pristine sites, ranging from 14% (forests; 12-16% CI) to 50% (wetlands; 14-87% CI). While restoration does increase carbon sequestration in SOC, it should not be viewed as a way to fully offset carbon losses in natural ecosystems, whose conservation has priority.

Ecosystem restoration is the process of returning modified or degraded land to natural ecosystems with similar levels of complexity, structural diversity, and services as pristine ecosystems<sup>1,2</sup>. Under global initiatives such as the Bonn challenge<sup>3</sup> and the UN Decade on Ecosystem Restoration<sup>4</sup>, countries have pledged to restore close to 1 billion hectares by 2030 worldwide<sup>5</sup> and to recognize restoration as an integrated solution to address multiple environmental issues<sup>2,6</sup>. Restoration may contribute to halting global biodiversity loss by increasing local species richness and abundance<sup>7,8</sup>, while simultaneously providing climate change adaptation through improved soil stabilization<sup>9</sup>, water availability<sup>10</sup>, and protection against flooding<sup>3</sup>. Ecosystem restoration can also mitigate climate change by enhanced uptake of atmospheric carbon in soils and biomass<sup>11</sup>, but the effectiveness and limitations of restoration as a climate mitigation strategy are objects of ongoing research.

Estimates of the global climate mitigation potential of ecosystem restoration range from 205 GtC sequestered by 2050 through forests restoration alone<sup>12</sup> up to 287 GtC sequestered by 2050 by restoring woody vegetation across all ecosystem types<sup>13</sup>. These model-based estimates extrapolate carbon stocks of pristine ecosystems to restorable land within the same ecoregion, assuming that restoration leads

to complete recovery<sup>13</sup>. Meta-analyses that combine the outcomes of empirical restoration studies have shown that carbon stocks in restored areas are consistently larger than before restoration<sup>9,14</sup> or those of neighboring non-restored areas<sup>15</sup>. However, complete recovery to pristine stocks may not always be achieved<sup>16,17</sup>. Carbon stock gains may vary across ecosystem type<sup>8</sup>, pre-restoration land use, e.g., cropland, pasture<sup>18</sup>, and, likely, also across restoration strategies<sup>19,20</sup>. Previous work has typically focused on specific regions, ecosystems, pre-restoration land uses and restoration strategies. However, evaluating the effectiveness of restoration as a climate change mitigation strategy requires simultaneously considering these different aspects in a complete global overview, as well as evaluating potential limitations of restoration by consistently comparing both degraded versus restored, and restored versus pristine carbon stocks.

Here, we provide such global empirically-based overview of the change in soil organic carbon (SOC) stocks resulting from restoration of degraded land. We systematically quantify the effect of ecosystem restoration on SOC sequestration with a second-order meta-analysis<sup>21</sup>. In this analysis we use mixed-effect regression models to combine, analyze and synthesize 41 pertinent restoration meta-analyses, which were based on 3953 primary studies and produced 380 summary

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effects (i.e., weighted averages of treatment versus control comparisons from primary studies). We systematically compare restored with degraded land to analyze SOC recovery, and contrast this to pristine ecosystems to assess whether SOC content can achieve that of pristine areas. In comparing restored and degraded land, we perform separate meta-regressions on forest, grassland, shrubland and wetland ecosystems and test the influence of pre-restoration land use and restoration strategy on SOC change. We hypothesize pre-restoration land use to affect the carbon content of restored sites, as some land uses such as mining and agriculture have long-lasting impacts on the environment that can influence recovery<sup>19</sup>. We analyze the soil carbon content in relation to the restoration strategy, as authors disagree on the influence of restoration approach on restoration outcomes<sup>20,22</sup>. The resulting comprehensive global overview enables a broader understanding of the climate mitigation benefits of restoration across different settings, as well as its limitations.

### Results

# Enhanced soil organic carbon stocks of restored ecosystems

Restored ecosystems on average store more SOC than degraded land (Fig. 1). Average SOC increases across ecosystems range from 25% in grasslands (10-39% range over the 95% confidence interval, Fig.1c), to 68% in forests (48-89% CI; Fig. 1b), to 79% in shrublands (38-120% CI, Fig. 1d), all with statistically significant summary effects. We do not find statistically significant SOC change in comparing restored with degraded mangroves (73%; -2 - 147% CI; Fig.1f) and wetlands (9%; -2 -19% CI; Fig. 1e) as the 95% confidence intervals overlap with zero. For all ecosystems combined, SOC increases in 90% of the summary effects, by an average of 45% (30-59% CI, Fig.1a). These values reflect current SOC increases in restoration projects across the world. Average SOC for these restoration projects will likely continue to increase over time, but we show that the fastest part of the recovery has already taken place and accounts for the majority of total SOC increase over the time period analyzed (Supplementary Information section S2). Further SOC increases are likely to occur at a slower pace, making them less relevant in the context of mitigating climate change.

While restoration of degraded ecosystems leads to SOC increases across most ecosystem types, pristine levels have not been reached for those ecosystems where empirical data on restored versus pristine SOC levels are available, i.e., wetlands, and mangroves and forests. These ecosystem types show significant SOC recovery deficits, as compared to the pristine state, of 50% in wetlands (14-87% CI; Fig. 2d), 28% in mangroves (12-44% CI; Fig. 2b) and 14% in forests (12-16% CI; Fig. 2c). When looking at all ecosystems combined, restored ecosystems exhibit lower SOC levels than pristine sites in 98% of the summary effects, with an average deficit of 38% (18-58% CI; Fig. 2a). Although no restoration age data was available for the comparison between restored and pristine ecosystems, recent literature shows pristine SOC levels may never or only very slowly be achieved<sup>16,23</sup>, due to impaired recovery trajectories<sup>24-26</sup>. For example, where physical, geochemical or biological conditions have been altered to a (near-)irreversible degree<sup>24-31</sup>.

Our results on wetlands stand out, as they show no statistically significant difference in SOC between the restored and degraded state and the largest deficit compared to the pristine state out of all analyzed ecosystem types. While their relatively short species and nutrient turnover times might be expected to result in a larger SOC recovery compared to, for instance, forests<sup>32</sup>, we find the reverse. This may stem from the difficulty of removing stressors like eutrophication<sup>23</sup> or the fact that certain wetlands have lower SOC than agricultural land<sup>14,33</sup>. Our results suggest that ecosystems further from recovery, like wetlands, may have a lower capacity to recover SOC after damage and thus their protection is crucial. It should be noted here that in the original, first-order meta-analyses, various wetland types were combined into a single category, a grouping that we therefore followed. The dynamics

of carbon sequestration and greenhouse gas emission, however, do vary across different wetland ecosystems. For example, due to larger sediment intake, coastal wetlands in tidal systems accumulate SOC more rapidly than inland freshwater wetlands and release less methane (CH<sub>4</sub>) after restoration<sup>34</sup>. Increased CH<sub>4</sub> and nitrous oxide (N<sub>2</sub>O) emissions can form a trade-off for inland wetlands restoration, as the warming effect of these greenhouse gas emissions may only be offset by CO<sub>2</sub> sequestration (including in the SOC pool) after 40–80 years following restoration<sup>35</sup>.

#### The influence of pre-restoration land use

Ecosystem restoration leads to a statistically significant SOC increase, compared to the degraded state, for 12 out of 16 pre-restoration landuse combinations. The average SOC increase ranges from 15% in grassland restored from pasture to 256% in forest restored from mining (Fig. 3, panels b and a). The exceptions for which we found no statistically significant SOC change are pastures restored to forests or wetlands (Fig. 3a, d), cropland restored to wetlands (Fig. 3d), and mining sites restored to grassland (Fig. 3b). Restoration of former pastures typically leads to relatively low SOC increase likely because pastures already have high SOC levels generally (e.g., 22-46 Mg/ha<sup>36</sup>), as pasture vegetation allocates more carbon to belowground pools to minimize carbon loss from grazing<sup>37</sup>. Furthermore, SOC levels have been shown to decline during the early stages of active restoration of pastures to forests due to soil disruption linked to replanting<sup>38</sup>. Restoration of cropland or pasture to wetlands may not result in a significant SOC increase likely because SOC levels in certain wetland types are lower than in agricultural land<sup>14</sup>. In addition, nutrient delivery from pre-restoration farming activities may continue to cause eutrophication and impair wetland recovery<sup>14,23,34</sup>, as was the case for wetland studies included in our analysis<sup>14</sup>. We find non-significant SOC change on former mining sites restored to grassland. This could be caused by some of the original studies finding SOC increase, while others find SOC decrease after restoration<sup>39</sup>. A reason for this could be that different types of mining have different effects on SOC measurements. In coal mines, for example, it can be challenging to distinguish between the coal particles left by the mine and carbon derived from plant decomposition<sup>40</sup>.

Specifically in forest ecosystems, different pre-restoration land uses significantly influence SOC recovery (Fig. 3a). Restoration of mining sites resulted in larger SOC increase than for all other prerestoration land uses, and restoration of barren land shows a larger SOC increase than restoration of former cropland and pasture. The differences between the pre-restoration land use categories reflect the level of degradation that is caused by the pre-restoration land use. For example, initial SOC levels are relatively low on former mining sites (e.g., 5.7 g/kg<sup>41</sup>), which suffer from severe soil organic matter depletion caused by land clearance, topsoil excavation and heavy metals use<sup>41</sup>. Likewise, barren land is characterized by relatively low SOC content<sup>9</sup>, as is degraded cropland (e.g., 14-19 g/kg<sup>36</sup>). The 'farmland' category was derived from meta-analyses that did not distinguish between cropland and pasture as pre-restoration land use and that largely originate from the Grain for Green<sup>42</sup> or the Three-North Shelter Forest<sup>15</sup> projects, launched to counteract the severe land erosion in China<sup>42</sup>. These projects typically begin from a severely degraded state, which then also results in a larger relative increase in SOC.

# The influence of restoration strategy

We distinguished three restoration strategies in our study: active replanting (active restoration), spontaneous revegetation (passive restoration), disturbance removal, and habitat rehabilitation (assisted restoration). Restoration of ecosystems led to significant SOC increases across most strategies, except for active restoration in grasslands (non-significant change) and in wetlands (SOC decrease), indicating that the analyzed strategies are generally effective in sequestering

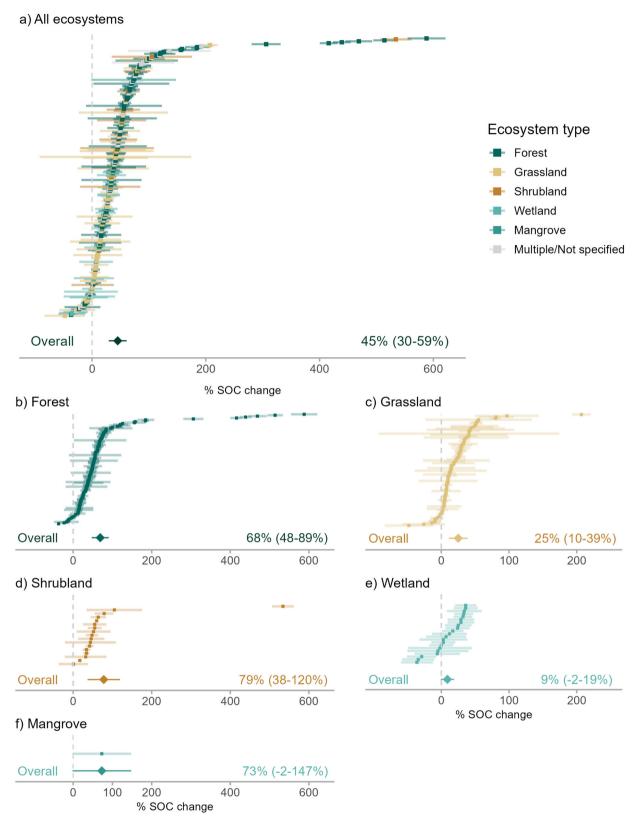
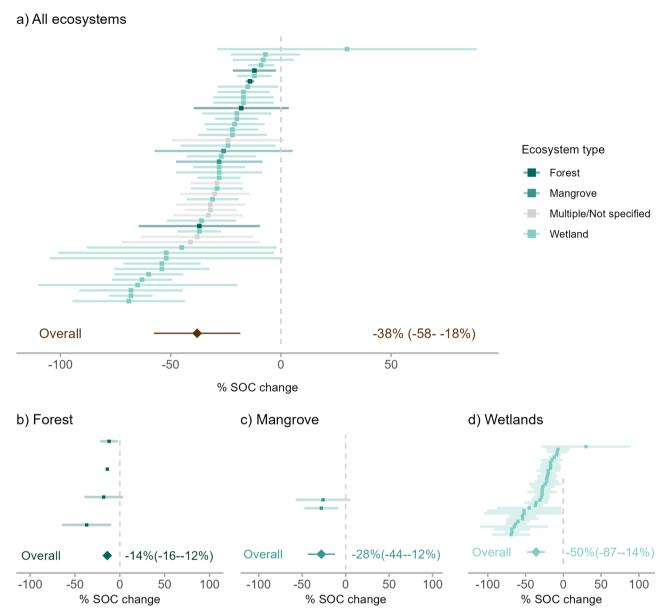


Fig. 1 | Change in Soil Organic Carbon (SOC) in restored ecosystems compared to degraded land. Panel a shows SOC change for all ecosystem types, while panels b-f show the same for individual ecosystems. Coloured squares are the summary effects extracted from meta-analyses, reported as percentage of SOC change. Lines indicate the 95% confidence interval. Coloured diamonds represent the average

summary effects for all ecosystems (a) and each ecosystem type separately (b-f). Positive values indicate a higher SOC in restored land (compared to degraded land), while negative values indicate the opposite. We consider average summary effects whose confidence interval does not overlap with zero as significantly different from zero, thus statistically significant.



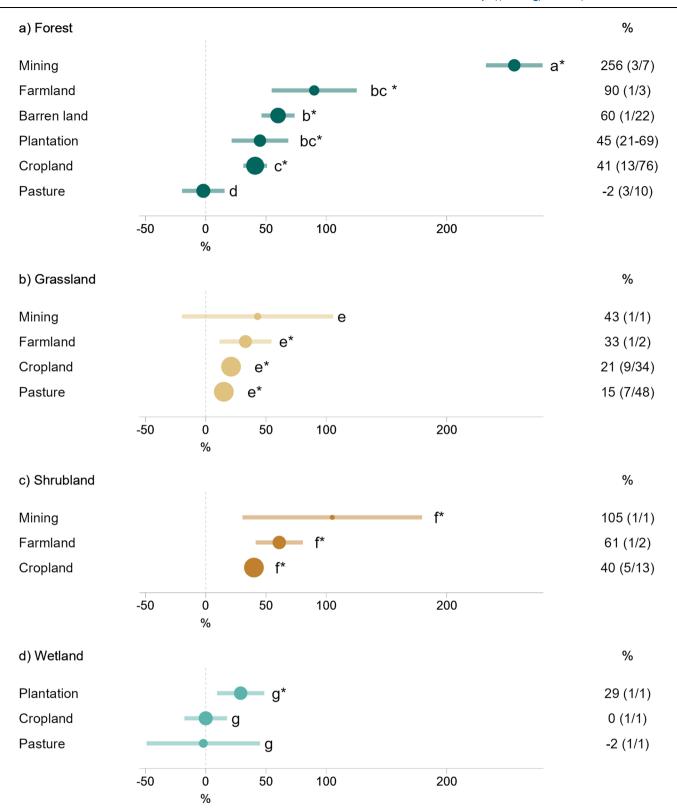
**Fig. 2** | **Change in Soil Organic Carbon (SOC) in restored ecosystems as compared to pristine ecosystems.** Panel **a** shows SOC change for all ecosystem types, while panels **b**, **c** and **d** show the same for forest, mangrove and wetland ecosystems, respectively. Coloured squares are the summary effects extracted from metanalyses, reported as percentage of SOC change. Lines indicate the 95% confidence interval. Coloured diamonds present the average summary effects for all

ecosystems (a) and each ecosystem type ( $\mathbf{b}$ ,  $\mathbf{c}$ ,  $\mathbf{d}$ ). Negative values indicate a lower SOC in restored land (compared to pristine ecosystems land), while positive values indicate the opposite. We consider average summary effects whose confidence interval does not overlap with zero as significantly different from zero, thus statistically significant.

carbon. We do not find statistically significant differences in SOC recovery between active versus passive restoration, with 56% (30–81% CI) compared to 95% (52 – 139% CI) SOC increases in forests, and 8% (–12 – 27% CI) compared to 24% (7 – 40% CI) in grasslands, respectively (Fig. 4a, b). This is in line with earlier work that showed that across ecosystem types, active restoration does not lead to faster or more complete overall ecosystem recovery than passive restoration  $^{23}$ . In tropical forests, previous work showed that passive restoration results in higher plant biodiversity and larger overall biomass increase, which likely increases SOC recovery, compared to actively restored sites  $^{20}$ .

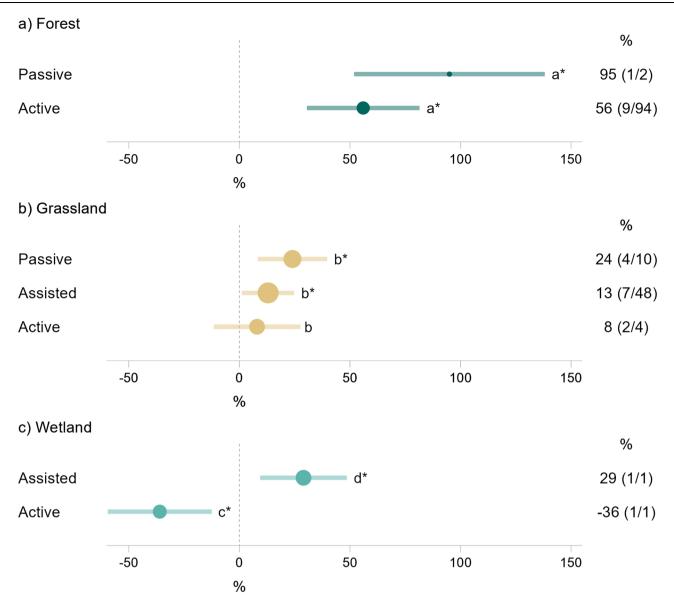
A key explanation for our finding that active restoration does not result in statistically different SOC responses than passive restoration could be that active restoration is more likely to be used in areas that are too degraded for SOC to recover without human intervention, whereas more resilient sites passively revegetate<sup>23</sup>. In fact, active

restoration may have been, and also should be<sup>23</sup>, applied in areas where passive restoration is unsuccesful. In the meta-analyses underlying our study, we see that actively restored grasslands were typically more degraded in their pre-restoration state than grasslands that underwent passive restoration<sup>42,43</sup>. As the history of individual sites can determine the choice of the restoration approach, pre-restoration land conditions and restoration strategy may be intertwined in our study. For the restoration of forests specfically, soil manipulation due to replanting can cause carbon loss that is only regained in time<sup>38</sup>. In wetlands specifically, restoration strategies were found to be statistically different with assisted restoration yielding a SOC increase of 29% (10 – 48% CI), and active restoration a SOC decrease of 36% (13 – 59% CI) (Fig. 4c). Our data on actively restored wetlands were based only on restored tidal wetlands, which were found to have lower SOC than their pre-restoration land use as cropland<sup>14</sup>. This explains the observed SOC



**Fig. 3** | Change in Soil Organic Carbon (SOC) in restored ecosystems as compared to degraded land across pre-restoration land uses. Different panels and colours represent different ecosystem types, namely forests (a), grasslands (b), shrublands (c), and wetlands (d). Circles are the average summary effects for a singular land use, reported as the percentage of SOC change, also showed in the column on the right. Parentheses include the number of meta-analyses and effect sizes included for each category presented in this figure. Lines indicate the 95% confidence interval. Circle size is the inverse of the standard error, i.e., larger circles indicate higher precision and, typically, smaller Cl. We consider average summary effects whose confidence interval does not overlap with zero as significant, i.e.,

statistically different from zero. Asterisks indicate statistically significant summary effects. Positive values indicate a higher SOC in restored ecosystems compared to degraded land, while negative values indicate the opposite. The category "farmland" refers to summary effects that encompass both cropland and pastureland. Letter annotations indicate statistically significant differences, where average summary effects indicated with different letters differ statistically from one another. The figure displays all pre-restoration land use categories besides "multiple" and "not specified". The number of effect sizes and meta-analyses included for all categories are given in Supplementary Table S21.



**Fig. 4** | **Change in Soil Organic Carbon (SOC) in restored ecosystems as compared to degraded land across restoration strategies.** Different panels and colours represent different ecosystem types, namely forests (**a**), grasslands (**b**), and wetlands (**c**). Circles are the average summary effects for a singular restoration strategy, reported as the percentage of SOC change, also showed in the column on the right. Parentheses include the number of meta-analyses and effect sizes included for each category presented in this figure. Lines indicate the 95% confidence interval. Circle size is the inverse of the standard error, i.e., larger circles indicate higher precision and are thus associated with smaller CI. We consider average

summary effects whose confidence interval does not overlap with zero as significant, i.e., statistically different from zero. Positive values indicate a higher SOC in restored ecosystems compared to degraded land, while negative values indicate the opposite. Letter annotations indicate statistically significant differences, where average summary effects indicated with different letters differ statistically from one another. The figure displays all restoration strategy categories besides "multiple" and "not specified". The number of effect sizes and meta-analyses included for all categories are given in Supplementary Table S22.

decrease but does not imply that active restoration is detrimental to SOC in all wetland types and pre-restoration land uses.

For assisted restoration of grasslands, we were also able to quantify stock changes in the above- and belowground biomass carbon pools in addition to SOC. Carbon stored in aboveground biomass (AGB) increased by an average of 68% (48–89% CI; Fig. S4a) after assisted restoration, while carbon stocks in belowground biomass (BGB) and SOC increased by 20% (3–36% CI; Fig. S4b) and 11% (–10–31% CI; Fig. S4c), respectively. The higher relative AGB recovery compared to SOC is likely because our data on assisted strategies predominantly reflects pastures being restored by grazing exclusion, where AGB is more depleted than BGB and SOC and thus recovers more after disturbance removal<sup>44</sup>. Moreover, addition of above-ground litter to the soil enhances microbial carbon decomposition and this priming effect

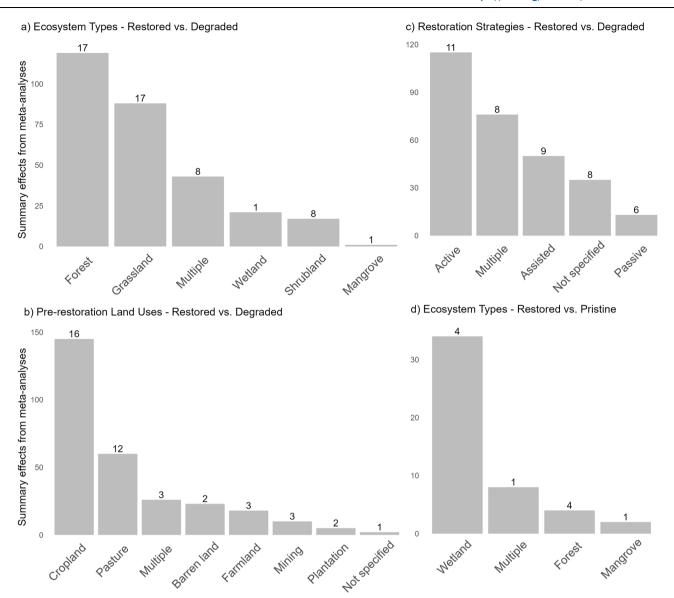
can cause SOC loss<sup>21</sup>. AGB is more sensitive to disturbances like droughts, wildfires, and insect outbreaks compared to below-ground stocks<sup>45</sup>, so while the increase of all carbon pools mitigates climate change, accumulation in AGB may have lower persistence compared to SOC<sup>11</sup>.

We studied the combined influence of pre-restoration land use and restoration strategy for cropland restoration to forest and grassland ecosystems and pasture to forest ecosystems (Fig. S5) but found no statistically significant combined effect.

#### Discussion

#### Sensitivities and limitations

The use of multiple existing first-order meta-analyses presented several limitations to this study. First, depending on their scope, the meta-



**Fig. 5** | **Number of summary effects extracted from first-order meta-analyses.** The number of summary effects are shown for restored versus degraded land across different ecosystem types (**a**), restored versus degraded land across different pre-restoration land uses (**b**), restored versus degraded land for different restoration strategies (**c**), and restored versus pristine land for different ecosystem

types (**d**). Meta-analyses can report a single summary effect for two or more levels of the predictor variable (e.g., two or more ecosystem types), or do not specify the level. These were reported as "Multiple" and "Not specified", respectively. Numbers on top of the bars represent the number of meta-analyses from which the summary effects were extracted.

analyses used here had in some cases pooled observations across different settings (e.g., multiple pre-restoration land uses or restoration strategies) into a single summary effect. As this obscures differences in SOC change between these different settings, we placed such combined summary effects into the 'multiple' category (Fig. 5), which was not used to assess SOC recovery across different pre-restoration land uses or restoration strategies. Moreover, as meta-analyses focus on entire ecosystems and/or countries, we could not assess SOC responses under different biomes, local climatic conditions and soil types.

Second, the meta-analyses used here report summary effects using various metrics. We limited our analysis to those that could be transformed to response ratios to allow for inter-comparison, possibly excluding valuable information. In addition, SOC measuring methodology and time elapsed (i.e., restoration age) may vary between moderators like ecosystem, previous land use and restoration strategy. Consequently, we believe that sharing the underlying data from individual meta-analyses would improve the

quality of future studies. Access to raw data points would enable researchers to conduct more comprehensive and accurate analyses, ultimately advancing knowledge and fostering informed decision-making.

Third, there was an overlap in primary studies used by the first-order meta-analyses (Figs. S6 and S7). We based our default results on excluding meta-analyses with more than 30% overlap<sup>21</sup>. Robustness analyses, in which meta-analyses with an overlap of more than 10% and 5% were excluded, did not result in statistically significant different outcomes from our default 30% cut-off (Tables S3 and S4). Restrictive cutoffs did result in wider confidence intervals as fewer data points were available. We also examined the robustness of our results on SOC changes against the control type and weighting method used by the meta-analyses included in this study. Our analysis shows that SOC changes are not sensitive to the type of control and to the different weighting methodologies used in the meta-analyses included in our study (Tables S5–S12). We performed these tests for the data representing SOC change for restored compared to degraded land, because

no varying types of controls or weighting methods existed in the restored vs. pristine land dataset.

Fourth, most meta-analyses used in this study focused on: i) terrestrial ecosystems, ii) croplands as pre-restoration land use, or iii) active strategies as restoration approaches when comparing restored areas with degraded land (Fig. 5, panels: a,b,c), as these focus areas may have been considered as most policy-relevant and cover a large geographical extent. Restoration aimed specifically at climate mitigation traditionally focuses on forests and (more recently) on mangroves, due to their large carbon pools and high sequestration rates<sup>46</sup>. Our systematic literature review allows us to pinpoint understudied settings and comparisons that may benefit from further research, such as restoration of wetlands in comparison to degraded land, submersed aquatic ecosystems, and restored grassland versus pristine land. Meta-analyses can suffer from publication biases when non-significant, negative results encounter publication issues. The results of the Egger's test, used to check for publication biases (see the Methods for a more in-depth explanation), indicate a high likelihood of bias in specific settings of our study, such as forests restored with active restoration and grasslands restored from pastures through assisted restoration (Table S2). However, across studies heterogeneity in mixed-effect models may also have an impact on Egger's test<sup>47</sup>.

Fifth, only few meta-analyses report restoration age data for restored versus degraded ecosystems, and no meta-analyses report this for restored versus pristine ecosystems. Therefore, we could not assess if SOC recovery is faster in some settings (e.g., different restoration strategies or pre-restoration land uses). More importantly, this lack of data meant we could not rule out the possibility that pristine SOC levels may in some systems be reached when enough time passes. However, based on our temporal regression of SOC increase in restored versus degraded systems (Supplementary Information section 2) and previous literature on SOC dynamics in a wide range of ecosystem types<sup>16,23</sup>, we deem it most likely that SOC increases rapidly after restoration and then stabilizes over time possibly never reaching pristine levels. Earlier empirical studies have for instance shown that a carbon recovery debt, analogous to our carbon deficit, continues to exist across different ecosystems globally (including wetlands, mangrove, and marine systems) as time passes<sup>16</sup> and that ecosystem recovery is incomplete over all analyzed restoration ages<sup>23</sup>, indicating that pristine SOC may in fact never be attained. As mentioned in the Results section, this may be due to the impaired recovery of ecosystems where conditions have been altered to a (near) irreversible degree<sup>24-26</sup>. Altered physical conditions could for example comprise the erosion of topsoils29 or permanently altered hydrology<sup>25</sup>. Altered chemical conditions could include effects of nutrient deposition<sup>27</sup> or various forms of pollution<sup>30</sup>. Altered biological conditions could include ecological feedbacks that sustain the degraded state<sup>24,26</sup>, the invasion of nonnative species<sup>24</sup>, or long recovery times for full ecological complexity<sup>28,31</sup>.

#### **Implications**

This study provides an overview of the relative global SOC change resulting from the restoration of degraded land, accounting for different pre-restoration land conditions, uses and restoration strategies. By systematically comparing restored sites with both degraded land and pristine ecosystems across the globe, we found that restoration consistently increases ecosystem SOC in different contexts, but (thus far) not to pristine levels. Existing model-based global estimates may thus be overly optimistic when assuming a full return to pristine levels. Future studies could explore absolute SOC increases through restoration by combining the SOC change ratios presented in this study with global maps on areas suitable for ecosystem restoration and SOC stocks in

pre-restoration land. Only for wetlands, unrealized carbon stock potential has been quantified globally by multiplying the carbon densities of different stocks with the area lost to degradation<sup>48</sup>. To our knowledge, such empirically-based assessments are lacking for the other ecosystems, whereas they are essential to evaluate the carbon sequestration potential of restoration in absolute terms.

Our findings imply that preventing carbon loss from land degradation is a more efficient strategy for mitigating climate change compared to ecosystem restoration. To guide decision-makers in the selection of natural-climate solutions, Cook-Patton et al.<sup>49</sup> find that conservation should be prioritized over restoration, because mitigation from restoration takes longer, is costlier and may be less effective in reducing GHG concentrations than avoided emissions for conservation. Our global study that compares restored ecosystems to both degraded and pristine states adds to their conclusions as we consistently show that attempting to compensate SOC depletion through ecosystem restoration would result in a carbon deficit. Although our results on SOC deficit do not include a temporal component, existing literature suggests that such deficits may never be fully offset<sup>16,23</sup>. Avoiding such a carbon deficit is particularly relevant, as a rapid reduction in greenhouse gas emissions is required across sectors to reach the temperature goals in the Paris Agreement<sup>50</sup>. Ecosystem restoration should therefore not be viewed as a way to fully offset SOC losses in natural ecosystems, whose conservation has priority. Instead, restoration should be regarded as a viable strategy to provide additional carbon sequestration (and associated ecosystem services) and be implemented in degraded areas while pristine lands remain intact.

#### Methods

#### Data collection and first-order meta-analysis selection criteria

We retrieved 410 meta-analyses and quantitative reviews on the soil carbon sequestration potential of restored ecosystems compared to degraded or pristine areas, using a search string (Table S1) in the Web of Knowledge database in January 2024. Of those, 41 were selected by abstract and full-text screening according to the following criteria:

- (i) Carbon sequestration is expressed as a change in carbon content between restored and human-managed or pristine areas and is reported for soil organic carbon (SOC), below-ground biomass (BGB) and above-ground biomass (AGB), in either stock (kg/ha) or concentration (g/kg).
- (ii) Results are presented as logarithm Response Ratios (lnRR) or closely related metrics such as percentage of change, which we transformed to lnRR. Following meta-analytical methods, lnRR is the natural logarithm of the ratio between the mean carbon content between restored and degraded or pristine areas. A positive lnRR indicates a higher amount of carbon in the restored ecosystem than that of the control, whilst a negative lnRR implies a higher carbon content in the control.
- (iii) Restoration does not consist of commercial plantations and/or afforestation, i.e., planting forest species in non-naturally forested contexts<sup>2</sup>. Restoration starts a process that eventually leads to adapted ecosystems that do not require management in the long term<sup>1</sup>.
- (iv) Meta-analyses unambiguously define the treatment as restoration and the control as either a) anthropogenically managed or altered land (defined here as degraded land), or b) unaltered vegetation (defined here as pristine); they specify variance components and the formulas used to compute them; they describe type and general structure of the models chosen to derive their results and the software package used to conduct the analyses.

To verify that meta-analyses were built on different sets of primary studies and to limit pseudo-replication, we only included meta-analyses that shared less than 30% of their primary studies with other selected meta-analyses. We first extracted the primary studies from the selected meta-analyses, and then checked the overlap between pairs of meta-analyses (SI, section 7.1). If two or more metaanalyses had an overlap higher than 30%, we discarded the metaanalysis with the fewer number of primary studies, following Tamburini et al.<sup>21</sup>. We conducted separate overlap checks, one for metaanalyses comparing restored ecosystems with degraded land and one for those comparing restored with pristine ecosystems. Five meta-analyses did not report a list of primary studies included in their research, thus we used the full reference list instead (SI, section 9.6); three meta-analyses reported only the last names and year of the studies included in their analyses (SI, section 9.7), so we searched manually for those references, and considered only those we managed to retrieve.

For each meta-analysis, we extracted the summary effects with 95% Confidence Intervals (CI). We extracted data on summary effects from text and tables, or from graphs using the online software Plot-Digitizer (Version 3.1.5) when necessary. When a meta-study reported multiple summary effects (e.g., on restored forests and restored grasslands), each summary effect was extracted individually. In three studies, summary effects were reported as organic matter concentration (SI, section 9.5), which we converted to SOC concentration by multiplying by a conversion factor of 0.5851. We also extracted weighting methodology of each meta-study, since not all analyses used inverse variance weighting, typical of the meta-analytical method52. Furthermore, if reported, we extracted the control type used to derive each summary effect, i.e., whether the control corresponds to the same area prior to restoration (temporal control) or to an adjacent site that is not restored (spatial control, also known as space-for-time control53).

### Moderator variables and levels description

If reported, we extracted ecosystem type, pre-restoration land use, restoration strategy and restoration age corresponding to each summary effect. Ecosystem types included forests, grassland, shrublands, mangroves, and wetlands (which included swamps, mires, bogs, fens, marshes, peatlands, and floodplains). Pre-restoration land use encompasses land utilization practices established for the extraction of natural resources, such as cropland, pasture, farmland (that includes both crops and pasture), tree plantations (including orchards), mines, or areas unvegetated because of such practices, included here as barren land<sup>9</sup>. We classified restoration as: *passive restoration*, i.e., spontaneous revegetation; active restoration, i.e., the direct planting on degraded areas, or assisted restoration, i.e., efforts that rehabilitating habitats, managing disturbances, and protecting spontaneously growing seedlings to trigger natural recover<sup>2</sup>. Assisted strategies in terrestrial ecosystems consists in weeding and establishing fences and firebreaks22; in aquatic ecosystems, they involve rewetting, especially for peatlands<sup>48</sup>, restoring inundation in marshes by, e.g., removing dikes<sup>54</sup>, and placing sediment to reverse land subsidence in coastal wetlands<sup>55</sup>.

#### **Data description**

Most of the selected meta-analyses (36 out of 41) were published after 2015 indicating a growing use of the methodology in the field of ecosystem restoration. 78% of the selected meta-studies used degraded land as a reference, 12% used pristine areas as a reference, and 10% used both. In total, this resulted in 332 summary effects for the degraded control (289 focused on SOC, 31 on AGB, and 12 on BGB) and 48 for the pristine control. Of the 289 summary effects on SOC with degraded control, the most frequently assessed ecosystem types are forests (41%; Fig. 5a) and the least are mangroves, for which

the only available data comes from a meta-analysis by Su et al. <sup>56</sup>. We show the results of that study here to ensure a complete overview of what is reported in literature. While cropland is the most frequently studied pre-restoration land use (50%; Fig. 5b), in terms of restoration strategies, most summary effects reflected active restoration (40%; Fig. 5c) followed by assisted (17%) and passive restoration (4%), with a large portion of multiple strategies (26%) or strategy not specified (12%). For the comparison between restored and pristine ecosystems, 71% of all summary effects reflected wetlands (Fig. 5d). In terms of geographical range covered, we included both meta-analyses with global scale and with a regional scale. Most included meta-analyses consider the global scale (40%) or focus on China (58%) (Fig. S3), as China has implemented some of the oldest and largest restoration projects to compensate the erosion caused by prolonged and intensive land use<sup>42</sup>.

#### Second-order meta-analysis

We studied the natural logarithm of the response ratios (lnRR) of carbon stocks. We compared restored with both degraded and pristine areas in different ecosystems by performing a series of mixed effect models using the metafor package<sup>57</sup> in R version 4.3.2<sup>58</sup>. The model had the general form:

$$LnRR \sim predictor, random = RES, V = SE^2$$

Where: LnRR are the summary effects (i.e., outcomes of the first-order meta-analyses); predictor is either pre-restoration land use or restoration strategy; RES is the random effect structure; V is the sampling error variance, the square of the standard error SE. We calculated SE from the 95% confidence intervals using the following equations (Eqs. 1, 2)<sup>57</sup>.

$$V = [SE]^2 \tag{1}$$

$$SE = \left(\frac{CI}{2}\right)/1.96\tag{2}$$

We used inverse-variance weighting, i.e., weighing the summary effects by 1/SE^259. For the random effect structure (RES), we selected summary effect ID nested within paper ID, which account for potential heterogeneity between sources and summary effects<sup>60</sup>. We ran models with several combinations of random effects and selected RES corresponding to the model with lowest Aikake Information Criteria (AIC) score. We ran a first meta-regression with intercept and random effects, but without predictors, to assess whether the resulting pooled summary effect was significantly higher or lower than zero, i.e., whether carbon content of restored ecosystems is higher or lower compared to the control. We considered pooled summary effects significantly different from zero if their 95%-CI did not overlap with zero. We performed the analysis separately for the degraded and the pristine control.

For the degraded control, we studied carbon change in relation to pre-restoration land use and restoration strategy for several ecosystem types. Data availability was insufficient to do the same analysis for the pristine control. Subgroup analyses were performed by dividing our database into subsets according to ecosystem type and running separate regressions. This was done to account for variation of residual heterogeneity within subgroups. For each ecosystem type, we first ran a regression without predictors to obtain the pooled summary effect per ecotype and, secondly, we ran models including each predictor separately (i.e., pre-restoration land use and restoration strategy), with and without the intercept. We ran these models with the intercept to test whether each predictor explained a statistically significant portion of the effect sizes

heterogeneity, which is indicated by the results of the omnibus test (Q moderation test)<sup>57</sup>. We then excluded the intercept to obtain the weighted mean summary effect per predictor level<sup>61</sup>, which were considered significantly different from zero if their 95% CI did not overlap with zero. Using the omnibus test, we studied the contrasts between predictor levels and assumed a significant difference if *p*-value relative to the test was lower than 0.05.

### Robustness of the analysis

We tested the effects on our results of applying two more stringent overlap thresholds. Specifically, we excluded meta-analyses exceeding 10% and 5% shared primary studies and compared the resulting SOC changes to those obtained using the 30% threshold. We ran further robustness analyses to test the impact of different weighting methodologies and control types used by meta-analyses on our results on SOC changes. We divided the meta-analyses into three categories based on their weighting methods: i) meta-analyses that adopt strict inverse-variance weighting (inverse-variance weighted), ii) metastudies that do not use the inverse-variance method but use other approaches, for example, weighting their results according to their sample size only14 (weighted), and iii) unweighted studies (unweighted). We included weighting method as a categorical predictor in mixed-effect models, with the three categories featuring as predictor levels. We then used the omnibus test to first check the significance of the variance portion explained by the weighting method and, second, to study the contrasts between different weighting methods and assess whether our results on SOC change were significantly affected by weighting methodology. We ran these tests for the full database and the ecosystems subset. Concerning control type, we distinguished two categories, spatial and temporal, and used the same procedure as for weighting method was to assess the robustness of SOC change to different control types.

Only few meta-analyses report restoration age data for restored versus degraded ecosystems, and no meta-analyses report this for restored versus pristine ecosystems. We, therefore, tested the response of SOC change to restoration age for the restored versus degraded states in ecosystems for which temporal data was available, i.e., forests and grasslands. In this analysis we included studies that reported restoration age as a single year or as range with a lower and upper bound. This resulted in subsets containing 17 and 54 effect sizes or 14% and 61% of the full datasets, for forests and grasslands respectively. These subsets accurately represent the overall dataset, as is indicated by the fact that the predicted SOC increase at the mean restoration age matches the observed SOC increase in the full dataset. This holds for both forest and grassland. Since meta-analyses mostly reported restoration age as a time range, we applied a bootstrapping procedure to sample from each time range randomly 1000 times. For the restoration age ranges starting before one year, the lower bound of the intervals was set to begin at 1 year. For each random sample across the studies, we then fitted a linear regression with the SOC change as the dependent variable and the logarithm of time as the independent variable. This resulted in 1000 regression models for each ecosystem type. We extracted the R<sup>2</sup> values to evaluate the fit of each model, and the regression slopes to infer the change of SOC with unit of time. We could not perform a similar analysis for restored vs. pristine ecosystems, due to a lack of reported restoration ages in the relevant metaanalyses.

Because statistically significant studies are more likely to be published, meta-analyses can be subjected to publication bias when the overrepresentation of significant studies leads to an overestimation of the true effect size. We tested for publication bias by performing Egger's tests per moderator level using the *metabias* function of the meta package, assuming high risk of publication bias if the *p*-value of the t-test was lower than 0.05.

# **Data availability**

The data generated in this study, as well as the datasets used as source input for the figures are available, without restrictions, under the repository https://doi.org/10.17026/LS/LBR3QO.

# **Code availability**

The codes required to replicate the analyses performed and to generate the figures are available at https://doi.org/10.17026/LS/LBR3Q0.

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#### **Author contributions**

I.A., S.V.H., J. P.H., M.A.J.H. and M.M.v.K. conceived and designed the study; I.A. performed the research; I.A. analyzed the data with contributions from S.V.H., J.P.H., M.A.J.H. and M.M.v.K; I.A. and S.V.H. wrote the manuscript; I.A., J.P.H., M.M.v.K. M.A.J.H., and S.V.H. provided revisions to the manuscript.

#### **Competing interests**

The authors declare no competing interests.

### Additional information

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