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Postprint: Long-Term Monitoring and Innovative Research Elucidating the Formation Processes and Mechanisms of Forest Ecosystem Functioning

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Abstract

Innovation serves as the wellspring of momentum for leading disciplinary development. With long-term support from the Chinese Academy of Sciences, the Ministry of Science and Technology, the National Natural Science Foundation of China, and Guangdong Province, the Dinghushan Forest Ecosystem Research Station of the South China Botanical Garden, Chinese Academy of Sciences (hereinafter referred to as “Dinghushan Station”), through long-term monitoring and innovative research, discovered the phenomenon of continuous organic carbon accumulation in mature forest soils. It elucidated the mechanisms and driving forces of forest soil organic carbon accumulation across different scales from macro to micro, led research on the response and adaptation patterns of forest ecosystem carbon-nitrogen-water cycling processes and their coupling to environmental changes, and promoted the establishment of ecosystem non-equilibrium theory. The station scientifically quantified the current status and potential of carbon sinks in national forest ecosystems, providing important scientific support for national environmental diplomacy. It proposed a global model of forest-water yield relationships and precisely determined the critical thresholds of climatic and watershed characteristic parameters controlling water yield, providing new interpretations for the debate on the relationship between forests and water yield. Additionally, it discovered that evergreen broadleaf forest communities have adapted to climate change by shifting toward shrubification over the past 30 years and elucidated the mechanisms by which they are influenced by major environmental factors. These research findings provide theoretical support for the scientific assessment of forest carbon sequestration and water resource effects, as well as for national needs in nature reserve and ecological environment construction. Dinghushan Station has become an irreplaceable field technology support platform both domestically and internation-

ally, a world-renowned scientific research base for forest ecosystem studies, and also a talent training base for ecology within the Chinese Academy of Sciences and the Guangdong region.

Full Text

Preamble

Innovation serves as the fundamental driving force for disciplinary development. With long-term support from the Chinese Academy of Sciences (CAS), the Ministry of Science and Technology of China, the National Natural Science Foundation of China, and Guangdong Province, the Dinghushan Forest Ecosystem Research Station of the South China Botanical Garden, CAS (hereinafter referred to as “Dinghushan Station”) employs long-term monitoring and innovative research to elucidate the processes and mechanisms underlying forest ecosystem function formation. The station discovered that mature forest soils can continuously accumulate organic carbon, clarified the mechanisms and driving forces of forest soil carbon accumulation across macro-to-micro scales, and pioneered research on carbon-nitrogen-water cycling processes and their coupling responses to environmental change and adaptation patterns, thereby promoting the establishment of ecosystem non-equilibrium theory. Dinghushan Station has scientifically quantified the current status and potential of carbon sequestration in China’ s forest ecosystems, providing crucial scientific support for national environmental diplomacy. The station proposed a global pattern of forest-water yield relationships and precisely identified critical threshold values for climate and watershed characteristic parameters controlling water yield, offering new interpretations for the long-standing debate on “forests and water yield.” Furthermore, the station revealed that evergreen broad-leaved forest communities have adapted to climate change over the past 30 years by shifting toward shrub-dominated structures and clarified the underlying mechanisms influenced by key environmental factors. These research achievements provide theoretical support for the scientific assessment of forest carbon sequestration and water resource effects, addressing national needs for nature reserve construction and ecological environmental protection. Dinghushan Station has become an irreplaceable field scientific support platform and internationally renowned research base for forest ecosystem science, as well as a talent cultivation hub for ecology in CAS and Guangdong Province.

Keywords: evergreen broad-leaved forest ecosystem, long-term monitoring and innovative research, carbon sequestration function, carbon-nitrogen-water coupling, forest and water yield

Located in the northeastern part of Zhaoqing City, Guangdong Province, Dinghushan lies near the Tropic of Cancer and hosts China’ s first nature reserve (established in 1956). As the only national nature reserve affiliated with CAS, it preserves intact zonal forests of the South Asian subtropical zone –specifically, South Asian subtropical monsoon evergreen broad-leaved forests

—along with rich transitional vegetation types. This provides an ideal natural research base for studying forest ecosystem succession processes and patterns, as well as for reference in degraded ecosystem restoration and reconstruction, earning its reputation as the undisputed “green pearl” on the Tropic of Cancer. During the 1960s–1970s, the International Biological Programme (IBP) organized by the International Council for Science (ICSU) and the Man and the Biosphere (MAB) Programme by UNESCO greatly advanced international ecological development. The 1978 National Science Conference ushered in a new era for Chinese science. Against this backdrop, based on the first domain of the MAB Programme— “the ecological effects of increasing human activities on tropical and subtropical forest ecosystems” —senior ecologists including Professor He Shaoyi from the South China Botanical Garden (formerly South China Institute of Botany) established the Dinghushan Forest Ecosystem Long-term Research Station, initiating long-term positioning studies of tropical and subtropical forest ecosystems. The station aims to reveal the structure-function and pattern-process relationships of natural forest ecosystems and their responses and adaptation to environmental change, providing scientific support for solving key scientific and technological problems in national and local ecological environmental protection and sustainable resource utilization, and offering theoretical foundations for degraded ecosystem restoration and reconstruction.

Discovery of Continuous Organic Carbon Accumulation in Mature Forest Soils: Advancing Ecosystem Carbon Balance Theory and Leading Global Research on Mature Forest Carbon Sinks

The 1980s witnessed the implementation of the World Climate Research Programme (WCRP) and the International Geosphere-Biosphere Programme (IGBP), sparking a global surge in global change ecology research. From the 1992 United Nations Framework Convention on Climate Change (UNFCCC) requiring signatory countries to submit greenhouse gas emission and conversion inventories, to the 1997 Kyoto Protocol emphasizing greenhouse gas emission reduction and linking CO₂ emissions to national economic development, countries worldwide have been motivated to accurately assess greenhouse gas emissions and seek measures to reduce CO₂ emissions while increasing carbon sequestration potential through ecosystem management strategies.

Forests, as the main component of terrestrial ecosystems, play a vital role in mitigating atmospheric CO₂ concentration increases. However, traditional ecosystem equilibrium theory posits that carbon pools in mature forest ecosystems, especially tropical and subtropical ones, are essentially balanced and contribute little to global carbon sinks [1]. This theory primarily assumes that biomass increments in terrestrial ecosystems are largely offset by respiration. Guided by this theory, relevant international organizations, treaties, and global carbon balance estimation models have never considered the carbon sequestration ca-

capacity of mature ecosystems. We argue that this theory may be flawed, as it fails to adequately account for soil carbon, particularly carbon migration, loss, and deposition processes during hydrological cycles, which may be one reason for the unknown “missing carbon sink” in global carbon balance studies. Based on this innovative concept and supported by CAS key directional projects, we integrated and analyzed long-term positioning observation data (1979–2003) and experimental results from Dinghushan Station. Through rigorous demonstration, we obtained the important finding that “mature forest soils can continuously accumulate organic carbon,” published in the top international journal *Science* (Figure 1 [Figure 1: see original paper]) [2]. International peers believe this finding gradually erodes the old carbon balance theory established decades ago regarding forest succession, fundamentally changing perspectives on ecosystem processes and calling for the establishment of an ecosystem non-equilibrium theoretical framework. This study convincingly demonstrates that mature forests are important carbon sinks—a significant original innovation. *Nature* magazine interviewed multiple global ecologists, including renowned Swedish ecologist Günter Hoch, who considered this discovery a major “surprise” for the ecological community that would benefit developing countries in environmental diplomacy negotiations and reduce pressure for implementing the Kyoto Protocol. It provides new explanations for the role of mature forests in mitigating global CO₂ concentration increases and offers fresh insights into revealing the destination of the “missing carbon sink,” representing a major breakthrough [3]. The Intergovernmental Panel on Climate Change (IPCC) noted in its 2007 report that this paper was among the nine most unignorable articles globally. This achievement was selected as one of China’s Top Ten News in Basic Research for 2006 and has led a wave of global research on mature forest carbon sink functions [4,5].

Due to the international impact of this research, the editorial board of the prestigious academic journal *New Phytologist* chose to co-host the “23rd New Phytologist Symposium: Carbon Cycling in Tropical Ecosystems” with Dinghushan Station in Guangzhou on November 17–20, 2009. This marked the first time the journal held such a symposium outside Europe and North America, with over 150 botanists and ecologists from more than ten countries and regions including the UK, USA, Australia, Canada, France, Italy, and China attending (Figure 2 [Figure 2: see original paper]). After the conference, participants visited Dinghushan Station for field inspections and highly praised its long-term positioning monitoring and systematic long-term experiments, deepening international understanding of China’s ecological research.

Mechanisms and Driving Forces of Forest Soil Carbon Accumulation: Providing Theoretical Foundations for Scientific Assessment of Carbon Balance and Sink Functions

To explore the processes and mechanisms of forest soil organic carbon accumulation, the Dinghushan research team proposed two hypotheses: (1) the

acidification-driven mechanism hypothesis—soil acidification affects microbial activity and organic matter decomposition rates, activates base cations especially Al^3 , stimulates the formation of macromolecular organic complexes, and facilitates soil carbon accumulation; and (2) the carbon-nitrogen coupling-driven mechanism hypothesis—increased nitrogen deposition accelerates soil acidification while enhancing soil nitrogen availability, stimulating coupling with carbon to form macromolecular organic compounds, reducing soil labile organic carbon content, decreasing organic carbon emissions and losses, and increasing soil carbon accumulation. To test these hypotheses, Dinghushan Station established a series of long-term control experiments including simulated acid deposition, simulated nitrogen deposition, open-top chamber CO_2 enrichment + nitrogen addition (carbon-nitrogen interaction), altered precipitation variability, and fully enclosed watersheds (for accurate input-output control), receiving strong support from the National Natural Science Foundation of China, the Ministry of Science and Technology, and CAS. Integrated analysis of long-term monitoring data and experimental results has yielded a series of important conclusions regarding forest soil organic carbon accumulation mechanisms.

Simulation experiments reveal mechanisms of forest soil organic carbon accumulation. Nitrogen deposition simulation experiments show that high nitrogen treatment significantly reduces soil respiration rates in mature forests, with the reduction occurring mainly during the rainy season (April–September annually, also the peak plant growth season). As soil microbial activity and fine root growth are suppressed, the temperature sensitivity of soil respiration (Q_{10}) decreases, ultimately reducing CO_2 emissions from mature forest soils (Figure 3 [Figure 3: see original paper]), indicating that nitrogen deposition can drive organic carbon accumulation in mature forest soils and that these soils will play an important role in mitigating atmospheric CO_2 concentration increases under nitrogen deposition scenarios [6]. Long-term nitrogen deposition can cause soil acidification and increase soil adsorption capacity through physicochemical control mechanisms (non-biological control mechanisms), reducing dissolved organic carbon (DOC) output from rhizosphere zones and thereby increasing ecosystem soil carbon storage [7]. Phosphorus addition experiments show that increased phosphorus significantly improves microbial composition in mature (nitrogen-saturated) forest soils and enhances CO_2 emissions, indicating that nitrogen deposition can limit microbial decomposition of organic carbon and promote organic carbon accumulation by reducing phosphorus availability [8]. However, because mature forest (late-succession) soils have higher phosphatase activity than other transitional forest types (mid- and early-succession), this offsets the phosphorus limitation effect on the forest community to some extent [9].

Carbon-nitrogen interaction experiment results show that combined high CO_2 (700 ppm) and high nitrogen ($100 \text{ kg ha}^{-1} \text{ yr}^{-1}$) treatments have additive interactive effects, promoting soil CO_2 emissions more than individual high CO_2 or high nitrogen treatments [10] and causing increased inorganic carbon loss [11]. However, because the interaction significantly promotes plant growth, enhanc-

ing ecosystem net primary productivity (NPP) and water use efficiency [12] (Figure 4 [Figure 4: see original paper]), it increases soil organic carbon sources (litter quantity, fine root biomass, and exudates), promoting soil carbon pool increases and indicating that carbon accumulation requires sufficient coupling with exogenous nitrogen. Under elevated atmospheric CO₂ conditions, increased exogenous nitrogen promotes the accumulation of readily oxidizable organic carbon (ROC) and particulate organic carbon (POC), ultimately benefiting total organic carbon (TOC) increase [13,14] (Figure 5 [Figure 5: see original paper]).

Simulated acid deposition treatment exacerbates forest soil acidification, inhibits soil microbial activity and fine root biomass, reduces soil CO₂ emissions, and increases surface soil organic carbon content [15], but promotes ion activation and significantly increases leaching of anions and cations including NO₃⁻, SO₄²⁻, Ca²⁺, K⁺, Mg²⁺, and dissolved organic carbon (DOC), while dramatically increasing Al³⁺ leaching [16]. Cation activation promotes macromolecular complex formation, facilitating soil organic carbon deposition.

Altered precipitation variability control experiments (no precipitation, control, and double precipitation treatments) show that drought (no precipitation treatment) reduces forest soil phosphorus mineralization. During the rainy season (April-September), double precipitation also inhibits phosphorus mineralization in mature forest soils. Reduced phosphorus availability limits microbial decomposition of organic carbon [17]. In the dry season (November-February), soil respiration and its temperature sensitivity increase with precipitation amount, while its moisture sensitivity decreases with precipitation amount. During the wet season, no precipitation treatment reduces soil respiration and temperature sensitivity while increasing moisture sensitivity. These results indicate that drought will reduce soil respiration in South Asian subtropical forests, but increased rainfall during the rainy season may inhibit soil respiration responses to temperature increases [18].

Clarifying driving mechanisms of soil organic carbon accumulation.

Based on analysis of long-term hydrological monitoring data (1950-2009) and SWAT model simulations for Dinghushan, annual total precipitation changed little, but soil moisture content decreased significantly. Monthly 7-day low flow also decreased significantly during 2000-2009. However, maximum daily runoff during wet seasons and groundwater levels in the phreatic zone increased significantly during the same period (Figure 6 [Figure 6: see original paper]). The significant decreasing trends in soil moisture content and low flow indicate the watershed is developing toward aridification, showing that climate change has indeed caused more extreme hydrological events (drought and flood) in this watershed. Significantly reduced soil moisture content leads to decreased soil respiration, while increased rainfall during rainy seasons also reduces soil respiration responses to temperature increases. Clearly, climate change-induced alterations in hydrothermal environments reduce soil organic carbon decomposition rates, extend soil organic carbon turnover times, and ultimately promote soil organic carbon accumulation [19].

Studies on carbon balance in forest ecosystems at different successional stages show that as forest communities undergo forward succession, biomass carbon accumulation gradually shifts toward soil organic carbon accumulation, with increasing proportions of organic carbon allocated to soils and richer sources of soil organic carbon, enabling higher accumulation rates in mature forest soils [20-22].

Current research on the mechanisms of continuous organic carbon accumulation in mature forest soils continues to deepen, with new results expected to emerge soon.

Scaling from Point to Plane: Quantifying the Current Status and Potential of China's Forest Ecosystem Carbon Sequestration

Based on rich accumulation in forest ecosystem carbon cycle research, Dinghushan Station was selected as the lead unit for the "Forest Ecosystem Carbon Sequestration Status, Rate, Mechanism, and Potential" project (referred to as the "Forest Project") under the CAS Strategic Priority Research Programme "Carbon Budget Certification and Related Issues for Climate Change Response" (2011-2015, referred to as the "Carbon Special Project"). The project covered broad areas with complex research objects. Dinghushan Station's core team overcame numerous difficulties and, through repeated demonstrations, completed the division of project areas, determination of national survey plot numbers, organization of sub-project settings and research teams, and formulated detailed research implementation plans and unified operational protocols. The project and sub-project budget proposals passed CAS review, and the project successfully launched. After initiation, more than 1,000 researchers collaborated diligently for over five years, completing the following scientific tasks:

- (1) Constructed a standard methodology system compliant with IPCC specifications that enables measurable, reportable, and verifiable forest ecosystem carbon pools, covering plot layout, survey, sampling, laboratory analysis, and data calculation, providing a demonstration model for future related research.
- (2) Established a series of typical forest ecosystem sample plots for long-term ecological research. Based on comprehensive understanding of China's forest resources and according to forest complexity, 7,800 representative sample plots were established, reflecting China's forest resource status and suitable for long-term ecological research.
- (3) Constructed over 200 species- and organ-specific biomass equations applicable to China's forest biomass estimation by extensively collecting literature and integrating project data.
- (4) Built a national-scale forest ecosystem database involving more than 120

data tables and over 10 million data entries.

- (5) Published more than 300 related research papers and provided six consultation reports to central and local governments.
- (6) Clarified the current status and potential of carbon sequestration in China's forest ecosystems, providing convincing scientific data for national environmental diplomacy negotiations. The project successfully achieved its objectives and passed project acceptance.

As the chief scientist of the project, the author was invited as a member of the CAS Carbon Special Project delegation to attend the 2015 United Nations Climate Change Conference in Paris in December 2015 (Figure 7 [Figure 7: see original paper]). At the China Pavilion side event themed “Tracking Carbon Footprints—Chinese Scientists in Action,” the presentation showcased the current status of China's forest ecosystem carbon sinks, explaining that Chinese scientists had discovered through quantitative assessment of national terrestrial carbon sink status and potential that existing and planned carbon sink measures have played and will continue to play important carbon sequestration roles. This received high praise from leaders of the National Development and Reform Commission. CCTV News Channel subsequently produced a documentary titled “Building a Community with a Shared Future for Mankind: 2015 China Delegation at the Paris Climate Conference” [23], with over 40 minutes of detailed coverage of the Carbon Special Project side event, highly affirming its contribution: “These voices increased the world's understanding of China and provided inexhaustible momentum for climate change action.”

Innovative Thinking Enables Broad Perspectives: Large-Scale Revelation of the Relationship Between Forest Ecosystem Water Resource Conservation and Carbon Sink Functions

The debate over whether afforestation reduces water resources has long persisted. After comprehensively collecting 50 years of monitoring data from nearly 200 meteorological and hydrological stations across Guangdong Province and quantitatively analyzing factors including rainfall, potential evapotranspiration, anthropogenic water consumption, and reservoir interception, the impact of large-scale afforestation activities on water yield was revealed. Results show that over the past 50 years, large-scale afforestation activities doubled Guangdong's forest coverage, yet total provincial water yield did not change significantly (Figure 8 [Figure 8: see original paper]), while the water yield pattern changed—dry season water yield increased significantly. This redistribution of rainfall kept annual total water yield basically unchanged while significantly reducing intra-annual variability, making water yield more uniform throughout the year [24]. This conclusion demonstrates that in regions where rainfall exceeds potential evapotranspiration, large-scale afforestation will not cause water supply reductions; in other words, increased forest carbon sequestration function does

not come at the cost of water resources.

Addressing the “paired watershed” experiments conducted over the past century that concluded “afforestation means water loss” [25], and based on years of case studies, the station elaborated the “global pattern of climate and land cover effects on water yield,” tested with over 2,600 global research cases. The pattern identifies serious design flaws in the nearly century-old “paired watershed” experiments worldwide and severe “pre-assumption” problems in their result interpretations. The pattern concludes that forest-water yield relationships can be negative, neutral, or positive, and precisely provides critical threshold values for climate and watershed characteristic parameters controlling these three effects [26] (Figure 9 [Figure 9: see original paper]). This theoretically clarifies the mechanisms through which climate and watershed properties affect water yield, ending over 100 years of debate on the “forest-water yield relationship.” It is considered “an original scientific contribution of significant value with potential influence.” Practically, it has important implications for how to plant forests according to climate conditions and watershed characteristics to increase forest cover, maintain water supply, and enhance carbon sink potential.

Integrating Macro- and Micro-Approaches to Reveal Response and Adaptation Patterns of Tropical and Subtropical Evergreen Broad-Leaved Forest Structure and Function to Climate Change

Analysis of over 30 years of permanent plot monitoring data reveals that the monsoon evergreen broad-leaved forest (mature forest) in Dinghushan has experienced increased plant individuals per unit area due to higher community recruitment rates than mortality rates, leading to changes in community species composition. Large individual diameter growth rates increased while small individual growth rates decreased, causing declines in community mean diameter at breast height (DBH) and ultimately reducing community biomass [27] (Figure 10 [Figure 10: see original paper]). Further analysis using long-term monitoring results from 20 permanent plots of evergreen broad-leaved forests in China’s subtropical region shows that over the past 30 years, the active organic carbon pool (leaf, root, small tree, shrub, and small individuals with DBH < 10 cm, referred to as the active carbon pool) of this vegetation community has accumulated at much higher rates than the non-active carbon pool (branch and trunk biomass carbon pools of individuals with DBH > 10 cm) [28].

Evergreen broad-leaved forests are undergoing transformation toward smaller individual sizes and small tree species composition, which will profoundly affect biodiversity conservation functions. Meanwhile, forest community structure changes have caused the leaf-to-root biomass ratio in mature forests across China’s evergreen broad-leaved forest region to increase, driving mature forest carbon budgets into a new non-equilibrium state pointing toward lower forest biomass carbon balance levels.

Based on 32 years (1978–2010) of community survey data from eight censuses of species individual numbers, plant DBH, and environmental factor changes in the Dinghushan evergreen broad-leaved forest permanent plot, combined with measurements of functional traits reflecting plant resource acquisition strategies (photosynthetic rate, hydraulic conductivity, leaf nitrogen and phosphorus content) and drought resistance (xylem vulnerability to cavitation, branch safety margin, turgor loss point) for 48 dominant species (accounting for 92% of total individuals), integrated analysis revealed that functional traits related to rapid plant growth and drought resistance strategies significantly correlate with abundance changes. This mechanistically explains that structural changes in South Asian subtropical monsoon evergreen broad-leaved forest communities represent an adaptation to regional climate change (temperature increase, forest soil drying, etc.) [29].

Since its establishment in 1978, Dinghushan Station has consistently focused on the overall objective of understanding relationships between forest ecosystem structure-function and pattern-process, as well as their response and adaptation to environmental change. The station systematically conducts long-term monitoring, research, and demonstration work, emphasizing platform resource utilization to serve scientific research, science education, environmental planning, and eco-tourism across various sectors. Through undertaking numerous national, CAS, and local research projects, the station has revealed mechanisms and driving forces of organic carbon accumulation in tropical and subtropical forest ecosystems, and clarified key processes and coupling relationships of carbon, nitrogen, and water cycles and their responses and adaptation to environmental change. Since the Knowledge Innovation Program launch, the station has published over 400 SCI papers, including more than 100 in top-tier journals such as *Science*, *Nature Communications*, *Ecology Letters*, *Global Change Biology*, *New Phytologist*, *Soil Biology & Biochemistry*, *Biogeochemistry*, *Agricultural and Forest Meteorology*, and *Water Resources Research*. Research achievements have independently won one second-class National Natural Science Award (with all awardees from Dinghushan Station), one China's Top Ten News in Basic Research, two first-class and one second-class Guangdong Provincial Science and Technology Awards, and one third-class award from the State Environmental Protection Administration. As a major participant, the station contributed to achievements that won one first-class and one second-class National Science and Technology Progress Award, and two first-class Guangdong Provincial Science and Technology Awards, while cultivating outstanding talents in ecosystem ecology research.

With its unique geographical advantages, comprehensive research facilities, long-term historical data accumulation, and rich research outputs, Dinghushan Station has become a renowned comprehensive research base for ecosystem ecology both domestically and internationally. With strong support from superior departments, Dinghushan Station will continue to play an important exemplary and leading role in long-term ecological research fields including ecosystem ecology, forest hydrology, and global change ecology.

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