













Optimizing cover crop practices as a sustainable solution for global agroecosystem services

Received: 5 November 2023

Accepted: 14 November 2024

Published online: 05 December 2024



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The practice of cover crops has gained popularity as a strategy to improve agricultural sustainability, but its full potential is often limited by environmental trade-offs. Using meta-analytic and data-driven quantifications of 2302 observations, we optimized cover crop practices and evaluated their benefits for global agroecosystems. Cover crops have historically boosted crop yields, soil carbon storage, and stability, but also stimulated greenhouse gas emissions. However, combining them with long-term implementation (five years or more) and climate-smart practices (such as no-tillage) can enhance these services synergistically. A biculture of legume and non-legume cover crops, terminated 25 days before planting the next crop and followed by residue mulching, is the optimal portfolio. Such optimized practices are projected to increase agroecosystem multiservices by 1.25%, equivalent to annual gains of 97.7 million metric tons in crop production, 21.7 billion metric tons in carbon dioxide sequestration, and 2.41 billion metric tons in soil erosion reduction. By 2100, the continued implementation of optimized practices could mitigate climate-related yield losses and contribute to climate neutrality and soil stabilization, especially in harsh and underdeveloped areas. These findings underscore the promising potential of optimized cover crop practices to achieve the synergy in food security and environmental protection.

To meet the ever-growing food demand, the globally unprecedented cropland expansion and agricultural intensification have caused a myriad of negative environmental impacts, such as climate change, biodiversity loss, and nitrogen (N) pollution^{1,2}. As these impacts escalate and break through the corresponding planetary boundaries, the sustainability of agroecosystems and their several critical services will be irreversibly undermined^{3,4}. Therefore, achieving higher yields with lower environmental costs—i.e., to synchronously achieve the inter-linked sustainable development goals (SDGs)—is an inevitable challenge⁵. Perceived as one of climate solutions⁶, cover crops (CCs)

represent a potential strategy to safeguard food production while reducing environmental impacts⁷.

CCs refer to the crops incorporated during the transition period between the growth cycles of two cash crops, offering various benefits to agroecosystems through surface coverage and crop diversification, including provision (e.g., food and feed supply), regulation (e.g., carbon (C) storage and climate mitigation), and support (e.g., soil stabilization and erosion control)⁷. For example, legume CCs substantially improve soil nutrition through biological N fixation, while some non-legume CCs enhance soil structure and penetration to support well-

developed root systems of primary crops⁸. CCs also accelerate the formation of microbial-derived C by providing diverse residues for microbes⁹. However, some investigations have demonstrated that CC implementation may interfere with the yield of subsequent crops by competing for soil moisture and nutrients¹⁰, and stimulate nitrous oxide (N₂O) and methane (CH₄) emissions through activated microbial metabolism^{11,12}, leading to an uncertain greenhouse gas (GHG) budget. Although CC practices are generally beneficial to soil microbiome and associated functions¹³, in some cases, such improvement in soil biological attributes does not translate into increased crop productivity¹⁴. These variable outcomes highlight the need to optimize CC practices to achieve both food security and environment-friendly services. This optimization requires careful consideration of CC type selection (including mixtures), termination timing, and residue management (Fig. 1a).

Although numerous research efforts aim to maximize the benefits of CCs for agroecosystem services^{7,8}, these studies are predominantly isolated experiments conducted under limited agronomic and biophysical conditions. Most of these efforts focus on individual target services, often lacking a quantitative evaluation of the trade-offs or synergies among them, especially concerning the interactions between CC practices and diverse environmental and management factors¹⁵. Such knowledge gap hinders our capacity to propose an ideal CC adoption paradigm and formulate effective measures that can fully harness its multiple benefits⁷. Additionally, current limitations within statistical procedures—such as the complicated assumptions in process-based modeling and the low predictive accuracy of empirical models—further contribute to a lack of quantitative tools for assessing potential CC benefits and extrapolating these benefits on a global scale, despite some successful regional simulations by crop models^{16,17}. Given the critical need for synergistic agroecosystem services, it becomes imperative to globally explore and implement the most-effective CC practices, leveraging ubiquitous data and emerging methodologies.

Here, we conducted a preliminary examination of the critical effects of CC practices on agroecosystem services using meta-analytic techniques, with a primary focus on food supply, C storage, climate mitigation, and soil stabilization (as measured by the mean weight diameter of soil aggregation, MWD). According to the observed performances across these dimensions, we identified the optimal CC portfolio, the key factors influencing its effectiveness, and their interactions. The optimization of CC portfolio was complemented by additional long-term field data on soil health and simulations from the Agricultural Production Systems sIMulator (APSIM). We further introduced an “agroecosystem multiservices” index (see “Methods”) to offer a holistic evaluation of the capability of CCs to simultaneously provide multiple benefits. Finally, we employed a machine-learning approach, which excels at handling variable interactions and non-linearities in the context of meta-analysis, to quantify the potential of optimized CC practices in enhancing synergies among agroecosystem services worldwide. Our hypothesis posits that optimizing CC practices can sustainably deliver spatial and temporal benefits for global agriculture, thereby markedly advancing the SDGs (Fig. 1b).

Results and discussion

Partial trade-offs of agroecosystem service promotion by historical CC practices

Drawing insights from 2302 field observations of 219 studies spanning the historical application of CC practices from 1978 to 2020, we determined the effects of CCs on five fundamental agroecosystem services (Supplementary Fig. 1). Overall, CCs significantly increase yields by 2.33% and SOC stocks by 6.46%, alongside an enhancement of 14.3% in MWD (Fig. 2a), illuminating their notable effectiveness in promoting soil C storage, erosion control, and subsequent crop yields⁷. Nonetheless, N₂O and CH₄ emissions are also greatly stimulated by 29.5% and 42.3%, respectively. These stimulations of GHGs hinge on cropland type, with N₂O emissions only rising in uplands and CH₄ emissions in paddy

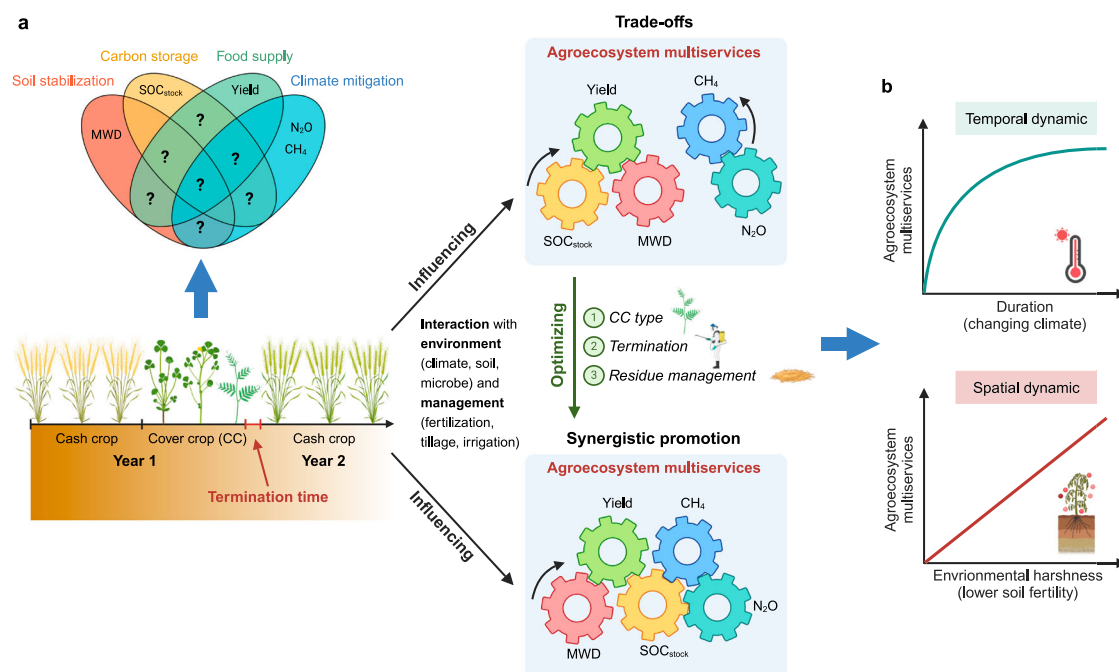


Fig. 1 | Hypothetical synergy of optimizing CC practices on multiple agroecosystem services, and its underlying benefits in different scenarios.

a Hypothetical shift from trade-offs to synergistic promotion of agroecosystem services by optimizing CC utilization and management, including its type, termination, and residue management. **b** Sustained benefits of optimizing CC practices.

We hypothesize that optimizing CC practices would have a lasting positive impact on agroecosystem multiservices with increasing climate change (temporal dynamic) and environmental harshness (spatial dynamic). Created in BioRender. Qiu, T. (2023) <https://BioRender.com/b58x621>.

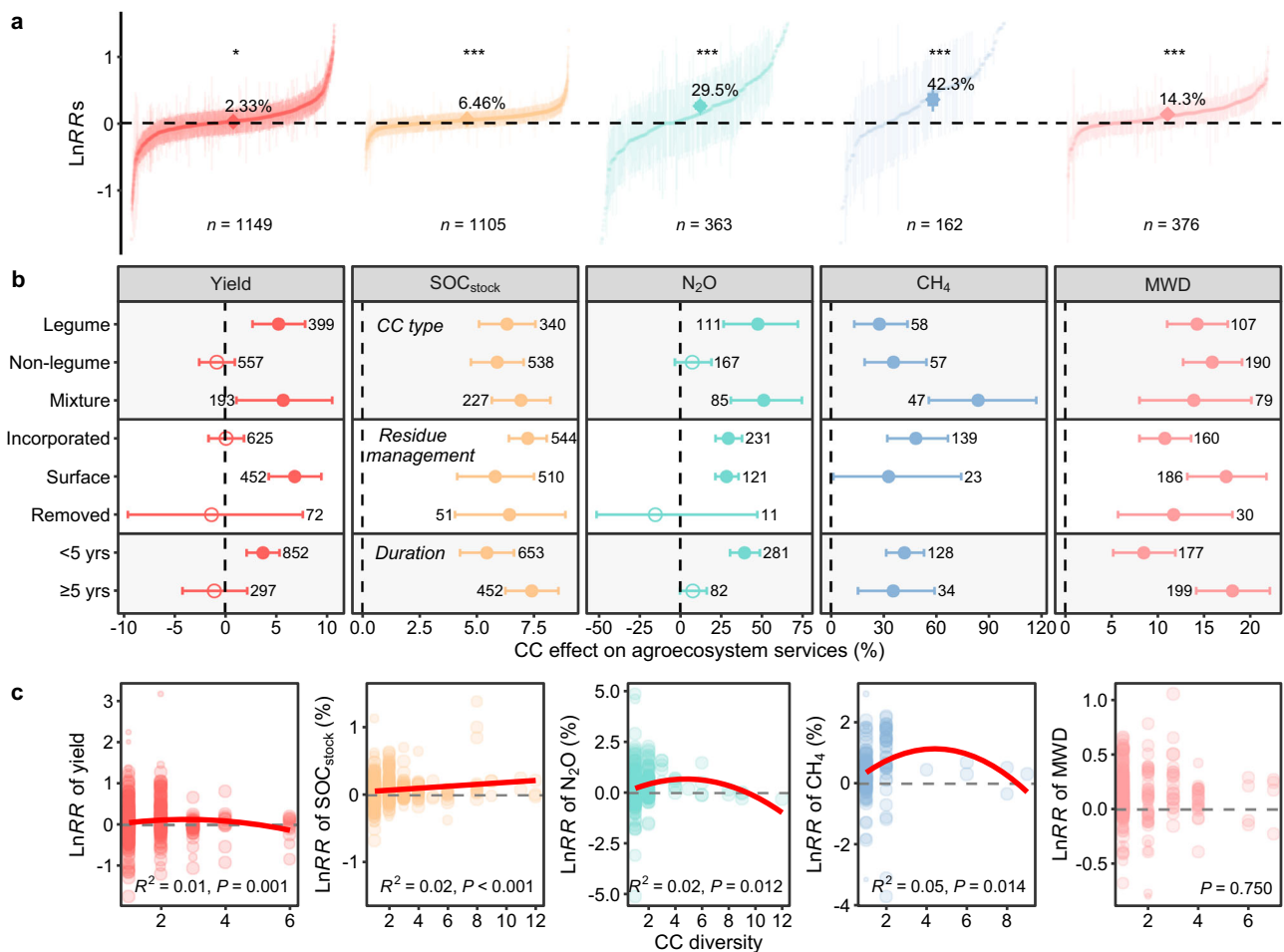


Fig. 2 | Effect of CCs on agroecosystem services and its dependence on practice characteristics. **a** Overall effects of CCs on five agroecosystem services (yield, SOC stock, N₂O, CH₄, and MWD). Dots represent the independent effect sizes (LnRRs) of individual observations and their 95% confidence intervals. Diamonds and figures above them denote the weighted effect sizes and the corresponding changes of agroecosystem services (%), respectively. *P < 0.05 and ***P < 0.001. **b** Control of CC practice characteristics including CC type, residue management, and duration.

Dots represent the overall effect sizes and their 95% confidence intervals. Solid and empty dots indicate significant and non-significant changes, respectively. Figures on the side of error bars refer to the number of observations. **c** Non-linear relationship between CC diversity and LnRRs of agroecosystem services. Red solid lines indicate the significant correlations (P < 0.05). MWD, mean weight diameter. Source data are provided as a Source Data file.

fields (Fig. 3a). Distinct from previous meta-analyses reporting no change or slight reduction^{10,18}, our findings indicate a context-dependent response of N₂O emissions to CCs, which can be attributed to the disproportionate contribution of nitrite and ammonium (primary products of CC residue decomposition in upland and paddy fields, respectively)¹⁹. Given the assignable role of N₂O in global warming and ozone depletion²⁰, there is an urgent need to implement appropriate mitigation measures to counteract such disservice induced by CCs⁷. Encouragingly, the implementation of long-term CC rotation (≥ 5 years) has shown potential to mitigate additional N₂O emissions without sacrificing crop yields (Fig. 2b). By continually providing adequate substrates (residues) and habitats, long-term CC practices are anticipated to increase the diversity of N₂O reductors (e.g., *nosZ* Clades I and II) and their survivability in the soil, thus reducing N₂O emissions^{21,22}. The long-term implementation can also effectively strengthen soil stability and C storage, potentially serving as a net sink of GHGs²³. In essence, CC practices promote several agroecosystem services but also pose a disservice risk, associated with a spectrum of factors. Identifying the key determinants of CC effects is therefore paramount to competently minimizing their trade-offs and maximizing their synergies.

Optimizing CC practices under the interactions with environmental and management factors

We propose that the characteristics and optimization of CC practices are key to synergistically promoting agroecosystem services (Fig. 1a). Compared to non-legume CCs, legumes and mixtures (a blend of legume and non-legume CCs) have been robustly observed to boost crop yields and N₂O emissions (Fig. 2b and Supplementary Fig. 2). For the residues of legumes and mixtures with a low C:N ratio, their sufficient available N not only contributes to crop uptake and growth, but may also exceed the microbial N requirements, thereby increasing soil N₂O production and emissions²⁴. This exemplifies a double-edged effect of their biological N fixation and highlights the importance of modulating microbial interactions within CC systems²⁵. Notably, these effects can be modified by CC diversification. The changes in yields and GHGs significantly display concave-down parabolic patterns, while SOC stocks rise linearly with increasing CC diversity (P < 0.05; Fig. 2c), manifesting the superiority of CC mixtures with a species number of 2 or 3. Additionally, mixtures have been found to enhance the root growth of subsequent crops and sequester more C in the surface soil (10–30 cm) than legume CCs alone (Supplementary Figs. 3, 4). These belowground benefits are supported by a 7-year rotation system, where CC mixtures can facilitate the accrual of mineral-associated

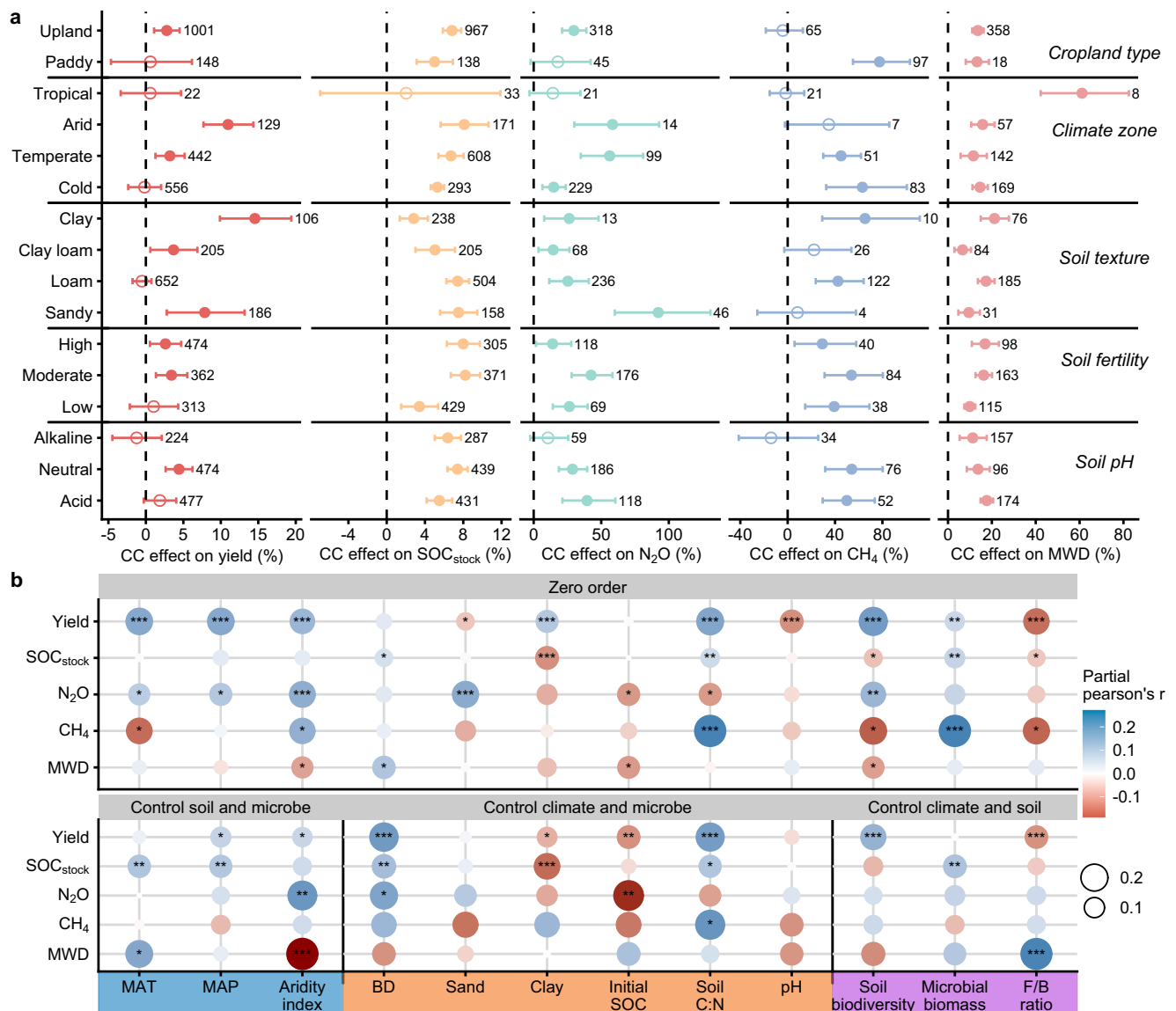


Fig. 3 | Mutual control of environmental factors on CC effects. a Varied CC effects among environments with different biophysical properties according to the classifications of cropland type, climate zone, soil texture, soil fertility, and pH. Dots represent the overall effect sizes and their 95% confidence intervals. Solid and empty dots indicate significant and non-significant changes, respectively. Figures on the side of error bars refer to the number of observations. **b** Partial correlation

analysis identifying the independent contribution of climate, soil and microbe to CC effects. Top texts of facets represent the controlled factors. Color scale and bubble size jointly indicate the partial Pearson's correlation coefficient (r). MWD, mean weight diameter. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Source data are provided as a Source Data file.

organic C fractions through increased root biomass²⁶. Our long-term observations further confirm that CC mixtures particularly promote the accumulation of mineral-associated organic C rather than particulate organic C (Supplementary Fig. 5a, b); the former can limit the accessibility of microbes and enzymes via mineral-organic matter interactions (e.g., adsorption and aggregation), thus exhibiting greater persistence^{27,28}. Given the lower production costs related to breeding and planting⁷, we cautiously recommend mixtures with a diversity of 2 (i.e., a biculture of legume and non-legume CCs) as the preferred CC type. This coincides with the perspective that a higher functional diversity, rather than species richness, of CCs predominantly supports multiple agroecosystem services¹⁵.

We adopted a meta-forest (MF) approach to capture the complex interactions of CC practices with environmental and management factors (Fig. 3–4 and Supplementary Fig. 6). Among these, soil biodiversity is identified as the most critical determinant of the CC effect on

yields (Supplementary Fig. 6a), plausibly attributed to key functions executed by diverse microbial groups, such as nutrient cycling and mutualism¹³. Partial correlation analysis robustly confirms this biological role even after controlling climate and soil variables ($P < 0.001$; Fig. 3b). Moreover, the response of crop yields is also dependent on climate, with arid regions experiencing the largest yield increase (Fig. 3a and Supplementary Fig. 2). This is largely due to the capacity of CCs to enhance soil water retention by reducing evaporation and increasing water infiltration⁸, especially when CC residues are mulched on the soil surface (Fig. 2b and Supplementary Fig. 2). Accordingly, CCs have a great potential to augment crop production in dryland farming systems²⁹. In contrast, the diminished CC biomass input post-termination³⁰ constrains soil C sequestration and yield improvements in cold climates (Fig. 3a and Supplementary Fig. 2), for which the high concentration of particulate organic C fraction may also account (Supplementary Fig. 5c). Regarding SOC stocks, the primary

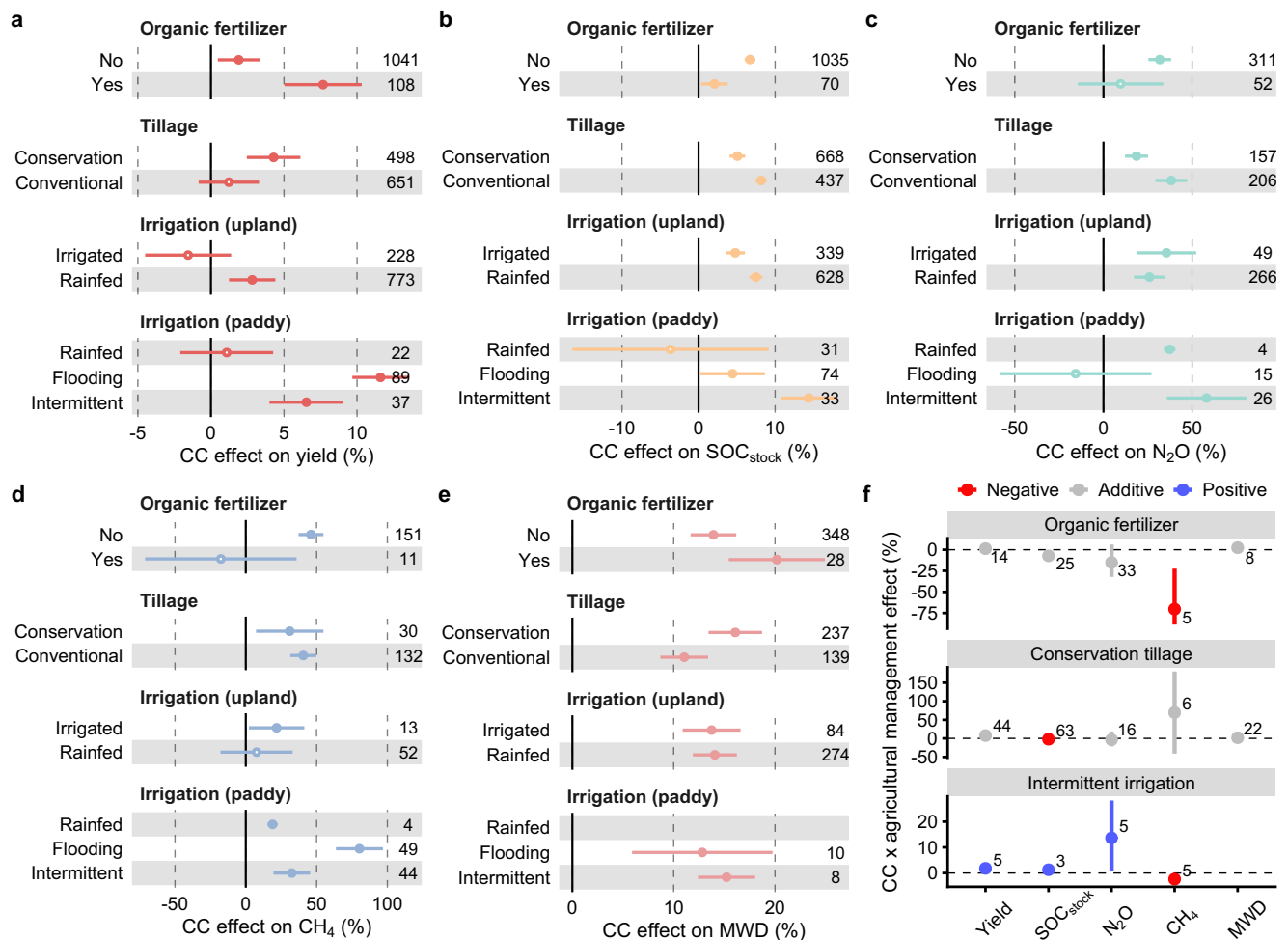


Fig. 4 | CC effects determined by agricultural managements and their interactions. a–e Control of CC effects by diverse agricultural managements, including organic fertilizer application, tillage, and irrigation. Dots represent the overall effect sizes and their 95% confidence intervals. Solid and empty dots indicate significant and non-significant changes, respectively. Figures on the right side refer to the number of observations. **f** Interactive effects of CCs and three climate-smart

managements on agroecosystem services (%). Red and blue dots represent negative (antagonistic) and positive (synergistic) interactions alongside with their 95% confidence intervals respectively, with gray dots denoting non-significant (additive) interactions. Figures around the dots refer to the number of observations. MWD, mean weight diameter. Source data are provided as a Source Data file.

moderators are initial SOC concentration and pH (Supplementary Fig. 6b), with their interactive effects varying across different soil depths ($P < 0.001$; Supplementary Table 1). This depth-dependent control limits C storage in surface and mid soil layers (Supplementary Fig. 4), probably due to microbial and enzymatic reactions sensitive to C concentration or pH. For instance, glucosaminidase and polyphenol oxidase activities were reported to correlate negatively with subsoil C stocks³¹. The greater, long-term stimulation of cellulase activity by CCs in surface and mid soil layers than in the topsoil (0–10 cm) supports this point (Supplementary Fig. 7a,b).

Soil texture, particularly clay content, dictates the CC effects on yields and SOC stocks as well. The negative relationship between SOC change and clay content ($P < 0.001$) suggests a heightened C sequestration potential and thus a notable yield gain of 7.86% in sandy soils³² (Fig. 3a,b), which is more evident in soils with lower fertility (Supplementary Fig. 8). This relationship also appears in SOC fractions, that is, their higher improvements occur in the soil texture with less clay and SOC, but not in the finest clay soils, especially for mineral-associated organic C (Supplementary Fig. 5c). Similarly, the positive relationship between yield gains and soil bulk density reveals that CCs can favor crop growth in highly compacted soils by fostering root penetration³³ (Fig. 3b). In humid tropical climates, CCs can significantly increase

MWD by 61.1%, reinforcing their role in mitigating soil hydraulic erosion⁸, largely through the contribution of high fungal-to-bacterial ratios ($P < 0.001$; Fig. 3b). The dominance of fungi in these systems leads to the substantial production of glomalin and other extracellular polysaccharides, as well as the formation of extensive hyphal networks, which physically bind soil particles into macroaggregates³⁴. This also highlights the supplementary benefits of CC residues beyond biomass input, as they act as organic binding agents that promote soil aggregation and erosion control¹³. More importantly, the duration of CC implementation emerges as the primary factor for enhancing MWD (Supplementary Fig. 6e), with long-term application leading to sustained soil stabilization and erosion control ($P < 0.001$; Fig. 2b and Supplementary Fig. 9). These insights demonstrate the higher benefits of CC practices into harsher environments and spotlight the intrinsic role of manipulating functional microbiota (e.g., N-fixers and mycorrhizal fungi) to strengthen the synergies among agroecosystem services in a changing environment^{13,25,34}.

Aligned with Basche et al.³⁵ and our previous observations, CC type significantly influences N₂O emissions (Supplementary Fig. 6c). This effect is particularly pronounced when leguminous species are included and in upland soils where residues are mainly decomposed into nitrite¹⁹ (Figs. 2b and 3a). Integrating conservation tillage with CC

practices, especially no-tillage combined with CC residue mulching³⁶, is expected to reduce N₂O emissions while boosting crop yields (Fig. 4a, c and Supplementary Fig. 2). By moderating soil temperature and aggregate stability²⁹, which in turn enhances the interaction of mycorrhizal fungi with living roots³⁷, mulching CC residues on the soil surface can markedly increase crop yields (Fig. 2b). In comparison, incorporating CC residues into the soil induces microbial turnover and nutrient immobilization³⁸, potentially limiting the yield benefits. The greater enhancement of cellulase activity also indicates the superior microbial functionality under no-tillage (Supplementary Fig. 7c); meanwhile, its active decomposition of organic matter contributes to the formation and stability of soil aggregates¹³. Furthermore, our analyses indicate that soil C:N ratio serves as a driving force behind CH₄ emissions (Fig. 3b and Supplementary Fig. 6d). An elevated C:N ratio exacerbates soil N limitation in general, under which CC biomass input accelerates microbial mineralization of organic matter via N mining, thereby priming CH₄ emissions³⁹. This priming effect varies by cropland type and irrigation method, with intermittent irrigation adeptly lowering CC-derived CH₄ emissions from paddies (Supplementary Fig. 10). Simultaneously, increasing N supply curbs the significant activation of cellulase and thus the opportunity for organic matter mineralization in paddy soils ($P < 0.001$; Supplementary Fig. 7d). Just as the synergies in increased yields, enhanced SOC stocks, and reduced CH₄ emissions (Fig. 4f), the co-implementation of CCs and intermittent irrigation facilitates both rice production and climate mitigation, chiefly through alleviated soil N limitation and improved aeration by drainage⁴⁰.

Accordingly, combined with climate-smart management practices⁶, CC benefits can be further amplified (Fig. 4). Via the potential promotion yield stability⁴¹ and soil microbial anabolism⁴², applying organic fertilizer largely increases the yield improvements based on CCs (Fig. 4a and Supplementary Fig. 2). This combination also effectively controls the production of GHGs (Fig. 4c, d), presenting a strong antagonism to CH₄ emissions by $\sim 70.3\%$ (Fig. 4f), probably due to the activation of methanotrophs and CH₄ oxidation⁴³. It is noteworthy that organic fertilizer and conservation tillage are also inclined to additionally enhance MWD (Fig. 4e), by virtue of their stronger cementation and less physical disruption of soil aggregates⁴⁴ as well as the amplified role of CC roots in soil stabilization⁷. N management is deemed as the cornerstone for agricultural and socio-economic sustainability^{45,46}. In this study, excessive N fertilizer application have been affirmed to nonlinearly decrease and even reverse CC-based yield gains once exceeding 100 kg N ha⁻¹, despite the high actual yields (Supplementary Fig. 11). Our APSIM results similarly prove that high N input ($> 100 \text{ kg ha}^{-1}$) will reduce the yield benefits from CCs (Supplementary Fig. 2). Under these circumstances, the larger N threshold and higher yield benefits accentuate the merits of CC mixtures in N fertilizer reduction and substitution (Supplementary Fig. 11). Fraiser et al.⁴⁷ suggested that the biculture of legume and non-legume CCs can enhance N availability and reduce N losses, thereby increasing subsequent crop yields. A life cycle assessment also revealed that utilizing CC mixtures will reduce N fertilizer rate by 25.0% while bolstering environmental footprint reduction and energy savings by 51.7%⁴⁸. Furthermore, N fate is largely governed by water management level. Overirrigation inevitably accelerates the leaching of surplus N and gaseous losses of C and N in (semi-)arid regions⁴⁹, accounting for the less soil C and yield improvements and greater GHG emissions from irrigated uplands (Fig. 4a–d). On the other hand, through water storage enhancement by increasing SOC and water evaporation reduction by residue mulching⁸, CCs are more conducive to the yield of rainfed crops in uplands (Fig. 4a and Supplementary Fig. 2).

Given the ascertained trade-offs, especially related to GHG emissions, we further quantified the associations among five services and their strengths of expected influence to narrow the actual gap in accurately evaluating CC applicability. In uplands, yields become the

keystone service with the greatest strength, followed by MWD, SOC stocks, and two GHGs (Fig. 5a). Beyond the direct support of SOC stocks for crop yields under CC practices³², the enhanced MWD will indirectly increase yields through improved soil fertility and connectivity (i.e., higher water, oxygen, and nutrient concentrations)¹³. Owing to the positive effects on food supply, C storage, and soil stabilization, CCs are anticipated to enhance agroecosystem multi-services (AMS) by 1.67% in uplands (Fig. 5c). Conversely, AMS experiences no significant promotion or even a decline in rice paddies, primarily attributed to the high expected influence of CH₄ (Fig. 5b, d). While CC biomass input promotes rice yields and soil C balance, it substantially increases CH₄ production under the anaerobic conditions of paddy soils¹² (Fig. 3a). Effective measures are, thus, necessary to reduce CH₄ emissions while maintaining rice productivity under CC practices, such as aerobic pre-digestion of CC residues⁵⁰ and intermittent irrigation (Fig. 4d, f). Structural equation modelling (SEM) show that climate is the dominant factor influencing AMS indirectly and directly in uplands and paddies, respectively (Fig. 5e–h), mainly by controlling water availability (precipitation and evapotranspiration; Supplementary Table 2). The direct influence of soil variables is also highly important to AMS. Specifically, soil C:N ratio is positively whereas initial clay and SOC concentrations are negatively associated with AMS, verifying the preferable benefits of CCs for harsh environments (i.e., soils with less organic matter and stronger N limitation or dryland areas; Fig. 1b). Meanwhile, integrating CCs with climate-smart management practices, including reducing N fertilizer rate, organic amendments, and mulching CC residues, has a definitely positive effect on AMS (Supplementary Table 2). Overall, these findings emphasize the importance of bridging the gap between local environment and managerial knowledge to design more sustainable CC systems with fewer trade-offs.

Global implications from optimizing CC practices

CC termination time, hereinafter defined as the time interval between CCs ending and the next cash crop planting (Fig. 1a), is acknowledged as the key factor affecting the magnitude and direction of multiple CC benefits^{7,29}. However, its importance is frequently overlooked. According to the maximum positive effect on AMS in moving window analysis (window size = 30 observations; see “Methods” for more details), we estimate an optimal CC termination time of 25 days across the globe (Supplementary Fig. 12). At this time point, there are also positive interactions of climate, soil, and microbial variables on AMS ($P < 0.001$; Supplementary Fig. 13). Our estimate is supported by Wang et al.⁵¹ who reveal that by terminating CCs around three weeks prior to the succeeding cash crop, soil water reserves and thus water use efficiency and yield of crops can be enhanced globally. Both premature and late CC termination are likely to restrict crop growth via insufficient nutrient input and water depletion, respectively²⁹. Though the optimal termination timing is largely site-specific, this macroscopic estimate has assisted the paradigm shift in CC utilization and management, marking an important step in evaluating the global applicability of optimizing CC practices. In the future, the alignment of termination timing with specific site conditions and crop requirements can further refine CC practices and ensure that their benefits are maximized.

Based on observed CC performances and interactions with the environment and management, we provide an optimized portfolio of CC practices here, i.e., the biculture of legume and non-legume CCs combined with surface mulching initiated after a termination period of 25 days. By integrating this portfolio with MF models and serial datasets of predictors (Supplementary Table 3), we scaled up the site-level CC effects to the globe (Fig. 6a–c). On average, these optimized practices are projected to increase global AMS by 1.25% for the current period (2020). The most significant gains occur in uplands, surpassing those from historical practices (1.86% vs. 1.67%; Fig. 5c), particularly in

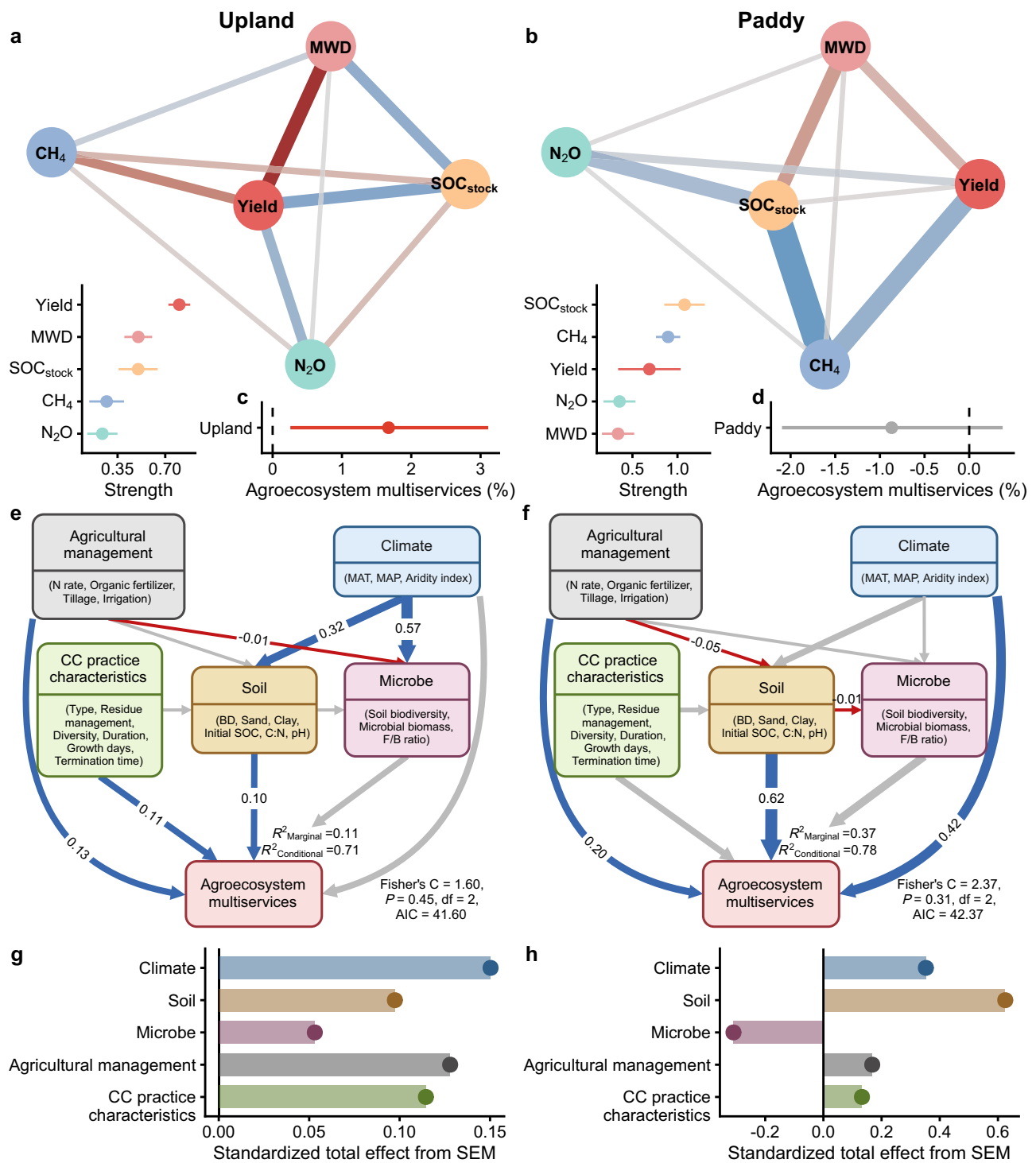


Fig. 5 | Agroecosystem multiservices and its drivers. Associations among CC effects on five agroecosystem services with their strengths from network analysis in upland (a) and paddy (b). Red and blue edges indicate negative and positive correlations, and edge width is proportional to correlation coefficient. Dots represent the bootstrapped strengths of individual services and their 95% confidence intervals. c, d Quantification of the changes of agroecosystem multiservices (%) under CC practices. Red and gray dots indicate significant and non-significant changes alongside with their 95% confidence intervals, respectively. e, f Direct and indirect effects of environmental and management factors on agroecosystem multiservices.

Red and blue pathways refer to negative and positive effects at a significant level ($P < 0.05$), with figures on them representing the standardized path coefficients from structural equation modelling (SEM). The conditional and marginal R^2 indicate the explained proportion of variance without and with random effects of “study”, respectively. AIC, Akaike information criterion. g, h Standardized effects of environmental and management factors from SEM. Total effect is the sum of standardized direct and indirect effects. $n = 2049$ and 253 data points for upland and paddy, respectively. MWD, mean weight diameter. Source data are provided as a Source Data file.

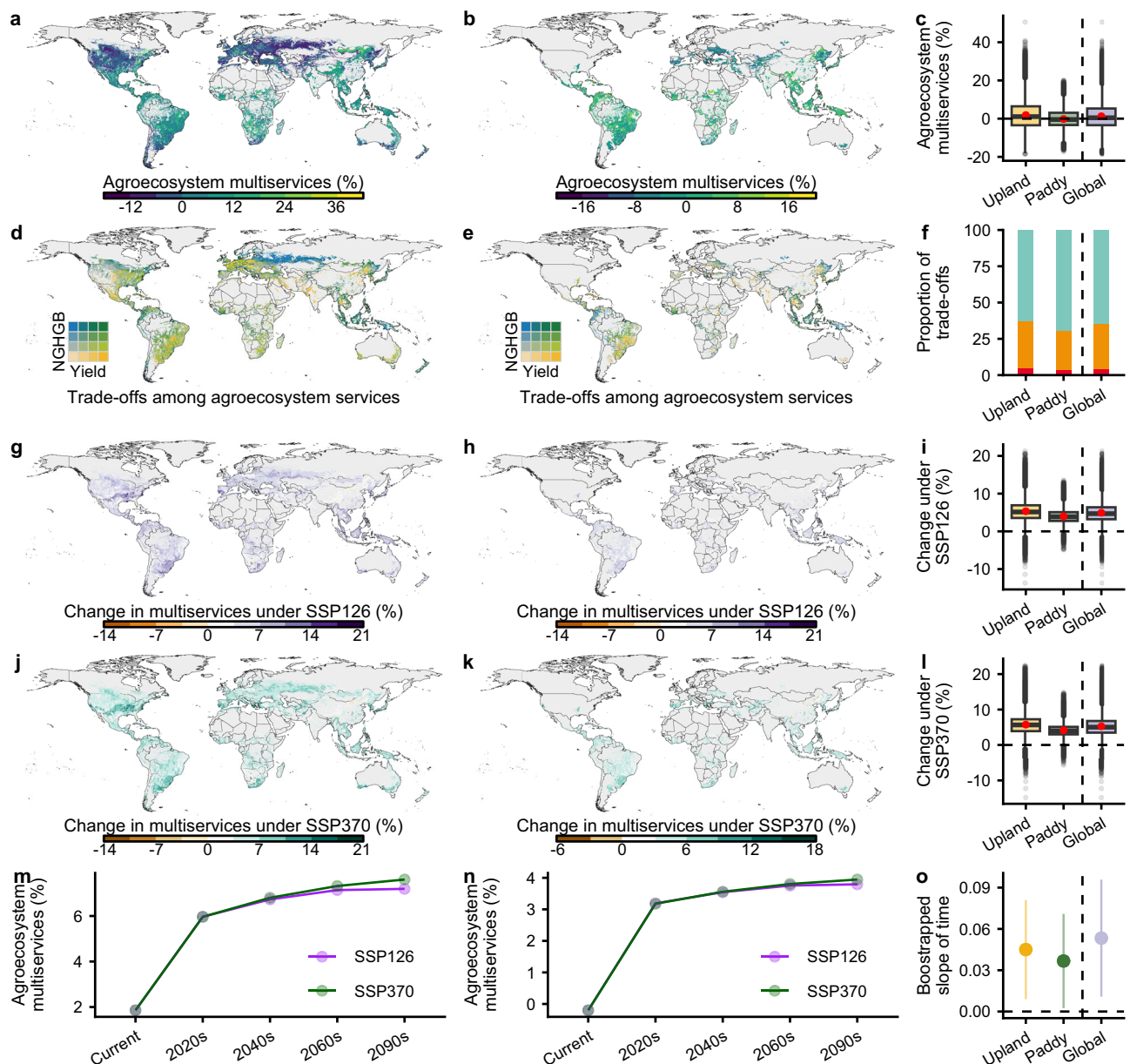


Fig. 6 | Global pattern of agroecosystem multiservices and its future trend under CC practices. Maps of CC effects on agroecosystem multiservices (%) for upland (a) and paddy (b). d, e Trade-offs or synergies between CC-derived actual crop production and net GHG budget. g, h Changes of CC effects on agroecosystem multiservices (%) between 2091–2100 and current (2020) under SSP126. j, k Changes of CC effects on agroecosystem multiservices (%) between 2091–2100 and current (2020) under SSP370. m, n Trend of agroecosystem multiservices during 2020–2100 under SSP126 (purple) and SSP370 (green). These spatial distributions are all aggregated by cropland type or globe (c, f, i, l, o) with the top-

down three colors in (f) representing synergy, trade-off, and negative proportions, respectively. Boxplots show the median (center line), the interquartile range between the first and third quartiles (box bounds), whiskers extending to 1.5 times the interquartile range from the quartiles, and any points beyond this range as outliers. Red dots indicate the mean values. o Bootstrapped regression slopes of time (duration) versus agroecosystem multiservices and their 95% confidence intervals. $n = 476,105$ and $199,449$ gridded values for upland and paddy respectively, with a total of $675,554$ gridded values for globe. Source data are provided as a Source Data file.

Africa, Latin America, and Northwest China. Moreover, the implementation of CC practices is expected to significantly improve crop yields and soil health in paddy fields across Southeast Asia (Fig. 6a). These benefits are pivotal to the diet and economy in this region and to global rice production⁴⁰. However, CC implementation also carries risks caused by reduced MWD and modest yield gains in North America, Europe, and temperate West Asia (Supplementary Figs. 14, 15). At the national scale, Colombia and India, benefiting from the substantially increased crop yields and SOC stocks, are the most applicable countries for CC practices in upland and paddy fields,

respectively (Supplementary Figs. 16, 17). In contrast, some European countries like Greece and Portugal may thoroughly experience adverse AMS consequences. Such regional inequality is related to the different climate, soil types, cropping systems, and even socio-economic conditions^{29,52}, but in general, CC practices offer potential to narrow it by delivering greater benefits to those countries with low crop production and high population density⁵³.

Optimizing CC practices is conducive to the synergies among agroecosystem services (Fig. 6d–f). Regardless of soil stabilization, CC benefits in crop yields and net GHG budget (NGHGB) reduction are

synergistically heightened in 64.9% areas, while merely 35.1% have trade-offs or negative responses. Paddy fields show a higher proportion of synergies compared to uplands (69.7% vs. 64.9%), likely due to their larger background C stocks and actual returns in mitigating NGHGB⁵⁴. These benefits can be converted into crop production by 97.7 Tg yr⁻¹ and CO₂ capture by 21.7 Pg yr⁻¹, equivalent to increases of 3.22% in staple crop yields and 0.87% in topsoil C stocks (0–30 cm) per year of global application (Supplementary Fig. 18a,b). However, there is a slight decrease in MWD by –2.11% during the current period, underscoring the significance of the duration of CC implementation (Supplementary Figs. 9 and 14). In line with our meta-analysis, long-term CC practices (≥ 5 years) will further increase SOC stocks, reduce N₂O emissions, and greatly enhance MWD without yield penalty (Fig. 2b and Supplementary Fig. 19). These positive feedbacks constantly intensify with time, offering temporally sustainable benefits for global AMS under a changing climate (Fig. 6g–o). Processed-based modelling assessments have also confirmed the clear advantages of long-term CC practices in soil C sequestration^{16,55,56} and erosion control¹⁷. We therefore estimate that after 5 years, optimized CC practices can reduce soil erosion displacement by 2.41 Pg annually, with 1.42 Pg in uplands and 0.99 Pg in paddy fields (Supplementary Fig. 18c). In addition, while CC-based yield gains are initially affected by climate change, their resistance and resilience markedly enhance over time, especially in rice paddies (Supplementary Fig. 20), thus aiding in combating the plausible yield losses and maintaining global food security⁵⁷.

Climate change impacts on AMS vary among cropland types and emission scenarios, but the larger positive changes always exist in warmer regions, even under the mid-high climate emission scenario of Shared Socioeconomic Pathway 370 (Supplementary Fig. 21). Soils in these warmer areas typically have less micronutrients, which often appears in underdeveloped countries⁵⁸. The use of CCs can replenish the removed soil micronutrients, maintaining their optimum levels that are crucial for crop productivity and soil health⁵⁹. By linking soil micronutrient concentrations (ref. 58) with their associated AMS, we strikingly discover that AMS benefits from CCs tend to be higher in regions with lower soil micronutrient levels (Supplementary Fig. 22). This reaffirms CC advantages for improving agricultural sustainability against harsh conditions and in dryland areas, because the equilibrium among all macro- and micronutrients can further improve water use efficiency of crops⁵⁹. More importantly, leveraging the national SDG performance data, we unravel the explicit support of optimizing CC practices for nations with limited progress towards the SDGs ($P < 0.001$; Supplementary Fig. 23), particularly in upland systems of the least-developed countries (SDG bundle 1 and 2)⁶⁰. However, despite of the huge potential in these countries (e.g., Nigeria and India; Supplementary Fig. 16), the widespread adoption of effective CC practices is still hindered by limited farmers' knowledge and subsidies⁷. To surmount this obstacle and achieve the common SDGs, international assistance and incentive policies (e.g., N Credit System⁴⁶ and Green Manure Planting Program⁶¹) are urgently needed. For developed countries with extensive CC experience but lacking in climate action (SDG bundle 5), new high-tech approaches and site-specific CC management are required to counteract adverse outcomes and realize further benefits^{52,62}.

Though we have presented considerable CC benefits across multiple independent observations, these findings should be taken with caution. First, our understanding of the underlying mechanisms remains limited. Beyond the accelerated microbial turnover and microbial-derived C accumulation under CC practices⁹, the positive link between MWD and SOC stocks in uplands partly implies the mineral-mediated SOC persistence during the aggregation process²⁸ (Fig. 5a). For more effective climate actions, it is essential to unveil the long-term effects of co-implementing CC practices with novel climate-smart managements (e.g., enhanced silicate rock weathering⁶³) and

their mechanisms (e.g., microbial growth and death pathways⁶⁴) on soil C sequestration. Second, there are some uncertainties in the predictions. Despite the well-assumed variable interactions and nonlinearities, as well as the weight of individual studies in MF models, the imbalanced data among different services and some regions will cause large estimation errors, such as CH₄ for the Mediterranean and MWD for Malaysia (Supplementary Fig. 24). Additionally, implementation duration is an indispensable factor for predicting CC effects, but most of the studies included are short-term (Supplementary Table 4). Excluding potential moderators of trade-offs among agroecosystem services may also miscalculate the CC benefits, such as elevated CO₂⁶⁵, management adaptability⁶⁶, and socio-economic factors⁶⁷.

Third, the representativeness of selected variables is controversial and subjective to a certain extent. In this study, five services related to food supply, C storage, climate mitigation, and soil stabilization have been applied to assess CC effects (Fig. 1a). While they represent provisioning, regulating, and supporting⁷, there are still some critical services omitted (e.g., N leaching), likely undermining the reliable estimation of AMS. Cautiously, we assigned weights to these services based on their expected influence and agricultural demand for AMS. This effort greatly avoids the deviation from auto-correlation and gap with reality in the absence of other important services⁶⁸. Finally, but perhaps most importantly, this study only involves crop rotations without consideration of the intercropping between CCs and perennial crops such as fruit trees. Although this approach targets sustainable agriculture, it neglects the probable returns of CC intercropping in agroforestry systems by increasing N retention and mitigating N leaching globally⁶⁹. In this framework, crop-specific responses are also not included. Future research should critically address these responses to better quantify the applicability of CC practices across diverse regions, particularly within the context of genotype × environment × management interactions⁷.

In conclusion, our comprehensive analyses underline the significant potential of optimizing CC practices for improving agricultural sustainability worldwide, particularly in a harmonious balance between food security and environmental protection. Given their notable ameliorative characteristics and sustainable benefits (Fig. 1b), CC practices are emerging as a nature-based solution poised to advance the SDGs. In light of these insights, it is imperative for future research to explore more management combinations to unlock the untapped potential of CC practices. Furthermore, we strongly advocate for the establishment of incentive policies and international collaboration to encourage the widespread adoption of these optimal practices. Achieving this vision will necessitate collaborative endeavors across both global and local sectors.

Methods

Data compilation

Working procedure of this study aims at evaluating CC benefits for global agroecosystems (Supplementary Fig. 25). We conducted a comprehensive search of all relevant peer-reviewed publications on the Web of Science before August 2022 to quantify the effects of CCs on multiple agroecosystem services. For agroecosystem services, we mainly focus on food supply, C storage, climate mitigation, and soil erosion control, which represent provisioning, regulating, and supporting roles. Thus, yield, SOC stock, N₂O, CH₄, and MWD were identified as target variables. We searched for titles and topics using the formula: (“cover crop” or “catch crop” or “green manure”) and (“yield” or “SOC” or “N₂O” or “CH₄” or “soil aggregate”) and (“cropland” or “farmland” or “agriculture”) while screening out meta-analyses, reviews, incubation, and pot experiments. Studies included into our dataset must conform to several criteria: (1) they must be field studies reporting mean values and replications of at least one target variable for the control and treatment (CC) groups; (2) both two groups share the same climatic and edaphic conditions before the experiment; (3)

geographical coordinates or location are described; (4) both the control and CC treatment are under the same management practices, including fertilization, tillage, and irrigation; (5) detailed management information is stated, even CC and crop calendars; (6) only the CC rotation systems are considered rather than CC intercropping with other perennial crops; (7) inclusion of the same data from other publications is not permitted. Finally, 218 studies from 241 publications were included. These screening procedures follow the PRISMA methodology (Supplementary Fig. 26).

For each study, we extracted the mean values and replications (n) of target variables, and the standard deviation (SD) as much as possible from the tables or figures using GetData software v. 2.25. If the study reported the standard error (SE), we transformed it using the formula: $SD = SE \times \sqrt{n}$; other unreported SDs were approximated by multiplying the mean values by the average coefficient of variation within each group. SOC data provided in concentration units were converted into stocks ($Mg\ ha^{-1}$) by soil bulk density and sample depth. Data on environmental conditions (climate, soil, and microbial properties) and management practices (N fertilizer rate, organic fertilizer application, tillage, and irrigation) were also extracted from the corresponding studies, and the missing values were filled by high-resolution global maps (Supplementary Table 3). These maps generally have a good capability to impute missing values, but for some soil variables at different depths, the uncertainties they introduce should be treated with caution (Supplementary Fig. 27). In addition, available information about CC practice characteristics (type, diversity, termination, residue management, and duration) was also recorded. Given the importance of CC termination in rotation systems, we noted the CC growth days and termination time (i.e., the time interval between CCs ending and the next cash crop planting). Based on the above steps, we eventually compiled a big dataset of 2302 field observations for meta-analysis and scaling up (Supplementary Data 1). Overall, our dataset covers five continents and 25 major agricultural countries with broad discrepancies in environment and management, so it can be ideally used to explore the global CC effects and their main drivers. Details are shown in Supplementary Table 4.

Meta-analysis

The natural log response ratio ($\ln RR$) was calculated to quantify the effect sizes of CCs on agroecosystem services: $\ln RR = \ln(\bar{X}_t/\bar{X}_c)$, where \bar{X}_t and \bar{X}_c are the mean values of CC treatment and control groups, respectively. On the basis of mean value, replication and SD, we calculated the effect size of each pair data and its variance by the *escalc* function in the R package *metafor*⁷⁰. Then we used the mixed-effects models from the *rma.mv* function to calculate the overall CC effects and the 95% bootstrapped confidence intervals (CI) for five target variables. These mixed-effects models were weighted by the inverse of variance, and included “study” (independent study sites) as a random effect. Moreover, we examined the presence or absence of publication bias using the funnel plots combined with Egger’s regressions (Supplementary Fig. 28). Desirably, no publication bias was found in all target variables, which supports the robustness of subsequent conclusions. The percentage change $((RR - 1) \times 100)$ was adopted to denote the weighted effect sizes. If the 95% CI did not overlap with 0, it indicated a substantial positive (> 0) or negative (< 0) effect of CCs on the agroecosystem service.

To investigate the potential controls of CC effects by environmental and management factors, we divided them into various categories. Cropland types were categorized into upland and paddy. Climate zones were classified into four groups: tropical, arid, temperate, and cold, according to the Köppen-Geiger climate classification⁷¹. Soil texture was also grouped into four types that were simplified based on the USDA classification, including clay, clay loam, loam, and sandy. According to the uniform distribution of initial SOC concentration in our dataset, soil fertility was categorized into low

($< 9.3\ g\ kg^{-1}$), moderate ($9.3\text{--}17.4\ g\ kg^{-1}$), and high levels of SOC concentration ($> 17.4\ g\ kg^{-1}$), which was attained by the R package *funModeling*⁷². Soil pH was classified into acid (< 6.5), neutral ($6.5\text{--}7.5$), and alkaline (> 7.5). To further investigate CC effects on belowground services, we used mixed-effects models to examine the responses of SOC stock at five depths (0–10 cm, 10–30 cm, 30–60 cm, 60–100 cm, and > 100 cm) and root biomass ($n = 152$, a subset of 11 studies; Supplementary Data 2) to different types of CCs. The CC types were categorized into three groups: legume, non-legume, and mixture. Residue management included CC residue incorporation into soil (incorporated), residue mulching on soil surface (surface), and residue removal (removed). Implementation duration was divided into short-term (< 5 years) and long-term (≥ 5 years). Besides CC practice characteristics, most studies also involved other agricultural management practices. Within these practices, we classified organic fertilizer application into yes and no, tillage into conservation and conventional tillage, irrigation in upland into rainfed and irrigated, and irrigation in paddy into rainfed, flooding, and intermittent irrigation.

Furthermore, we tested the interaction between CCs and agricultural management using 37 two-factor experiments in our dataset, including CC \times organic fertilizer, CC \times conservation tillage, and CC \times intermittent irrigation. For example, the interactions between CCs and organic fertilizer were calculated as: $\ln RR = \ln(\bar{X}_{AB}/\bar{X}_B) - \ln(\bar{X}_A/\bar{X}_C)$, where \bar{X}_{AB} , \bar{X}_B , \bar{X}_A , and \bar{X}_C are the mean values of treatment A plus B (CCs plus organic fertilizer), treatment B (only organic fertilizer), treatment A (only CCs), and control (no CCs and organic fertilizer), respectively. Similarly, if the 95% CI did not overlap with 0, the interaction was considered as a positive (> 0) or negative (< 0) interaction; otherwise, there was only an additive effect. Meta-regressions were employed to test the dependence of CC effects on continuously predictive variables, including CC diversity, N fertilizer rate, duration, and initial clay and SOC concentrations. Independent associations of CC effects with climate, soil, and microbial properties were validated using partial correlation analyses.

Long-term field data and APSIM model

To complement additional support for the positive effects of CC practices on soil health, we retrieved data on SOC fractions (mineral-associated organic C and particulate organic C; $n = 82$, 18 studies; Supplementary Data 3) and cellulase activity ($n = 305$, 13 studies; Supplementary Data 4) from long-term CC experiments, similarly following the PRISMA procedure. We examined CC effects on two SOC fractions and their proportion among various CC types, climate zones, and soil types. For cellulase activity, its responses to long-term CC practices along soil profiles, as well as in combination with tillage and N fertilizer management, were examined. There was also no publication bias found (Supplementary Fig. 29).

We used APSIM v. 7.10-r4218, a flexible crop model that can effectively simulate agricultural systems under a diverse range of complex crop, environmental, and management interactions^{16,17}, to further provide evidence for the long-term CC benefits to global main crop yields and SOC stocks. Specifically, we selected wheat (Wedgetail) as the modelled cash crop and simulated its production in four scenarios: no CCs, legume CCs (field pea), non-legume CCs (oats), and CC mixtures (field pea and oats). Regarding CC mixtures, field pea and oats were treated as intercrops and linked up with the APSIM-canopy module⁷³. All crops in the sequences were sown at $150\ plants\ m^{-2}$, with a row spacing of $300\ mm$ ⁷⁴. We collected a suite of observations from sites with a long history of CC practices to optimize the relevant parameters within crop and soil modules, and calibrate the model (Supplementary Data 5). The calibrated model has a relatively good capability to simulate wheat yields and SOC stocks for all scenarios ($R^2 > 0.60$), with relative root mean square errors of 0.35 and 0.31, respectively (Supplementary Fig. 30). Details of the cultivar and soil parameters can be found in Supplementary Table 5. Combined with

meteorological, soil, and management data, we finally obtained the outputs of wheat yields and SOC stocks from 1981 to 2020. The model results are shown as the 40-year average CC effects.

Meta-forest analysis

We performed MF analyses using the R package *metaforest*⁷⁵ to quantify the relative importance of environmental and management factors for CC effects on five agroecosystem services (ln RRs). MF analysis is a machine-learning method that integrates meta-analysis (the variance and weight of each study) and random forest algorithm, while considering the potential nonlinear relationships and interactions between predictors^{65,75}. Specifically, we first checked the convergence of our original models including all predictors, and then optimized the tuning parameters using the *train* function in R package *caret*⁷⁶ without the predictors of negative importance. In the original models, CC growth days and termination time were included because they jointly determine the input and nutrient release of CC residues and the subsequent benefits to agroecosystem services⁷. Given the distinct mechanisms of upland and paddy in many processes, we also incorporated cropland type into the models as a predictor. Each final model was obtained based on 10-fold cross-validation with 75% of the dataset used for model fitting and 25% for validation, which had the minimum root mean square error. Moreover, the mean absolute error, out-of-bag R^2 , and R^2 between the predicted and observed values were used to assess the predictive performance of five MF models (Supplementary Table 6 and Supplementary Fig. 31).

Network analysis and SEM

Based on MF predictions, network analysis was conducted to evaluate the associations among five services under CC practices and their relative roles for AMS. First, partial correlation networks were estimated by pairwise Markov random field using the R package *bootnet*, based on the extended Bayesian information criterion⁷⁷. Second, the correlation stability of networks was bootstrapped by 1000 iterations, after which the robust centrality metrics (strength) were calculated. Third, each lnRR was weighted by its strength to quantify AMS. It is notable that we adopted the framework proposed by Manning, et al.⁶⁸ to assign weights to different agroecosystem services based on their relative importance for agricultural demand (supply-benefit relationship). Specifically, a weight of 0.9 was assigned to crop yield due to its priority in intensive agriculture, while a weight of 0.6 was assigned to soil carbon storage, climate mitigation, and soil stabilization, given their secondary yet critical roles in agricultural sustainability⁶⁸. Last, we calculated the percentage changes of AMS in both upland and paddy fields, as well as their 95% bootstrapped CIs.

Piecewise SEM was performed using the R package *piecewiseSEM*⁷⁸ to ascertain the direct and indirect effects of environmental and management factors on AMS. All the predictors were divided into five composite factors (climate, soil, microbe, agricultural management, and CC practice characteristics) based on their standardized coefficients with AMS. Then the piecewise SEM was estimated by computing these composite factors in mixed-effects models from the R package *lme4*⁷⁹. Marginal and conditional R^2 were used to jointly evaluate the interpretability of AMS, with smaller Fisher's C ($P > 0.05$) and Akaike information criterion for selecting models with higher goodness. Standardized total effects from SEM referred to various contributions of composite factors to AMS. Two additional multivariate mixed-effects models were used to complementally quantify the individual effects of all predictors on AMS in upland and paddy fields.

Scaling up and future projection

Well-trained MF models were applied to scale up CC effects on five agroecosystem services (%) with a batch of global gridded datasets (Supplementary Table 3). For CC practice characteristics, we selected their optimal portfolio according to our meta-analyses to evaluate

the global applicability of optimizing CC practices and its potential benefits. Optimal CC termination time was estimated by moving window analysis, with a window size of 30 consecutive observations sorted by termination time. Briefly, we performed a mixed-effects model to explore how much termination time would exert the maximum positive effect on AMS. The model included CC termination time, climate, soil, microbe, and their multi-order interactions as fixed effects, with a random effect of “study”. Bootstrapped standardized effects fitted nonlinearly with CC termination time and displayed a bimodal pattern, so the optimal CC termination time was determined as the threshold at concave peak. Then, the gridded dataset of CC growth days was accordingly predicted by optimal CC termination time and growth days of main crops from GGCMI Phase 3⁸⁰ (Supplementary Fig. 32). Separating upland from paddy, we generated several global maps of five services and AMS at a resolution of $0.1^\circ \times 0.1^\circ$ for the current period (2020). The associated SD maps were used for evaluating the uncertainties of scaled-up CC effects. Furthermore, we meticulously calculated the actual benefits of CC practices on crop production, net GHG budget (NGHGB), and soil erosion control by multiplying our scaled-up CC effects with a series of baseline datasets, including cropland area, crop yields, SOC stocks (0–30 cm), GHG emissions, and soil erosion (see more details in Supplementary Table 7). Based on the 100-year global warming potential (GWP) values from the Sixth Assessment Report of the IPCC, the conversion factors ($\text{CO}_2\text{-eq.}$) for N_2O and CH_4 to calculate NGHGB were 273 and 27²⁰. The NGHGB estimates the capacity for CO_2 sequestration of various agroecosystems under CC practices. It was calculated as the difference between the decrease in GWP due to larger SOC stocks and the increase in GWP derived from direct N_2O and CH_4 emissions¹⁰: $\text{NGHGB} (\text{Pg CO}_2 \text{ yr}^{-1}) = 44/12 \times \text{SOC}_{\text{stock}} - 273 \times \text{N}_2\text{O} - 27 \times \text{CH}_4$.

To explore whether optimizing CC practices can sustain benefits to global agroecosystems under future changing climate conditions, we projected CC effects in two scenarios of Shared Socioeconomic Pathway (SSP) using five bias-corrected climate model outputs provided by the ISIMIP3b simulation (GFDL-ESM-4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL)⁸¹. These daily model outputs are complementary in terms of model structure and climate sensitivity, derived from CMIP6 (Supplementary Table 8). The two scenarios representing low (SSP126) and mid-high (SSP370) emission scenarios were used to simulate the future changes of CC benefits. In our future projections, we did not consider the adaptability of environment and management caused by climate change, but only its own changes, including temperature, precipitation, and aridity. The future aridity index was calculated by combining temperature and precipitation data from CMIP6 using the R package *SPEI*⁸². Specifically, daily mean temperature data were aggregated to a monthly scale for each decade (e.g., 2021–2030). The aggregated monthly temperature was converted into annual potential evapotranspiration using the Thornthwaite function, which was then combined with annual precipitation data to obtain the 10-year average aridity index. The projected changes in future climate variables and CC benefits were calculated as the difference between 2091–2100 and current period (2020), and we examined the relationships among these changes in two scenarios to determine the impact of climate change. Climatic resistance of yield change was calculated as the ratio of current yield increase to its reduction caused by climate change: $R = Y_{\text{current}} / (Y_{\text{current}} - Y_{\text{future}})$, where R represents the climatic resistance, Y_{current} and Y_{future} are current and future CC-based yield changes, respectively. We also extracted soil micronutrient concentrations from 1,306 sites worldwide (ref. 58) and national SDG data in 2020 (ref. 60) to check their associations with the corresponding values of AMS. All analyses were performed using R statistical software version 4.1.2⁸³. The data and code used in this study are publicly available in Zenodo (<https://doi.org/10.5281/zenodo.14025624>) (ref. 84).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data used in this study has been deposited in GitHub (<https://github.com/TianyiQiu13/Cover-crop-multiservices>). Climate model outputs from ISIMIP3b are available at <https://data.isimip.org>. The global soil micronutrient concentration and national SDG index data were obtained from a public dataset (<https://figshare.com/s/8ff4083eb0ddb84ba056>) and SDG transformation center (<https://sdgtransformationcenter.org>), respectively. Other baseline data can be found in Supplementary Information. Source data are provided as a Source Data file. Source data are provided with this paper.

Code availability

The code that supports the findings of this study has been deposited in Zenodo (<https://doi.org/10.5281/zenodo.14025624>) (ref. 84).

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Acknowledgements

This study was financially supported by the National Key Research and Development Program of China (2021YFD1901205), the Strategic Priority Research Program of Chinese Academy of Sciences (XDB40020202), and the National Science & Technology Fundamental Resources Investigation Project of China (2021FY100500). J.P. and J.S. were supported by the Spanish Government grants TED2021-132627B-I00 and PID2022-140808NB-I00 funded by MCIN, AEI/10.13039/501100011033 and the European Union NextGenerationEU/PRTR, and the Catalan Government grant SGR2021-1333.

Author contributions

L.F. and T.Q. conceived the study. T.Q. collected and analyzed the data, and wrote the first draft of the paper. Y.S., J.P., J.S., F.Z., and S.P. discussed the design and analyses of this study, with conceptual inputs to improve the manuscript. T.Q., Y.S., and Q.H. configured and ran the APSIM model. J.L., Q.C., L.X., W.Y., S.Z., J.J., W.Z., M.H., and W.T. advised on the interpretation of the results and revised the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41467-024-54536-z>.

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Peer review information *Nature Communications* thanks the anonymous reviewers for their contribution to the peer review of this work. A peer review file is available.

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