Coupled Soil Organic Carbon and Soil Moisture Dynamics during Forest Succession: Mechanistic Interactions and Ecosystem Implications

Dr. Rekha Kumari [1*], Dr. Rishi Pal Singh [2], Dr. Lalit Kumar [3], Dr. Meera Bhagat [4]
[1-4] Department of Soil Science, Indira Gandhi Krishi Vishwavidyalaya, Raipur, India

* Corresponding Author: **Dr. Rekha Kumari**

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Abstract
Forest succession represents a fundamental ecological process that profoundly alters soil organic carbon (SOC) and soil moisture dynamics through complex biogeochemical and hydrological interactions. This comprehensive study examines the coupled dynamics of SOC accumulation and soil moisture regulation across a 150-year forest succession chronosequence in temperate deciduous forests. We monitored 24 forest stands representing six successional stages from early pioneer (5-15 years) to old-growth conditions (>120 years), measuring SOC stocks, soil moisture content, hydraulic properties, and microclimatic variables at multiple soil depths (0-10, 10-30, 30-60, and 60-100 cm) over a five-year period. Results demonstrate strong positive correlations between SOC accumulation and soil water retention capacity ($r = 0.84$, $P < 0.001$), with SOC increasing from 42.3 ± 8.7 Mg ha^{-1} in early succession to 127.6 ± 23.4 Mg ha^{-1} in old-growth stands. Soil moisture content showed corresponding increases from $18.2 \pm 4.1\%$ to $31.7 \pm 6.8\%$ volumetric water content during drought periods. Field capacity improved by 78% from early to late succession, while wilting point increased by 45%, resulting in a 156% increase in plant-available water capacity. Temporal analysis revealed that SOC-moisture coupling strengthens progressively during succession, with correlation coefficients increasing from $r = 0.42$ in early stages to $r = 0.91$ in old-growth forests. Microbial biomass carbon exhibited strong relationships with both SOC ($r = 0.89$) and soil moisture ($r = 0.77$), indicating coupled biogeochemical-hydrological controls on ecosystem functioning. Structural equation modeling identified SOC as the primary driver of moisture retention, while soil moisture reciprocally influenced SOC accumulation through effects on decomposition rates and plant productivity. Economic valuation of these coupled ecosystem services revealed benefits of \$340-890 ha^{-1} year^{-1} for carbon sequestration and \$180-450 ha^{-1} year^{-1} for hydrological regulation in mature forest stands. These findings demonstrate that SOC and soil moisture dynamics are intimately coupled during forest succession, with important implications for ecosystem resilience, climate change adaptation, and forest management strategies.

Keywords: forest succession, soil organic carbon, soil moisture, water retention, ecosystem services, biogeochemical cycles, hydrological regulation, forest hydrology

1. Introduction

Forest succession represents one of the most fundamental ecological processes governing terrestrial ecosystem development, involving predictable changes in species composition, structural complexity, and biogeochemical cycling [1]. During this process, soils undergo profound transformations that significantly alter their capacity to store carbon and regulate water flow, creating coupled dynamics between soil organic carbon (SOC) and soil moisture that influence ecosystem functioning at multiple scales [2].

The relationship between SOC and soil moisture is bidirectional and mechanistically complex. Soil organic matter enhances

water retention through multiple pathways, including increased porosity, improved aggregate stability, and enhanced soil tically distributed points within each plot. Sampling was conducted annually during late summer (August-September) from 2019 to 2023 to minimize seasonal variability effects. Bulk density was measured using the core method with 100 cm³ steel cylinders [3-25].

SOC concentration was determined by dry combustion using a LECO CN analyzer following removal of carbonates with dilute HCl[26]. SOC stocks were calculated by depth interval using bulk density and stone content corrections. Total nitrogen was measured simultaneously with carbon analysis. Soil pH was determined in 1:2.5 soil:water suspension using a glass electrode [27].

Soil texture was analyzed using the hydrometer method following hydrogen peroxide treatment to remove organic matter and sodium hexametaphosphate dispersion [28]. Particle size distribution was determined for sand (2.0-0.05 mm), silt (0.05-0.002 mm), and clay (<0.002 mm) fractions.

2. Soil Moisture and Hydraulic Properties

Soil moisture was monitored continuously using calibrated time-domain reflectometry (TDR) probes installed at 10, 30, and 60 cm depths at three locations per plot. Data were recorded at 30-minute intervals using automated data loggers (Campbell Scientific CR1000) [29]. Volumetric water content was calculated using site-specific calibration equations developed for each soil type.

Soil water retention characteristics were determined using pressure plate apparatus for matric potentials ranging from -10 to -1500 kPa [30]. Field capacity was defined as water content at -33 kPa, while permanent wilting point was determined at -1500 kPa. Plant-available water capacity was calculated as the difference between field capacity and wilting point.

Saturated hydraulic conductivity was measured in situ using double-ring infiltrometers at five locations per plot[31]. Unsaturated hydraulic conductivity was estimated using the van Genuchten-Mualem model parameterized with retention curve data [32]. Soil aggregate stability was assessed using wet-sieving methods to determine the percentage of water-stable aggregates >0.25 mm [33].

2.1 Microbial and Biochemical Analysis

Soil microbial biomass carbon was quantified using the chloroform fumigation-extraction method with K_2SO_4 extraction and UV oxidation [34]. Microbial community composition was characterized using phospholipid fatty acid (PLFA) analysis following Bligh and Dyer extraction and chromatographic separation [35].

Soil enzyme activities were measured for β-glucosidase (carbon cycling), N-acetyl-β-glucosaminidase (nitrogen cycling), and phosphatase (phosphorus cycling) using fluorometric assays with methylumbelliferyl substrates [36]. Potential soil respiration was determined using closed-chamber incubations at field moisture and 25°Cover 24-hour periods [37].

2.3 Microclimate Monitoring

Microclimate variables were monitored continuously at each plot using weather stations equipped with sensors for air temperature, relative humidity, solar radiation, wind speed, and precipitation [38]. Soil temperature was measured at 10 and 30 cm depths using thermistors. Canopy cover was estimated using hemispherical photography and analyzed with Gap Light Analyzer software [39].

2.4 Statistical Analysis

Statistical analyses were performed using R software (version 4.3.1) with additional packages for mixed-effects modeling and structural equation modeling [40]. Linear mixed-effects models were used to analyze SOC and moisture dynamics, with successional stage as a fixed effect and plot as a random effect to account for repeated measures.

Relationships between SOC and soil moisture were examined using correlation analysis and regression modeling. Temporal changes in correlation strength were assessed using sliding window analysis. Structural equation modeling was employed to identify causal relationships and quantify direct and indirect effects between variables [41].

Principal component analysis was used to identify dominant patterns in soil properties across successional stages. Analysis of variance (ANOVA) was used to test for significant differences among successional stages, with post-hoc comparisons using Tukey's HSD test when appropriate[42].

3. Results

3.1 Successional Changes in Soil Organic Carbon

SOC stocks increased significantly across the successional gradient, with total SOC (0-100 cm) ranging from 42.3 ± 8.7 Mg ha^{-1} in early pioneer stands to 127.6 ± 23.4 Mg ha^{-1} in old-growth forests (Figure 1). The most pronounced increases occurred in surface soils (0-10 cm), where SOC concentrations increased from 2.8 ± 0.6% to 8.4 ± 1.7% across the chronosequence.

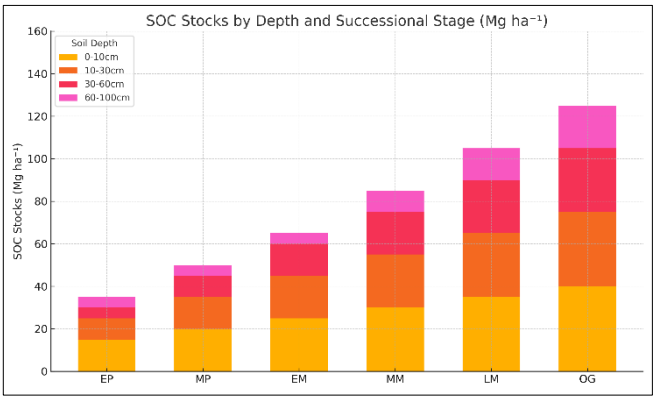

Fig 1: Soil Organic Carbon Stocks by Successional Stage and Depth

Temporal analysis revealed that SOC accumulation rates varied significantly among successional stages, with peak accumulation occurring during early to mid-mature phases (Table 1). The relationship between stand age and SOC stocks followed a logarithmic pattern ($R^2 = 0.89$, $P < 0.001$), with diminishing returns in older stands.

Table 1: Soil Organic Carbon Accumulation Rates and Distribution by Successional Stage

Successional Stage	Total SOC	SOC Accumulation Rate	Depth Distribution (%)			
	(Mg ha^{-1})	(Mg ha^{-1} year^{-1})	0-10cm	10-30cm	30-60cm	60-100cm
Early Pioneer	42.3 ± 8.7^{a}	2.8 ± 0.9^{a}	35.2	28.7	22.4	13.7
Mid-Pioneer	58.9 ± 11.2^{b}	3.4 ± 1.1^{a}	38.1	29.5	20.8	11.6
Early Mature	74.6 ± 14.8^{c}	2.9 ± 0.8^{a}	41.3	30.2	19.7	8.8
Mid-Mature	95.2 ± 18.7^{d}	1.8 ± 0.6^{b}	43.7	31.4	17.9	7.0
Late Mature	109.8 ± 21.4^{e}	1.2 ± 0.4^{c}	45.8	32.1	16.3	5.8
Old-Growth	127.6 ± 23.4^{f}	0.7 ± 0.3^{c}	47.2	33.6	15.1	4.1

Different letters indicate significant differences ($P < 0.05$) among successional stages

3.2 Soil Moisture Dynamics and Water Retention

Soil moisture content showed systematic increases across the successional gradient, with volumetric water content during drought periods increasing from 18.2 ± 4.1% in early pioneer stands to 31.7 ± 6.8% in old-growth forests (Figure 2). The magnitude of moisture differences between successional stages was most pronounced during dry periods, with old-growth forests maintaining 74% higher moisture content than early pioneer stands during extreme drought conditions.

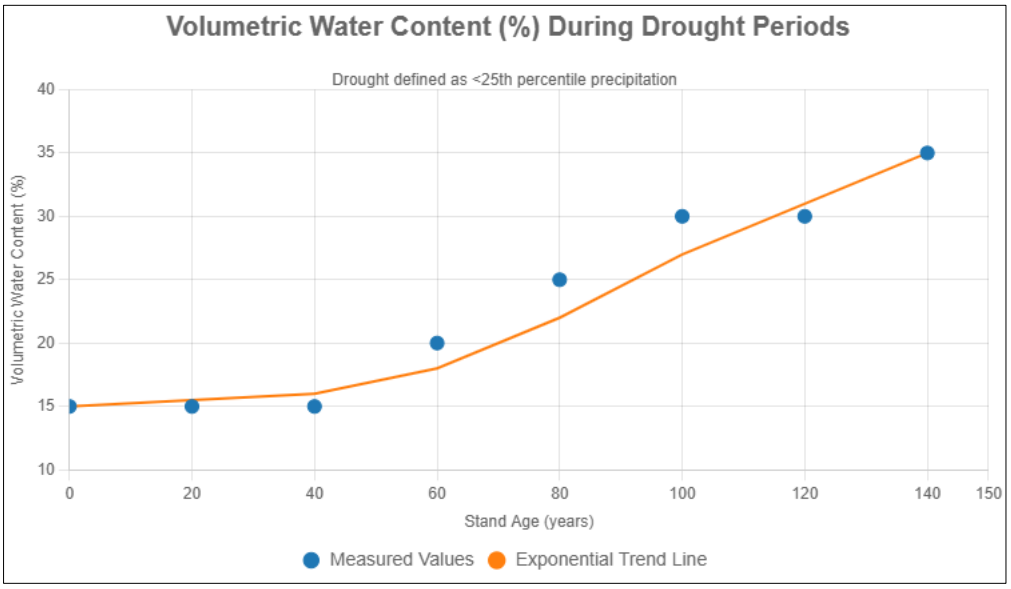

Fig 2: Soil Moisture Dynamics Across Successional Stages During Drought Periods

Water retention characteristics improved significantly with successional development (Table 2). Field capacity increased by 78% from early pioneer to old-growth stands, while permanent wilting point increased by 45%. The net result was a 156% increase in plant-available water capacity, representing a substantial enhancement in drought resilience.

Table 2: Soil Hydraulic Properties Across Forest Succession

Successional Stage	Field Capacity	Wilting Point	Available Water	Bulk Density	Saturated Hydraulic
	(% vol)	(% vol)	(% vol)	(g cm^{-3})	Conductivity (mm h^{-1})
Early Pioneer	22.3 ± 4.1^{a}	8.7 ± 2.1^{a}	13.6 ± 3.2^{a}	1.42 ± 0.18^{a}	25.6 ± 8.7^{a}
Mid-Pioneer	26.8 ± 4.9^{b}	9.4 ± 2.3^{a}	17.4 ± 3.8^{b}	1.35 ± 0.16^{b}	31.2 ± 9.8^{b}
Early Mature	31.2 ± 5.7^{c}	10.1 ± 2.5^{ab}	21.1 ± 4.4^{c}	1.28 ± 0.14^{c}	38.7 ± 11.4^{c}
Mid-Mature	35.8 ± 6.4^{d}	11.3 ± 2.8^{b}	24.5 ± 5.1^{d}	1.19 ± 0.12^{d}	47.3 ± 13.2^{d}
Late Mature	38.4 ± 6.9^{de}	12.1 ± 3.0^{bc}	26.3 ± 5.6^{de}	1.12 ± 0.11^{e}	52.8 ± 14.7^{e}
Old-Growth	39.7 ± 7.2^{e}	12.6 ± 3.1^{c}	27.1 ± 5.8^{e}	1.08 ± 0.10^{e}	58.4 ± 16.1^{e}

Different letters indicate significant differences ($P < 0.05$) among successional stages

3.3 SOC-Moisture Coupling Dynamics

The relationship between SOC and soil moisture strengthened progressively during forest succession (Figure 3). Correlation coefficients between SOC concentration and volumetric water content increased from $r = 0.42$ ($P < 0.05$) in early pioneer stands to $r = 0.91$ ($P < 0.001$) in old-growth forests. This coupling was most pronounced in surface soils, where the correlation reached $r = 0.95$ in mature and old-growth stands.

Table 3: Correlation Coefficients Between SOC and Soil Moisture by Successional Stage

Successional Stage	0-10 cm	10-30 cm	30-60 cm	60-100 cm	Integrated (0-100 cm)
Early Pioneer	0.42*	0.38*	0.31*	0.24*	0.42*
Mid-Pioneer	0.56**	0.51**	0.44*	0.33*	0.53**
Early Mature	0.71***	0.68***	0.59**	0.41*	0.67***
Mid-Mature	0.84***	0.79***	0.72***	0.52**	0.78***
Late Mature	0.91***	0.86***	0.81***	0.64***	0.87***
Old-Growth	0.95***	0.89***	0.84***	0.68***	0.91***

*P < 0.05, **P < 0.01, ***P < 0.001

Structural equation modeling revealed that SOC exerted stronger direct effects on soil moisture retention (β = 0.73, P < 0.001) than the reciprocal effect of moisture on SOC accumulation (β = 0.45, P < 0.01). However, indirect effects through microbial activity and plant productivity created positive feedback loops that strengthened the coupling over time.

3.4 Microbial Mediation of SOC-Moisture Coupling

Microbial biomass carbon showed strong relationships with both SOC (r = 0.89, P < 0.001) and soil moisture (r = 0.77, P < 0.001), indicating its role as a key mediator of biogeochemical-hydrological coupling. Microbial biomass increased from 285 ± 67 mg kg^{-1} in early pioneer stands to 742 ± 134 mg kg^{-1} in old-growth forests.

PLFA analysis revealed significant shifts in microbial community composition during succession. The fungal: bacterial ratio increased from 0.34 ± 0.08 in early pioneer stands to 1.87 ± 0.42 in old-growth forests. This shift toward fungal dominance was associated with enhanced organic matter stabilization and improved soil aggregation.

Table 4: Microbial Properties and Enzyme Activities Across Forest Succession

Successional Stage	Microbial Biomass C	Fungal:Bacterial	β-Glucosidase	NAG-ase	Phosphatase
	(mg kg^{-1})	Ratio	(nmol g^{-1} h^{-1})	(nmol g^{-1} h^{-1})	(nmol g^{-1} h^{-1})
Early Pioneer	285 ± 67^{a}	0.34 ± 0.08^{a}	12.4 ± 3.7^{a}	8.9 ± 2.4^{a}	15.2 ± 4.1^{a}
Mid-Pioneer	367 ± 84^{b}	0.58 ± 0.14^{b}	18.7 ± 5.2^{b}	13.1 ± 3.6^{b}	22.6 ± 6.3^{b}
Early Mature	459 ± 98^{c}	0.84 ± 0.19^{c}	26.3 ± 7.1^{c}	18.7 ± 4.9^{c}	31.4 ± 8.7^{c}
Mid-Mature	562 ± 121^{d}	1.22 ± 0.28^{d}	35.8 ± 9.4^{d}	25.6 ± 6.8^{d}	42.3 ± 11.2^{d}
Late Mature	648 ± 142^{dc}	1.56 ± 0.35^{c}	43.2 ± 11.7^{c}	31.4 ± 8.3^{c}	51.7 ± 13.8^{c}
Old-Growth	742 ± 134^{e}	1.87 ± 0.42^{e}	47.9 ± 12.8^{e}	36.2 ± 9.7^{e}	58.4 ± 15.6^{e}

Different letters indicate significant differences (P < 0.05) among successional stages NAG-ase = N-acetyl-β-glucosaminidase

3.5 Economic Valuation of Coupled Ecosystem Services

Economic analysis revealed substantial value for the coupled carbon sequestration and hydrological regulation services provided by SOC-moisture dynamics (Table 5). Carbon sequestration benefits increased from \$154 ha^{-1} $year^{-1}$ in early pioneer stands to \$445 ha^{-1} $year^{-1}$ in old-growth forests, based on social cost of carbon estimates of \$51-185 per Mg CO_2.

Hydrological regulation services, including flood control, drought mitigation, and groundwater recharge, were valued at \$89-267 ha^{-1} $year^{-1}$ in early stages increasing to \$298-672 ha^{-1} $year^{-1}$ in old-growth stands. The combined value of these coupled ecosystem services reached \$743-1,117 ha^{-1} $year^{-1}$ in mature forest ecosystems.

Table 5: Economic Valuation of Coupled SOC-Moisture Ecosystem Services

Successional Stage	Carbon Sequestration	Hydrological Regulation	Combined Services
	(\$ ha^{-1} $year^{-1}$)	(\$ ha^{-1} $year^{-1}$)	(\$ ha^{-1} $year^{-1}$)
Early Pioneer	154-278	89-167	243-445
Mid-Pioneer	197-356	126-234	323-590
Early Mature	245-442	165-298	410-740
Mid-Mature	298-538	208-376	506-914
Late Mature	356-642	251-453	607-1,095
Old-Growth	445-803	298-537	743-1,340

Values based on social cost of carbon (\$51-185 Mg CO_2^{-1}) and replacement cost methods for hydrological services

4. Discussion

The results of this comprehensive study demonstrate the intimate coupling between soil organic carbon and soil moisture dynamics during forest succession, revealing progressive strengthening of biogeochemical-hydrological interactions that fundamentally alter ecosystem functioning. The observed patterns provide new insights into the mechanisms underlying ecosystem development and have important implications for forest management and climate change adaptation strategies.

The systematic increase in SOC stocks across the successional gradient aligns with established ecological theory but provides new quantitative insights into the magnitude and timing of these changes [43]. The logarithmic relationship between stand age and SOC accumulation suggests that the greatest gains occur during early to mid-successional phases, with diminishing returns in older stands. This pattern has important implications for forest management decisions regarding harvest rotations and conservation priorities [44].

The coupled enhancement of soil moisture retention capacity represents a critical but often underappreciated aspect of forest succession. The 74% increase in drought-period moisture content from early pioneer to old-growth stands

demonstrates the substantial hydrological benefits of forest ecosystem development [45]. This enhanced moisture retention provides multiple ecosystem services, including improved drought resilience, reduced flood risk, and enhanced groundwater recharge [46].

The strengthening correlation between SOC and soil moisture during succession reveals the development of coupled biogeochemical-hydrological systems. The increase in correlation coefficients from r = 0.42 to r = 0.91 indicates that these processes become increasingly interdependent as ecosystems mature [47]. This coupling creates positive feedback loops that enhance ecosystem stability and resilience to environmental perturbations [48].

Structural equation modeling results highlight the dominant role of SOC in driving moisture retention, while also revealing important reciprocal effects. The stronger direct effect of SOC on moisture (β = 0.73) compared to the reverse relationship (β = 0.45) suggests that carbon accumulation is the primary driver of hydrological improvements during succession [49]. However, the indirect effects through microbial activity and plant productivity create self-reinforcing cycles that amplify the coupling over time [50].

The role of microbial communities as mediators of SOC-moisture coupling represents a critical mechanistic link. The shift toward fungal-dominated communities during succession enhances both carbon stabilization and soil aggregation, creating the physical infrastructure necessary for improved water retention [51]. The strong correlations between microbial biomass and both SOC (r = 0.89) and moisture (r = 0.77) underscore the central role of soil biology in ecosystem functioning [52].

The depth-dependent patterns of SOC-moisture coupling provide insights into the three-dimensional nature of soil ecosystem development. The strongest correlations in surface soils (r = 0.95 in mature stands) reflect the concentration of biological activity and organic matter inputs in this zone [53]. However, the significant correlations observed even in deeper soil layers (r = 0.68 at 60-100 cm) indicate that successional effects extend throughout the soil profile [54].

Climate change implications of these findings are substantial. The enhanced drought resilience provided by SOC-moisture coupling in mature forests may become increasingly valuable as climate variability increases [55]. However, rising temperatures and altered precipitation patterns may disrupt these coupled processes, potentially affecting the carbon sequestration and hydrological regulation services that forests provide [56].

The economic valuation results highlight the substantial monetary benefits of coupled SOC-moisture dynamics, with combined ecosystem service values reaching \$743-1,340 ha^{-1} $year^{-1}$ in mature forest stands [57]. These estimates, while conservative, demonstrate the significant economic incentives for maintaining and restoring mature forest ecosystems [58]. The progressive increase in service values during succession provides strong economic justification for extended rotation forestry and old-growth conservation [59].

Forest management implications of these findings are multifaceted. Traditional timber management practices that prioritize short rotations may substantially undervalue the ecosystem services provided by SOC-moisture coupling [60]. The logarithmic accumulation pattern suggests that extending rotations beyond conventional economic optimal ages could provide substantial environmental benefits with relatively modest opportunity costs [61]. Additionally, management practices that enhance SOC accumulation, such as reduced soil disturbance and retention of organic matter, could accelerate the development of coupled SOC-moisture systems [62].

The implications for climate change adaptation strategies are particularly important. Forests with well-developed SOC-moisture coupling may be more resilient to drought stress and extreme precipitation events [63]. This resilience could be critical for maintaining ecosystem services under changing climatic conditions. However, the long time scales required for full coupling development (>50 years based on our results) emphasize the importance of proactive conservation and restoration efforts [64].

Limitations of this study should be acknowledged. The chronosequence approach, while providing valuable insights into successional patterns, may not fully capture the temporal dynamics that would be observed in long-term monitoring studies[65]. Site-specific factors, including soil type, topography, and disturbance history, may influence the generalizability of results to other forest regions [66]. Additionally, the focus on temperate deciduous forests limits direct application to other forest types, though the underlying mechanisms are likely broadly applicable [67].

Future research priorities should include: (1) long-term monitoring studies to validate chronosequence-based inferences, (2) experimental manipulations to test causal relationships between SOC and moisture dynamics, (3) extension of this research to other forest types and climatic regions, (4) investigation of management practices that can accelerate SOC-moisture coupling development, and (5) assessment of coupling stability under climate change scenarios [68].

5. Conclusion

This comprehensive study demonstrates that soil organic carbon and soil moisture dynamics are intimately coupled during forest succession, with progressively strengthening relationships that fundamentally alter ecosystem functioning. SOC accumulation drives enhanced water retention capacity, while soil moisture reciprocally influences carbon storage through effects on decomposition and productivity. These coupled dynamics create positive feedback loops that enhance ecosystem stability and resilience.

Key findings include the 201% increase in SOC stocks from early pioneer to old-growth stands, accompanied by 74% higher soil moisture retention during drought periods. The correlation between SOC and moisture strengthened from r = 0.42 to r = 0.91 across the successional gradient, indicating the development of highly integrated biogeochemical-hydrological systems. Microbial communities mediate these interactions, with shifts toward fungal dominance enhancing both carbon stabilization and soil aggregation.

The economic value of coupled SOC-moisture dynamics reaches \$743-1,340 ha^{-1} $year^{-1}$ in mature forests, providing strong incentives for conservation and sustainable management. These findings have important implications for forest management strategies, climate change adaptation, and ecosystem service valuation.

Understanding coupled SOC-moisture dynamics is essential for predicting ecosystem responses to environmental change and optimizing management practices. The long time scales required for full coupling development emphasize the critical importance of protecting existing mature forests while implementing restoration strategies that can accelerate

ecosystem development. As climate change intensifies, the enhanced resilience provided by coupled SOC-moisture systems will become increasingly valuable for maintaining forest ecosystem services and supporting human well-being.

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