

Advancing ecosystem ecology through innovative research methods and techniques

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Abstract Terrestrial ecosystems are experiencing rapid and unprecedented changes driven by global warming, precipitation changes, increasing atmospheric CO₂, nitrogen enrichment, and land-use change. Understanding and predicting ecosystem responses to these interacting factors requires integrative approaches that combine empirical observations with advanced analytical and modeling frameworks. Over the past several decades, Luo Ecolab and its collaborators have pioneered a suite of innovative research methodologies, including long-term manipulative field experiments, global-scale meta-analyses, data assimilation, matrix-based modeling, and artificial intelligence (AI)-enabled data–model integration. In this review, we synthesize key advances across six thematic areas and demonstrate how these complementary approaches enhance mechanistic understanding and predictive capacity in ecosystem ecology. Specifically, experimental warming studies reveal that ecosystem responses are dynamic and frequently constrained by water and nutrient availability, and subject to acclimation over time. Meta-analyses provide robust quantitative syntheses

across ecosystems, identifying consistent yet context-dependent effects of global change on ecosystem productivity, soil carbon cycling, and greenhouse gas emissions. Data assimilation bridges observations and process-based models, reducing uncertainty and improving predictions at site, regional, and global scales. The matrix modeling framework offers a unifying mathematical structure for carbon cycle models, enabling efficient computation, traceability analysis, and systematic diagnosis of model uncertainty. Emerging AI approaches, particularly knowledge-guided machine learning, further advance the integration of big data with ecological theory, unlocking new pathways for scientific discovery. Collectively, these advances demonstrate that ecosystem responses to global change are governed by complex interactions among climate, nutrient availability, and microbial processes. By integrating empirical data, theoretical frameworks, and computational innovations, this body of work provides a robust foundation for next-generation ecosystem modeling and ecological forecasting in an era of accelerating environmental change.

Keywords Ecolab, global change, carbon cycling, field experiments, meta-analyses, data assimilation, matrix-based modeling, artificial intelligence

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1 Introduction

Rapid anthropogenic global change has created an urgent need to understand how terrestrial ecosystems respond to shifts in temperature, rising CO₂ concentrations, precipitation change, nutrient enrichment, and accelerating land-use transformation (Luo et al., 2001). To address these issues, various approaches can be applied, including manipulative field experiments, meta-analysis, data-model assimilation, advanced matrix modeling, and artificial intelligence (AI)-process integrated method (Fig. 1).

Field experiments can directly address the impacts of treatment factors and reveal the mechanistic responses of ecosystem properties to treatment factors. Field experiments also generate data that are critical for other approaches. As a result, field studies are fundamental methods for global change ecology (Luo et al., 2001; Wan et al., 2002, 2005; Zhou et al., 2007a; Niu et al., 2010). One shortcoming of field studies is that they are often constrained by site-specific conditions, methodological variation, and limited spatial or temporal scale. Meta-analysis provides a powerful tool to overcome these limitations by integrating results across biomes, harmonizing diverse experimental approaches, and revealing emergent global patterns (Wan et al., 2001; Luo et al., 2006; Zhou et al., 2007a; Lu et al., 2011a, 2011b; Song et al., 2019; Hui et al., 2025). It is a statistical method that combines the results of multiple individual studies and provides a more robust and quantitative conclusion. Since it integrates multiple studies, it increases sample size and statistical power,

often leading to a more robust and accurate estimation of the true effect size. As a result, meta-analysis can resolve conflicting results, provide more reliable responses to the treatments, and help guide policy-making and future research.

Data assimilation (DA) or data-model fusion integrates observational data with process-based models through mathematical algorithms to optimize model parameters and reduce model uncertainty (Luo et al., 2003; Xu et al., 2006; Zhou et al., 2012; Zhou et al., 2013; Luo et al., 2015). By doing so, DA improves model predictive ability and enables more accurate estimation of ecosystem state variables and fluxes. In essence, DA functions as a methodological “bridge” that links theoretical understanding with real-world observations, connecting process-based models with empirical data. Moreover, DA facilitates the integration of processes across different spatiotemporal scales by linking instantaneous, site-level observations (e.g., flux tower measurements) with regional-scale and long-term process simulations.

The matrix approach provides a coherent mathematical foundation for advancing terrestrial C cycle modeling (Luo et al., 2003, 2017, 2022; Xia et al., 2013; Du et al., 2018; Zhou et al., 2020; Liao et al., 2022). As land surface models continue to expand in scope and complexity, differences in their structures, process representations, and parameterizations have made it increasingly difficult to compare behaviors, improve computational efficiency, and diagnose sources of uncertainty. By formulating ecosystem carbon (C) dynamics into a compact matrix representation, this framework offers a systematic way to represent model

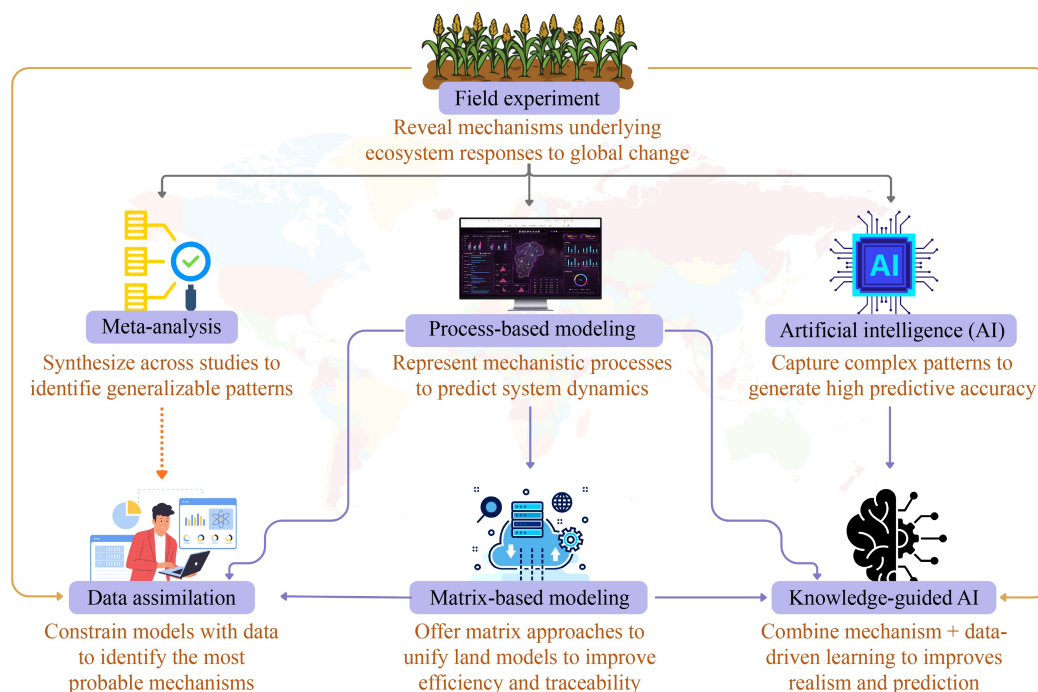


Fig. 1 A suite of methods and techniques used in Ecolab to advance science in ecosystem ecology.

processes, streamline numerical procedures, and enable transparent attribution of modeled outcomes. In this way, the matrix approach acts as a unifying methodological framework that integrates diverse model structures, enhances computational efficiency, and supports rigorous process-based evaluation across model ensembles.

Artificial intelligence (AI) provides new opportunities to integrate diverse big data and process-based models, thereby accelerating scientific discoveries (Tao et al., 2020, 2023, 2024; Huang, 2024; Xu et al., 2025; Fan et al., 2026). Hybrid modeling approaches, also referred to as knowledge-guided machine learning (KGML), have been proposed to improve process understanding in Earth system science using big data. In these approaches, physical or knowledge-based constraints, such as conservation of mass and energy, empirical functional relationships or governing partial differential equations, are incorporated into an AI-based structure, such as a neural network. Predictions of AI will be further constrained by those physical or knowledge-based constraints in addition to labeled observations. More importantly, unlike the neuron-related parameters in a conventional neural network, the latent variables and parameters embedded in the neural network to formulate physical or knowledge-based constraints explicitly represent physical or biological variables or processes, empowering additional mechanistic interpretability to the neural network in making predictions.

Over the past several decades, Luo Ecolab and collaborators have developed methods and tools to investigate the impacts of global change on different ecosystem properties, including productivity, plant functional traits, soil C cycling, microbial community dynamics, and greenhouse gas fluxes (e.g., Luo et al., 2001; Wan et al., 2001; Luo et al., 2006; Zhou et al., 2007b; Xia et al., 2020; Luo et al., 2022; Tao et al., 2024). In this review, we highlight Ecolab's scientific contributions and technological advancements. We begin by outlining the methodological framework, then summarize major findings across six thematic areas. We conclude by discussing how these contributions and tools have advanced ecological theory, strengthened the predictive capacity of ecosystem models, and influenced the broader trajectory of ecosystem ecology.

2 Manipulative warming experiments in a Tallgrass prairie: plant productivity and soil carbon cycling

2.1 Warming experiments conducted by Ecolab

Temperature has fundamental roles in regulating biological and biogeochemical processes, including plant growth, microbial metabolism and related C, water, and nutrient cycling. Consequently, climate warming can profoundly influence ecosystem structure and functions.

Numerous warming experiments have been conducted across forests, grasslands, tundra, agricultural systems, and bioenergy cropping systems (Wan et al., 2002; Song et al., 2019). Long-term warming experiments are particularly valuable because they reveal ecosystem responses that may evolve over time due to acclimation, adaptation, and resource limitation (Melillo et al., 2002; Rudgers et al., 2014). This section synthesizes findings from manipulative warming experiments in a tallgrass prairie conducted since 1999.

The first warming experiment, using infrared radiators, was initiated in Norman, Oklahoma, in 1999 (Luo et al., 2001; Wan et al., 2002; Fig. 2). Mowing treatment was nested within the unwarmed and warmed plots. The second set of experiments combined warming and precipitation manipulations, conducted both in situ in Oklahoma and with transplanted soil monoliths in the EcoCELL facility in Reno, Nevada (Arnold et al., 2008).

2.2 Effects of warming on plant phenology, productivity, community structure, and stability

2.2.1 Plant phenology and productivity

Warming accelerates leaf development, enhances photosynthetic capacity, and advances spring phenology. Experimental evidence shows that warming advances flowering and fruiting in early-season species, but delays reproduction in late-season species, resulting in divergent phenological shifts across the growing season (Sherry et al., 2007). These responses exhibit strong legacy effects and depend on species identity and precipitation (Sherry et al., 2008).

Phenological shifts alter ecosystem C processes by modifying the timing and duration of C uptake. Earlier leaf emergence may increase seasonal C assimilation, while delayed senescence may prolong photosynthetic activity. Ecolab's work distinguished direct warming effects (temperature increase) from indirect effects (extending growing season and enhanced soil N mineralization). Warming increased leaf photosynthesis

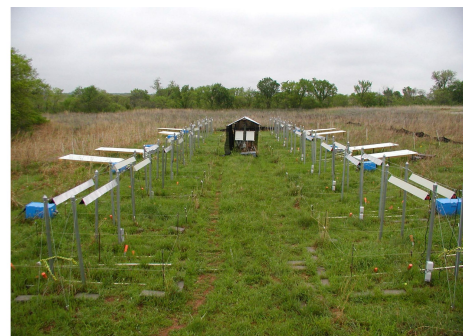


Fig. 2 Field warming experiment using the infrared heaters in Norman, OK, USA. (Photo credit: Y. Luo)

in spring, decreased it in early fall, and stimulated dark respiration until mid-summer (Zhou et al., 2007a, 2007b). Both processes exhibited acclimation, varying among plant species (Zhou et al., 2007a; Peng et al., 2019).

These seasonal responses led to increased green biomass in spring and autumn and total biomass in summer (Wan et al., 2005). Warming also enhanced belowground net primary productivity (BNPP) and increased the BNPP:NPP ratio (Xu et al., 2012a, 2012b), without altering its vertical distribution (Xu et al., 2014). Consequently, C storage increased in the aboveground plant, root, and litter pools. Optimum air temperature and precipitation ranges for BNPP were lower than those for ANPP (Jung et al., 2022), highlighting differential sensitivities of above- and belowground productivity. Overall, productivity and phenological responses were strongly mediated by precipitation and soil water availability (Sherry et al., 2008; Jung et al., 2022).

Nitrogen (N) availability plays a central role in regulating plant growth and C-climate feedbacks. In this system, warming reduced leaf N concentration and resorption efficiency, increased C:N ratio, and enhanced N use efficiency (NUE) by stimulating plant N uptake (An et al., 2005; Niu et al., 2010). Increased NUE in C₄ grasses appears to be a key mechanism driving enhanced biomass production under warming.

2.2.2 Community structure

Due to physiologic differences among species, warming can alter species interactions, community composition, and biodiversity. In tallgrass prairie, community composition remained relatively stable during the first seven years but began to shift after year eight, largely driven by changes in one invasive species and three dominant species. However, overall plant diversity (species richness, evenness, and diversity indices) showed little response, except during an extreme wet year (Shi et al., 2015a, 2015b).

Changes in community structure influence ecosystem function and stability. For example, warming-induced increases in the proportion of C₃ forbs explained differences in soil respiration responses between early (2000–2006) and later (2007–2012) experimental periods (Xu et al., 2015). Warming also enhanced temporal stability by promoting dominant C₄ species, highlighting the combined roles of dominant functional group and biodiversity in regulating ecosystem stability under global change (Shi et al., 2015a, 2015b).

2.3 Soil carbon cycling and decomposition responses to warming

2.3.1 Soil respiration

Soil respiration is a major C flux between terrestrial

ecosystems and the atmosphere. Because soil microbial and root activities are strongly temperature dependent, warming generally increases soil CO₂ emissions. Temperature sensitivity of soil respiration is commonly described by the Q₁₀ coefficient. While many models assume a constant Q₁₀, Ecolab demonstrated, for the first time, acclimation of soil respiration (i.e., declining Q₁₀) under warming in tallgrass prairie (Luo et al., 2001), suggesting a weakening of positive C–climate feedbacks over time. Warming stimulated soil respiration, including both autotrophic and heterotrophic respiration (Zhou et al., 2007b; Jia et al., 2014). However, responses varied with land use (mowing), precipitation, and experimental duration, partly due to shifts in plant functional groups and community structure (Zhou et al., 2007a, 2007b; Jia et al., 2014; Xu et al., 2015). Sustained increases in soil C release were largely driven by enhanced plant productivity, especially in spring and autumn, increased BNPP, and greater C inputs to soil, which provided C substrates for soil microbial and root respiration (Wan et al., 2005; Xu et al., 2012a, 2013, 2015; Jung et al., 2022).

2.3.2 Substrate regulation of decomposition

In addition to temperature, substrate availability strongly regulates decomposition (Xu et al., 2012a). Warming increased litter decomposition by more than 40% after 14 years, primarily accelerating turnover of labile C rather than recalcitrant pools (Stuble et al., 2019). As labile soil organic C (SOC) was depleted, overall SOC residence time increased, likely due to a greater contribution of recalcitrant C (Xu et al., 2012a, 2012b; Zhou et al., 2018a). Long-term warming also promoted decomposition of subsoil organic matter with long turnover times, likely driven by shifts of microbial functional groups as substrate composition changed (Cheng et al., 2017; Feng et al., 2017). These findings highlight the importance of both temperature and substrate availability in regulating long-term soil C dynamics.

2.3.3 Soil carbon loss and stabilization

Accelerated decomposition under warming has important implications for soil C storage. While warming initially increased microbial biomass C and labile C pools (first 2.5 years; Belay-Tedla et al., 2009), long-term responses differed. Over nine years, labile organic C declined, while SOC remained relatively stable (Xu et al., 2012a). This decline was likely driven by increased soil respiration, enhanced soil erosion (Xue et al., 2011), and shifts toward C₄ dominance under warming (Cheng et al., 2011).

Synthesizing results from these field warming experiments, several consistent patterns emerge. Warming generally enhances plant productivity through extended growing seasons and increased physiologic activity, although responses are strongly mediated by water and nutrient availability. Soil respiration typically increases due to enhanced microbial activity and decomposition, but long-term responses may attenuate due to substrate depletion, acclimation, or ecosystem restructuring. Warming also influences microbial community composition, enzyme activity, and C use efficiency, thereby altering soil C turnover and ecosystem C balance. Overall, these findings highlight the dynamic and context-dependent nature of ecosystem responses to climate warming. Continued long-term experiments and integration with ecosystem models are critical for improving predictions of terrestrial C cycling under future warming scenarios.

3 Meta-analysis of global change on ecosystem responses

3.1 Meta-analysis: concept and methods

Meta-analysis is a quantitative approach that synthesizes results from independent studies to generate robust, generalizable conclusions. By increasing sample size and statistical power, it improves estimates of treatment effects, reconciles conflicting results, and supports evidence-based decision-making.

Meta-analysis typically begins with a systematic literature search across major databases (e.g., Web of Science, Scopus, and Google Scholar) to identify peer-reviewed studies that experimentally manipulate key global change drivers such as elevated CO₂, warming, precipitation, or N enrichment. Extracted data (means, variance, sample size) are used to calculate standardized effect sizes, often log response ratios (lnRR). Random- or mixed effects models estimate overall effects, while moderator analyses assess the influences of ecosystem type, climate, or experimental duration. Publication bias and heterogeneity are evaluated to ensure robustness.

3.2 Major scientific contributions from Ecolab meta-analyses

Over the past several decades, Ecolab has conducted more than 50 meta-analyses, providing a comprehensive understanding of terrestrial ecosystem responses to global change. Early work on fire effects (Wan et al., 2001) showed reduced fuel N availability (−58%) and increased soil NH₄⁺ (+152%) (Fig. 3(a)), with later syntheses confirming reductions in C and N pools in tropical ecosystems (Jiang et al., 2022).

Across studies, consistent response patterns emerge.

For example, warming increases soil respiration (~12%–18%) and accelerates C turnover. Elevated CO₂ enhances plant biomass (~17%–21%) but yields limited soil C gains. Nitrogen addition enhances productivity (~25%–35%) but reduces microbial diversity and increases nitrous oxide (N₂O) emissions. Reduced precipitation suppresses productivity (−19% to −29%), whereas increases have modest positive effects. Land-use practices substantially alter soil C and nutrient dynamics. These syntheses provide a quantitative foundation for understanding ecosystem responses and guiding future research.

3.3 Responses of terrestrial ecosystems to global warming, elevated CO₂, and precipitation changes

3.3.1 Warming effects

Meta-analyses show that warming increases productivity, decomposition, and soil respiration, although responses often acclimate over time. For example, Lu et al. (2013) reported enhanced plant productivity (e.g., GPP, NPP), C pools, and litter decomposition, with limited change in soil C stocks (Fig. 3(b)). Warming also significantly enhances ligninase activities and greenhouse gas emissions, reducing net C sink strength (Chen et al., 2018; Liu et al., 2020; Yan et al., 2022). Overall, these studies highlight strong short-term sensitivity and long-term acclimation of C processes.

3.3.2 Elevated CO₂ effects

Elevated CO₂ stimulates photosynthesis, net primary productivity, and plant biomass, but responses diminish over time due to progressive N limitation. Luo et al. (2006) showed increases in above- and belowground biomass (Fig. 3(c)), while subsequent studies found that increased C inputs are offset by accelerated decomposition (van Groenigen et al., 2014). Changes in plant and soil stoichiometry further indicate progressive nutrient limitation (Yang and Luo, 2011; Deng et al., 2015). These findings clarify constraints on long-term CO₂ fertilization effects.

3.3.3 Precipitation effects

Precipitation changes strongly regulate ecosystem C processes. Drought typically reduces productivity and soil respiration, whereas increased precipitation can stimulate short-term C fluxes. Importantly, responses are nonlinear and asymmetric: productivity is often more sensitive to increased precipitation in dry ecosystems and to decreased precipitation in humid regions (Wilcox et al., 2017). Reduced precipitation consistently slows C cycling, while interactions among drivers are typically weak (Song et al., 2019).

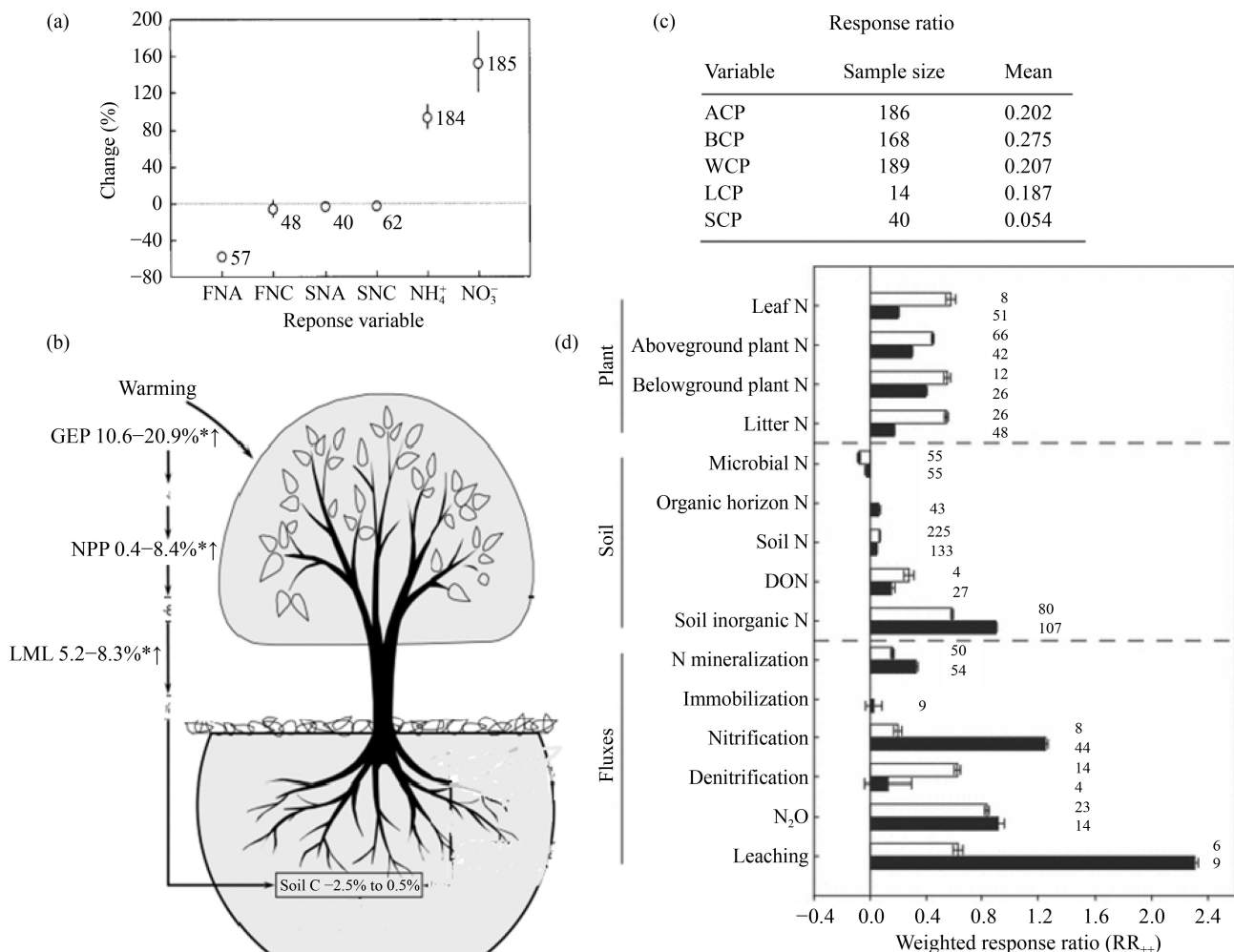


Fig. 3 Examples of meta-analyses of the effects of fire (a), adapted from Wan et al. (2001), warming (b), adapted from Lu et al. (2013), elevated CO₂ (c), adapted from Luo et al. (2006), and N addition (d), adapted from Lu et al. (2011a) on ecosystem responses. Abbreviations are FNA, fuel N amount; FNC, fuel N concentration; NH₄⁺, soil ammonium pool; GEP, gross ecosystem photosynthesis; NPP, net primary production; and DON, dissolved organic N. ACP, BCP, WCP, LCP, and SCP are aboveground, belowground, whole plant, litter, and soil C pool, respectively.

3.4 Nutrient enrichment and land-use change

3.4.1 Nutrient enrichment effects

Meta-analyses show that nutrient additions strongly influence ecosystem structure and function. Nitrogen addition increases productivity but reduces biodiversity and alters microbial activity and enzyme dynamics (Jian et al., 2016; Yan et al., 2022). Evidence also highlights widespread phosphorus and potassium limitations, challenging the assumption of dominant N limitation globally (Chen et al., 2024). For example, N addition increased crop yield but reduced species richness, while enhanced-efficiency fertilizers reduced soil N₂O emissions without yield loss (Zheng et al., 2022; Hui et al., 2025). Nitrogen addition enhanced leaf N, soil inorganic N, and soil N₂O emission in both agricultural and nonagricultural soils (Lu et al., 2011a; Fig. 3(d)). Globally, N limitation dominates many ecosystems, whereas P limitation is more common in tropical regions,

with widespread N–P co-limitation. Despite increased plant inputs, soil C responses are generally modest, indicating complex controls on SOC dynamics.

3.4.2 Land use and management effects

Land-use changes and management practices exert impacts comparable to climate drivers. Meta-analyses show that practices such as afforestation and cover cropping can enhance soil C storage, whereas plantation establishment and forest degradation often reduce soil C, N, and microbial biomass (Li et al., 2012; Liao et al., 2012; Zhou et al., 2018b; Huang et al., 2025). Nitrogen addition alters microbial community structure, reducing diversity and fungal dominance, and alters soil respiration (Zhou et al., 2014; Zhou et al., 2017). These findings highlight the critical role of land management in regulating ecosystem C and N dynamics.

Collectively, these meta-analyses reveal consistent and

mechanistic patterns in ecosystem responses to global change. Moisture availability, nutrient limitation, and microbial processes emerge as dominant controls of ecosystem sensitivity. The compiled global data sets and analytical frameworks provide essential benchmarks for improving process-based models and machine learning approaches. Together, this body of work strengthens predictive understanding of land C cycle and supports strategies for climate mitigation, C management, and sustainable land use.

4 Data assimilation of ecosystem processes

4.1 Data assimilation methods

Data assimilation (DA), also known as data-mode fusion, integrates observational data with process-based models to optimize model parameters, reduce uncertainty, and improve model predictive performance. It links mechanistic models with real-world observations and connects processes across spatiotemporal scales, from site-level observations to regional and global simulations (Luo et al., 2015, 2016).

DA has two primary applications (Luo et al., 2011). The first is parameter optimization (model calibration), which minimizes the difference between simulations and observations by identifying optimal parameter sets. The second is state data assimilation, which dynamically updates model variables (e.g., soil moisture and leaf area index) during model execution, improving realism and process representation.

Ecolab was among the first to apply DA in terrestrial C-cycle research, contributing to its development and application across site, regional, and global scales, including the advancement of DA methods under non-equilibrium conditions and the integration of DA with big-data research frameworks.

4.2 Data assimilation at the site scale

Ecolab initially applied inverse analysis to FACE experiments to quantify C residence time and its response to elevated CO₂ (Luo et al., 2003; White et al., 2005). Based on the Duke Forest FACE experiments, six observational data sets (e.g., biomass, litter, and soil respiration) were integrated with a process-based C-cycle model representing major C pools. A DA framework was developed to estimate key parameters such as C residence times in plant and soil pools. Parameter estimation was achieved using the Levenberg-Marquardt method combined with quasi-Monte Carlo approaches.

Subsequently, Bayesian probability inversion and Markov chain Monte Carlo (MCMC) techniques were introduced to quantify parameter and prediction

uncertainty. Xu et al. (2006) developed a framework using prior parameter distributions and likelihood functions to derive posterior probability density functions via Metropolis Hastings algorithm, establishing a standardized approach for uncertainty analysis.

This framework was later applied to long-term warming experiments. For example, Shi et al. (2015b) integrated multi-year observations from a tallgrass prairie warming study to estimate the posterior probability distributions of key model parameters controlling C allocation and turnover. The study quantified uncertainty in long-term C storage and revealed mechanisms underlying warming effects on ecosystem C dynamics.

4.3 Data assimilation at the regional scale

At the regional scale, Ecolab integrated remote sensing and multi-source observations to improve C-cycle modeling. Zhou and Luo (2008) developed a regional DA framework for North America by coupling multiple models (TECO-R, CASA, VAST) and optimizing C pools and fluxes using genetic algorithms. This study quantified C residence time and mapped its spatial distribution for the first time, revealing its role in regulating C uptake and allocation.

Subsequent work applied MCMC methods to assess uncertainty in key parameters controlling C turnover (Zhou et al., 2013). These approaches were extended to other regions, producing spatial estimates of C turnover time in Chinese forests (Zhou et al., 2010) and temperature sensitivity (Q_{10}) of soil respiration (Zhou et al., 2009).

4.4 Data assimilation at the global scale

At the global scale, DA has been used to improve simulations of SOC and quantify uncertainty. For example, Hararuk et al. (2014) combined global SOC observations with the CLM-CASA model using Bayesian MCMC methods, increasing model explanatory power from 27% to 41%. The study also identified high uncertainty in tropical and high-latitude regions. Zhou et al. (2009) estimated global spatial patterns of Q_{10} of soil respiration using inverse modeling. Accounting for spatial heterogeneity significantly increased the estimated C-climate feedback strength (3.21 vs. 1.88 Pg C^{∘C}⁻¹), highlighting the importance of spatial variability in model predictions.

4.5 Data assimilation under non-equilibrium conditions

A major limitation in large-scale modeling is the assumption of steady-state C balance. In reality, ecosystems are rarely in equilibrium due to climate change and disturbances. To address this, Ecolab developed DA approaches for non-equilibrium

conditions. Zhou et al. (2013) proposed a two-step DA framework integrating multi-source observations (e.g., NPP, biomass, SOC) with spatial data sets (e.g., NDVI, climate, soil properties), enabling direct estimation of regional C sinks without equilibrium assumptions. This approach improved parameter estimation and produced simulations consistent with observations.

Building on this framework, Zhou et al. (2015) demonstrated age-dependent variation in forest C sinks, shifting from steady-state assumptions to dynamic inversion. Ge et al. (2019) further quantified biases introduced by steady-state assumptions and proposed correction methods based on forest age, providing a framework for assessing C sinks in developing forests.

4.6 Data assimilation with Earth system models

Ecolab has also advanced DA applications in Earth system models (ESMs) to improve prediction accuracy and computational efficiency. Luo et al. (2016) identified three major sources of uncertainty in soil C simulations—model structure, parameters, and external drivers—and emphasized Bayesian DA as a key tool for reducing uncertainty. Du et al. (2017) used DA to evaluate the impact of N processes in C-cycle models, showing that incorporating N dynamics significantly influences C stock predictions. Further work (Du et al., 2018) demonstrated how DA can guide model structure improvement.

To systematically diagnose uncertainties, Zhou et al. (2021) developed a cloud-based model evaluation framework that integrates distributed data sets and traceability analysis. This system enabled comparison of multiple CMIP6 models and attributed uncertainty in C storage to components such as NPP and C residence time. Wei et al. (2022b) extended this work by comparing CMIP5 and CMIP6 models, identifying key deficiencies—particularly in nutrient limitation and soil processes—that lead to underestimation of C storage. These findings provide important guidance for next-generation Earth system model development.

5 A matrix approach for advancing ecosystem carbon cycle modeling

The matrix approach provides a unified mathematical framework for modern terrestrial C cycle modeling. As land models grow in complexity, differences in structure, process representation, and parameterization hinder model comparison, efficiency, and uncertainty diagnosis. By expressing ecosystem C dynamics in a compact matrix form, this approach standardizes model representation, improves computational efficiency, and enables transparent attribution of model outputs.

5.1 Unifying carbon cycle models into one matrix equation

Divergence among land C models has led to large discrepancies in simulated soil C storage across model intercomparison studies (Todd-Brown et al., 2013). These differences arise from variations in C transfer networks, process formulations, parameterization, and forcing data, complicating attribution of model uncertainty (Xu et al., 2006).

To address this, Luo et al. (2017) developed a matrix-based framework that represents diverse models within a unified equation. Most terrestrial C models can be described as nonautonomous, multi-compartmental systems (Rasmussen et al., 2016; Sierra et al., 2018; Luo et al., 2022), expressed as Eq. (1):

$$\frac{dX(t)}{dt} = B(t)\mu(t) - A(t)\xi(t)KX(t), \quad (1)$$

where $B(t)$ represents plant C allocation, $\mu(t)$ represents C input, $A(t)$ C represents transfer coefficients, $\xi(t)$ represents environmental modifiers, and K represents turnover rates. This formulation accommodates models of varying complexity and provides a consistent basis for analysis.

The adoption of the matrix approach has rapidly adopted to represent increasingly complex model structures, from simple C pools to systems incorporating N cycling and vertically resolved soil processes. It was first implemented in the Terrestrial Ecosystem Model (TECO) with eight C pools (Xu et al., 2006), and later extended to other models such as the Community Atmosphere Biosphere Land Exchange (CABLE, nine pools; Xia et al., 2012), CLM-CASA (12 pools) (Hararuk et al., 2014), and BEPS (13 pools) (Chen et al., 2015). Subsequent developments incorporated N cycling to address key uncertainty in terrestrial C sequestration identified in CMIP5 models (Zaehle et al., 2015). Matrix representations for organic N pools were developed in CABLE (Xia et al., 2013) and TECO (Du et al., 2018), effectively doubling the number of pools. Additional extensions incorporated mineral N pools in coupled C-N models (Shi et al., 2016). Dynamic vegetation models have also proven compatible with the matrix framework (Ahlström et al., 2015), and processes such as phenology, mortality, and non-structural C dynamics have been incorporated into the matrix representation of CLM5 (Lu et al., 2020), raising the prospect of a unified matrix-based representation of all terrestrial ecosystem processes.

A major advance was the representation of vertical mixing processes using tridiagonal matrix structures. Models such as CLM4.5 (Huang et al., 2018a), CLM5 (Lu et al., 2020), and ORCHIDEE-MICT (Huang et al., 2018b) have successfully implemented matrix representations of vertically resolved soil C dynamics with 70–140 pools, demonstrating the scalability and

robustness of the matrix approach even for highly complex systems. This achievement provides a strong foundation and confidence for extending matrix representations to other terrestrial ecosystem models.

Matrix representations also enhance model modularity and facilitate process-based attribution of uncertainty. For example, exchanging C-cycle processes within the LPJ-GUESS matrix framework identified NPP and soil decomposition as dominant drivers of uncertainty in global C uptake (Ahlström et al., 2015). Similarly, through the exchange of matrix components in CLM4.5, the contributions of different processes to the CO₂ fertilization effect on steady-state soil C stocks were identified (Huang et al., 2018a). Photosynthesis drives positive CO₂ fertilization effects, while warming-induced decomposition offsets these gains, especially at high latitudes. The comprehensive matrix framework implemented in CLM5 (Lu et al., 2020) further enables attribution of ecosystem C responses to multiple, simultaneous climate change drivers (e.g., warming, elevated CO₂, N deposition, and drought) and to specific underlying processes such as phenology, mortality, C allocation, soil decomposition, and soil vertical mixing.

The growing adoption of matrix representations also enables across-model comparison on a unified platform. Early studies simplified complex models to identify key uncertainty components (Zhou et al., 2018a), while more recent efforts, such as the Matrix-based Ensemble Model Inter-comparison Platform (MEMIP) (Liao et al., 2022) and MatrixMIP (Hou et al., 2023), allow precise identification of uncertainties arising from model structure and process representation, providing clear guidance for improving predictions of land C dynamics.

5.2 Saving computational cost for spinning-up models

The matrix approach provides a paradigm-shifting solution to the spin-up bottleneck in terrestrial ecosystem and land surface modeling. Spin-up is a critical yet computationally expensive step used to bring C and N

pools into dynamic equilibrium under pre-industrial conditions, thereby establishing the baseline for transient simulations in model initialization (Thornton and Rosenbloom, 2005; Randerson et al., 2009). Traditional native dynamics (ND) spin-up requires multi-millennial simulations that repeatedly compute the system state using multi-year forcing data, resulting in exceptionally high computational cost (Thornton and Rosenbloom, 2005; Shi et al., 2013). The cost increases even further as models incorporate additional biogeochemical processes, such as phosphorus cycling, and adopt finer spatial resolutions.

By reformulating the core biogeochemical equations into an algebra framework, Semi-analytical Spin-Up (SASU) method enables direct calculation of steady-state conditions, bypassing lengthy transient simulations (Fig. 4). For matrix-form models with vertical soil layers, steady-state pool sizes can be derived analytically by setting Eq. (2) to zero:

$$\frac{dX}{dt} = B(t)U(t) - (A\xi(t)K + V(t))X(t) = 0. \quad (2)$$

Then, Eq. (2) can be solved to obtain the steady-state as

$$X_{ss} = (A\bar{\xi}K + \bar{V})^{-1}\bar{B}\bar{U}, \quad (3)$$

where the $\bar{\xi}$, \bar{V} , \bar{B} , and \bar{U} denote mean values of $\xi(t)$, $V(t)$, $B(t)$, and $U(t)$ over multi-year forcing, respectively. For linear systems, the steady-state solution can be derived analytically by solving a straightforward matrix equation. For more complex nonlinear systems, this solution provides a quasi-equilibrium starting point that accelerates convergence (Fig. 4(a)).

SASU has demonstrated substantial efficiency gains in complex models. In CABLE, spin-up time was reduced by over 85%–90% (Xia et al., 2012; Fig. 4), and in CLM5, by up to 98.0% across global grid cells (Fig. 4(b)). It also outperforms the standard Accelerated Decomposition (AD) (Liao et al., 2023) method, being about eight times faster. In global applications, CLM5

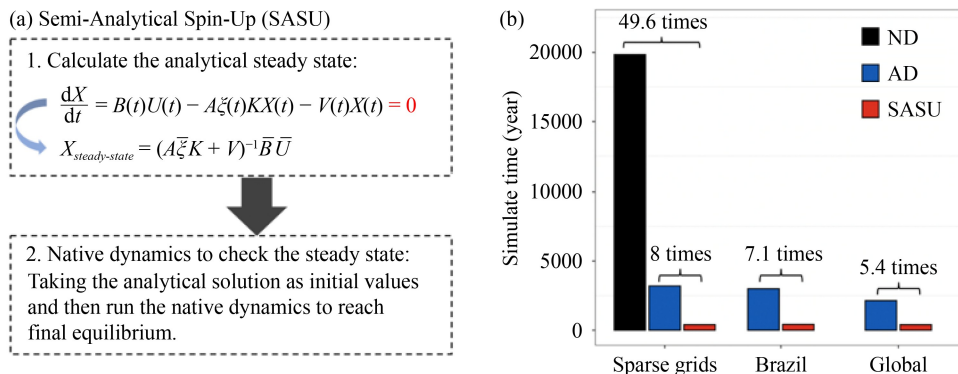


Fig. 4 An overview of the SASU workflow (a) and a comparison of spin-up methods' efficiency (b). Specifically, (b) illustrates the number of model years required to attain equilibrium across various spin-up methods, evaluated at 400 sparse global grid cells, a site in Brazil, and on a global scale within the CLM5 framework.

with SASU reached steady-state within 400 simulation years, compared to > 2000 years with AD (Fig. 4). In practice, simulations that once required months of computation can now be completed in days (Liao et al., 2023).

These improvements make computationally intensive analyses feasible, including large ensemble simulations and parameter sensitivity studies. For example, large parameter perturbation experiments with thousands of simulations across 211 parameters with CLM5 become tractable due to reduced spin-up time (Kennedy et al., 2025). SASU reduced the spin-up time of CLM5 to approximately 190 years, dramatically lowering the computational burden for each simulation and making large ensemble analyses much more tractable. In addition, this computational efficiency advanced applications such as DA and machine learning, which require repeated model evaluations (Reichstein et al., 2019; Raoult et al., 2025). By enabling efficient coupling with diverse observational data sets, SASU supports a new generation of data-informed modeling and improves predictions of terrestrial C dynamics under changing climate conditions (Luo and Schuur, 2020; Tao et al., 2020).

5.3 Traceability analysis of C cycle uncertainty among models

Another major application of the matrix approach is its ability to enable the traceability analysis of uncertainties within model ensembles. Despite decades of development, projections of the global land C sink still show large inter-model spread in IPCC Assessments (Luo et al., 2022). Traditional model intercomparison projects (e.g., CMIP6, MsTMIP, and TRENDY) typically describe uncertainty but lack explicit attribution of its sources. As model complexity increases, frameworks that can track how uncertainty propagates through model components are increasingly needed. The matrix approach addresses this by decomposing C dynamics into traceable components, making discrepancies both between models and observations and among models themselves traceable and diagnosable.

The first application was carried out in CABLE, where Xia et al. (2013) decomposed steady-state modeled ecosystem C storage capacity ($X_c(t)$) into ecosystem C input (e.g., NPP) and residence time (τ_E , i.e., $(A(t)K\xi(t))^{-1}B(t)$), and further traced τ_E into baseline residence time (τ_E') and environmental scalars (ξ). This framework was later extended to transient dynamics (Eq. (4)), decomposing C dynamics into storage capacity ($X_c(t)$) and storage potential ($X_p(t)$) (Luo et al., 2017), with $X_p(t)$ further linked to C chasing time ($\tau_{ch}(t)$, i.e., $(A(t)K\xi(t))^{-1}$) and net pool change ($X'(t)$). It has also extended models with vertically resolved soil processes (Huang et al., 2018b):

$$X(t) = \underbrace{(A(t)K\xi(t))^{-1}B(t)u(t)}_{X_c(t)} - \underbrace{(A(t)K\xi(t))^{-1}X'(t)}_{X_p(t)}. \quad (4)$$

The traceability framework has been widely applied in model inter-comparison projects. For example, Wei et al. (2022a) traced uncertainty in terrestrial C storage from CMIP5 to CMIP6, showing that uncertainty remains over 60% of the land surface and is largely driven by productivity-related processes (Wei and Xia, 2024). Tools such as TraceME further enable automated diagnostics of terrestrial C cycling in ESMs (Zhou et al., 2020).

Beyond model intercomparison, the framework has been applied to quantify process contributions. For example, when applied to the cohort-based DGVM LPJ-GUESS across 13 climate-forcing scenarios, the framework attributed 49%, 17%, and 33% of the uncertainty in modeled global C uptake to NPP, vegetation dynamics turnover, and soil decomposition rates, respectively (Ahlström et al., 2015). It has also been extended to vegetation demographic model (VDM) BiomeE to investigate successional C dynamics in a subtropical evergreen broadleaf forest. Furthermore, Cui et al. (2019) decomposed GPP within the traceability framework into a loop of C-accumulation processes and associated vegetation functional properties based on 15 terrestrial biosphere models (TBMs). With regard to nutrient limitation, Xia et al. (2013) used CABLE model to compare outputs and traceable components between C-only and CN-coupled model configurations. Wei et al. (2022b) further used CABLE to evaluate the effects of N and P limitations on the terrestrial C cycle, while Bian and Xia (2023) extended traceability analysis to a CNP version, which decomposes C, N, and P stocks into traceable components.

Together, traceability analysis provides a unified framework to attribute C cycle uncertainty to specific structures, parameters, and forcing drivers (Fig. 5). By converting ensemble spread into contributions from well-defined traceable components, it transforms discrepancies in model behavior into quantitative, process-based diagnostics. This capability is essential for model development, for integrating emerging observational constraints, and ultimately for reducing uncertainty in land C-climate feedbacks across ESM ensembles.

6 Artificial intelligence facilitates knowledge discovery

6.1 Conventional paradigms in knowledge discovery

Data syntheses and process-based modeling are two fundamental approaches for advancing scientific discoveries in land C cycle research. Conventional site-level measurements and controlled experiments provide valuable insights into soil C dynamics under specified

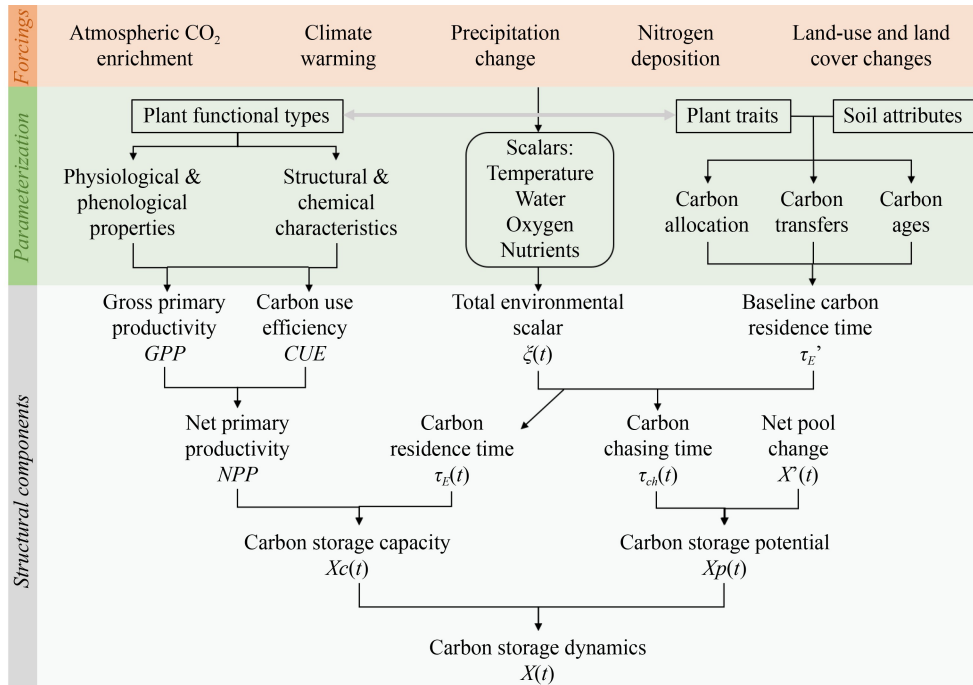


Fig. 5 Traceability framework of the terrestrial carbon cycle in land carbon cycle models, adapted from Xia et al. (2020).

environmental conditions. For example, data from well-designed experiments have challenged previous hypotheses regarding the relative importance of mineral protection versus substrate quality in preserving SOC (Hemingway et al., 2019). Similarly, long-term warming experiments have revealed temporally varying ecosystem responses in forest systems (Melillo et al., 2002). With the emergence of big data of environmental measurements, leveraging cross-site data and machine learning techniques has enabled the identification of global patterns in land ecosystem ecology, including soil C storage and turnover, plant productivity and biomass, and tree covers (Ma et al., 2017; Shi et al., 2020). However, most machine learning approaches primarily capture statistical relationships rather than causal mechanisms. Consequently, linking observed patterns to underlying processes remains challenging. Developing new research paradigms that better integrate field measured data with mechanistic understanding is therefore essential to improve our understanding of land ecosystem ecology across spatial and temporal scales.

Process-based models provide a mechanistic framework to study the land ecosystem ecology and underlying processes. By translating mechanistic understanding into mathematical formulations, these models encode our knowledge of biogeochemical processes and empirical relationships governing ecosystem dynamics. In addition to the external environmental variables that drive simulations, process-based models are defined by their model structure and parameterization. Model structures represent key system features such as C pool classifications, kinetics, and C transfer pathways, while parameter values quantify the magnitude and properties of specific processes within the

investigated system (Luo and Schuur, 2020; Tao et al., 2024). Although these models represent complex interactions and feedbacks within the terrestrial ecosystems and provide robust predictions under changing environmental conditions, substantial uncertainty persists across model predictions. Improving predictive reliability therefore requires better integration of observational data with mechanistic models to accurately reflect real-world system dynamics.

6.2 Data-model integration

As described above, integrating observational data with process-based models, commonly referred to as data assimilation, is essential for improving model prediction and extracting new scientific insights from observational data sets (Luo et al., 2016). DA represents a suite of approaches that integrate observations into model simulations to optimize model performance. Various techniques have been developed for this purpose, including Bayesian inference-based Markov Chain Monte Carlo (MCMC) methods (Xu et al., 2006) and evolutionary algorithms such as genetic algorithms. By adjusting model parameters or state variables, these approaches enable process-based models to better reproduce observed ecosystem dynamics. In soil C modeling, for example, models with different structures may initially produce divergent spatial patterns of SOC storage. However, these discrepancies can be largely reduced once their parameters are constrained by common observational data sets through data assimilation (Tao et al., 2024).

Beyond improving model performance, DA also provides insights into ecosystem processes. For example,

Liang et al. (2018) integrated time series data from a warming experiment into the Terrestrial ECOSystem (TECO) model using Bayesian data assimilation and revealed strong temporal shifts in parameters representing key ecosystem processes, such as light use efficiency and turnovers of different C pools. These parameter changes suggested gradual physiological acclimation of plants and soil microbes under prolonged warming, providing mechanistic insights into ecosystem responses to climate change. Despite these strengths, conventional DA approaches are computationally intensive and often limited in their ability to represent spatial and temporal heterogeneity in key ecosystem biogeochemical processes, constraining their scalability and predictive performance (Tao et al., 2020).

6.3 Empower AI with reasoning for knowledge discovery

Advances in artificial intelligence provide new opportunities to integrate large data sets with process-based models more efficiently, potentially leading to new scientific discoveries. Hybrid modeling approaches, also referred to as knowledge-guided machine learning (KGML), have been proposed to improve process understanding in Earth system science from big data (Reichstein et al., 2019; Cohrs et al., 2024; Jin et al., 2026). These approaches incorporate physical or knowledge-based constraints (i.e., reasoning), such as mass or energy conservation laws, empirical relationships, or differential equations into AI-based architectures such as neural networks (Karniadakis et al., 2021; Kraft et al., 2022; Fang and Gentine, 2024). By embedding such constraints into AI models, predictions are guided not only by observational data but also by established physical principles. More importantly, unlike conventional neuron-related parameters in a conventional neural network, hybrid approaches introduce latent variables and parameters that correspond to biophysical processes. This design enhances the mechanistic interpretability of AI-based prediction and enables AI to contribute to scientific discovery rather than purely statistical prediction.

However, current implementations remain limited. Significant challenges remain in empowering AI with reasoning capabilities. Most existing hybrid modeling has focused on relatively simple systems or a small set of constraints, such as a small number of empirical relationships in photosynthesis or simplified mass- or energy-conservation frameworks (Kraft et al., 2019; Fang and Gentine, 2024; ElGhawi et al., 2025). In more complex systems such as hydrological fluid dynamics, research has often focused on predicting state variable dynamics (e.g., velocity and pressure) while adhering to known physical principles, rather than identifying how key parameters governing system processes regulate system behaviors (Karniadakis et al., 2021). Increasing

evidence suggests that parameter dynamics may be more important than model structures for large-scale predictions (Tao et al., 2024). Consequently, a major challenge is to use AI to extract mechanistic insights from large observational data sets to understand spatial and temporal variability in biogeochemically interpretable parameters and establish quantitative relationships between these parameters and environmental drivers.

6.4 Emerging AI-process integration approaches

Recent developments highlight the potential of integrating AI with process-based modeling (AI-process integration). For example, Tao et al. (2020) developed the PROcess-guided deep learning and DATA-driven modeling (PRODA) framework to leverage large soil data sets for advancing our understanding of global SOC storage (Tao et al., 2023, 2024). By integrating deep learning, Bayesian DA, and mechanistic modeling, PRODA utilizes more than 57000 vertical SOC profiles to constrain key processes controlling SOC dynamics. As one of the earliest frameworks to combine large observational data sets with mechanistic models, PRODA significantly improved the predictive accuracy of SOC simulations, achieving performance comparable to purely data-driven machine learning approaches (Tao et al., 2020; Tao and Luo, 2024). Moreover, PRODA-based analyses revealed the relative importance of key components in the soil C cycle and highlighted microbial C use efficiency as a dominant control on global SOC storage and its spatial variation, exceeding the influence of other processes such as plant C input, decomposition, and vertical transport (Tao et al., 2023). The PRODA approach is one of the first-of-its-kind methods that bridges big data with process-based models to uncover new insights into the global soil C cycle and has proven to be instrumental in reducing the large inter-model simulation uncertainty that has long plagued accurate global C budget assessments. These results demonstrate the power of data-model integration in constraining uncertainty and advancing the mechanistic understanding of the global soil C cycle. Nevertheless, the Bayesian DA embedded within PRODA is computationally intensive, limiting its scalability for large-scale applications and real-time prediction.

The recently developed Biogeochemistry-Informed Neural Network (BINN) (Fan et al., 2025; Xu et al., 2025) offers a promising alternative to address these limitations. In this framework, a fully vectorized process-based soil C cycle model, derived from the soil component of the Community Land Model version 5 (CLM5) and comprising 70 partial differential equations, is embedded directly within a neural network structure (Xu et al., 2025). This design enables efficient optimization of large-scale SOC simulations while simultaneously retrieving spatially explicit parameters

governing key processes, including temperature sensitivity of respiration, C transformation rates, and vertical transport.

Beyond improving model performance, BINN offers several key advantages. First, it maintains strong biogeochemical interpretability by explicitly linking model parameters to underlying processes, enabling mechanistic insights from large data sets. Second, its end-to-end integration of neural networks, vectorized process-based models, and large observational data sets enhances computational efficiency, achieving more than 50-fold speedup compared to PRODA. Third, BINN flexibly incorporates diverse data sets across multiple observation sites, enabling multi-source data constraints during model optimization. Finally, by introducing a Kolmogorov-Arnold network (KAN) (Fan et al., 2025), BINN provides a fully interpretable AI architecture capable of revealing critical functional relationships between environmental drivers and biogeochemical parameters.

Looking ahead, integrating frameworks such as BINN with advanced land ecosystem models and expanding global observational data sets offers a pathway toward developing predictive and interpretable foundation models for terrestrial ecosystems (Fig. 6). Such approaches will not only advance our mechanistic understanding of C cycle processes but also support the development of science-based solutions for climate change mitigation.

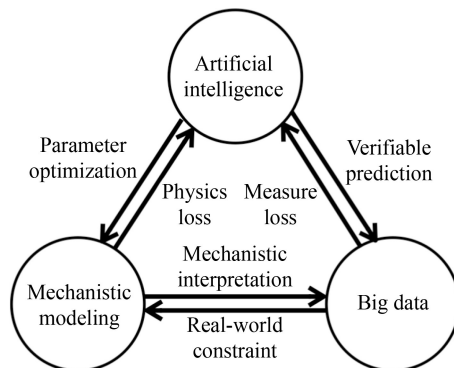


Fig. 6 Relationships of big data analytics, mechanistic modeling, and AI.

7 Conceptual, theoretical, and technical advances made by Ecolab

7.1 New concepts and terms developed by Ecolab

7.1.1 Acclimation and adaptation of ecosystem-scale processes

Ecolab was among the first to demonstrate that ecosystem-scale processes can acclimate and adapt to climate change. While acclimation of leaf photosynthesis and plant respiration has been well documented since

1970, whether ecosystem-level processes, such as gross primary production (GPP), soil respiration, and ecosystem respiration, exhibit similar responses remained unclear. Luo and his colleagues discovered that soil respiration acclimates to experimental warming in an ecosystem warming experiment in Oklahoma (Luo et al., 2001), sparking extensive discussion on the mechanisms and magnitude of this response. Subsequent studies expanded this concept. Niu et al. (2012) studied acclimation and adaptation of net ecosystem exchange of CO₂ to temperature change. Collaborative research was done on acclimation and adaptation of vegetation production (Huang et al., 2019a). Niu has continued studying in her own laboratory on acclimation and adaptation of ecosystem respiration (Chen et al., 2023) and its implications for earth system modeling (Niu et al., 2024).

7.1.2 Moving attractors of the land carbon cycle

Ecolab has advanced the concept of “moving attractor” to describe a ubiquitous phenomenon in the natural world that C state variables, such as plant and soil pools, always change in a direction toward a trajectory when a terrestrial ecosystem is at a time without suffering disturbances (Luo, 2024). The trajectory could be well defined at a given location with its prevailing climate, edaphic and biological conditions. After disturbances, C state variables move back toward the trajectory. This concept is adopted from applied mathematics for studying nonautonomous systems (Rasmussen et al., 2016; Wang, 2024). State variables in a nonautonomous system will be pulled back toward some trajectories (i.e., moving attractor or pullback attractor) when the system properties satisfy the condition for exponential stability (Rasmussen et al., 2016). Recognizing the moving attractor as a ubiquitous phenomenon in terrestrial biogeochemistry helps understand dynamic disequilibrium and predictability of land carbon cycle.

7.1.3 Donor pool-dominated control of carbon transfer among compartments

Ecolab has established solid empirical evidence that C transfer among ecosystem compartments is predominantly controlled by donor rather than recipient pools from observed macroscopic patterns. Donor pool-dominated C transfer is phenomenally obvious for litterfall from donor to recipient pools and documented in almost all studies of litter and soil organic matter decomposition (Xu et al., 2006; Zhang et al., 2008; Luo and Weng, 2011; Schädel et al., 2014; Cai et al., 2018). This concept is at odd with intuitive views that emphasize the regulation by receiving pools, such as microbial regulation of litter and SOC decomposition. While microbes likely regulate litter and SOC decomposition,

this concept offers strong constraints on model development and theoretical analysis.

7.2 New theoretical frameworks

7.2.1 Progressive nitrogen limitation

Understanding how N availability regulates terrestrial C sequestration is crucial for predicting future global terrestrial C sequestration. Luo led a group of international experts and developed a conceptual framework of progressive N limitation (PNL) for studying the interactions between C and N in terrestrial ecosystems in response to rising atmospheric CO₂ concentration (Hungate et al., 2003; Luo et al., 2004). Luo organized a special feature with eight case studies of PNL in various ecosystems, published in *Ecology*, including his own synthesis study (Luo et al., 2006). In addition, Ecolab studied how C and N interact under global change in dozens of publications (e.g., Liao et al., 2008; Li et al., 2012). Moreover, the PNL framework has been used to study long-term regulations of C cycle dynamics by N availability by many scientists in the research community (e.g., Mason et al., 2022; Bassett et al., 2026).

7.2.2 Dynamic disequilibrium of the land carbon cycle

Luo and Weng (2011) proposed the dynamic disequilibrium framework to study system behaviors of the land C cycle in response to global change. How ecosystem processes work together to determine system behaviors of C cycle has not been carefully studied, especially its transient dynamics under global change. Luo and Weng (2011), for the first time, proposed the theoretical framework, dynamic disequilibrium of the C cycle, which recognizes internal ecosystem processes that drive the C cycle toward equilibrium and external forces that create disequilibrium. Dynamic disequilibrium can be quantified by three parameters: C input, residence time, and C storage potential (Luo et al., 2017) and offers a theoretical foundation to precisely pinpoint sources of model uncertainty via traceability analysis (Hou et al., 2023).

7.2.3 Transient dynamics of the land carbon cycle

Olson (1963) is probably among the first to examine organic matter storage in forest floors from a system perspective. His analysis approximated steady-state storage of organic matter as a balance of litter producers and decomposers for different forest types. Since then, not much theoretical study has been done to understand the system behavior of the land carbon cycle. Luo et al. (2017) developed a framework for understanding transient dynamics of terrestrial C storage, which is

determined by three parameters: C input, residence time, and C storage potential. The first two parameters determine the C storage capacity, the maximum amount of C that an ecosystem can store at the given environmental condition at a point of time. As terrestrial carbon sequestration or loss occurs only at transient states, this study on transient dynamics of land carbon cycle offers a theoretical framework for quantifying carbon sequestration.

7.3 New techniques created by Ecolab

Ecolab has developed a variety of new techniques to facilitate research in ecosystem ecology. As described in Section 5, Ecolab developed the matrix approach to unify land biogeochemical cycle models, including carbon, nitrogen and phosphorus models. The matrix approach also offers new methods, such as traceability analysis, to underpin sources of model uncertainty. Section 6 highlighted the development of PRODA and BINN, two artificial intelligence (AI) methods for scientific discovery from process-based modeling and big data analysis. In addition, Ecolab developed a Terrestrial Ecosystem (TECO) model. TECO has been widely used to explore ecosystem C and N dynamics in response to climate change (Weng and Luo, 2008) with different versions for modeling ecosystem responses (including CH₄) to warming and elevated CO₂ in peatlands (Ma et al., 2017) and altered precipitation in drylands (Hou et al., 2021). Xia's group at East China Normal University has developed a TECO-CNP version with data assimilation (Wan et al., 2025). Moreover, Ecolab has developed an Ecological Platform for Assimilation of Data (EcoPAD) as a platform for data assimilation and ecological forecasting (Huang et al., 2019b). EcoPAD is a web-based software system that automates data transfer and processing from sensor networks to ecological forecasting through data management, model simulation, data assimilation, forecasting, and visualization. It facilitates interactive data–model integration from which the model is recursively improved through updated data while data are systematically refined under the guidance of model. EcoPAD was implemented at a peatland global change experiment to realize an ecological forecast from 2016 to 2023.

8 Summary and future research

Over the past several decades, Luo EcoLab has advanced ecosystem ecology through innovative methods across six major thematic areas: experimental studies, meta-analysis, data assimilation, matrix modeling, artificial intelligence, and theoretical frameworks. This review synthesizes their impact on understanding terrestrial ecosystem responses to global change. A central

conclusion emerging from this synthesis is that ecosystem responses to global change are highly context-dependent and regulated by the interactions among climate conditions, nutrient availability, and microbial processes. Field experiments provide critical mechanistic insights but remain scale-limited, while meta-analyses reveal generalizable patterns across ecosystems. Data assimilation integrates observations with process-based models to reduce uncertainty and improve predictive accuracy across spatial and temporal scales. The matrix modeling approach unifies C cycle models into a shared mathematical framework, boosting computational efficiency and enabling traceability analysis. Meanwhile, AI and hybrid models fuse large, heterogeneous data sets with mechanistic principles, accelerating knowledge discovery and improving forecast accuracy.

In addition to methodological advances, EcoLab has contributed key theoretical frameworks—such as progressive N limitation and dynamic disequilibrium—that provide a conceptual foundation for interpreting ecosystem dynamics under global change. These frameworks, together with newly developed tools such as PRODA and BINN, illustrate the power of combining theory, data, and computation. Future research should prioritize multi-source data integration, advanced modeling techniques, and AI-driven approaches to better capture ecosystem complexity and heterogeneity. Key focuses should include improving representations of nutrient constraints, microbial processes, and transient ecosystem dynamics in Earth system models. Strengthening the linkage between empirical observations and model development will be essential for reducing uncertainty in projections of C–climate feedbacks. Overall, this interdisciplinary framework represents a significant step forward in ecosystem ecology. It not only enhances our understanding of terrestrial C cycling but also provides critical tools and insights for addressing global challenges related to climate change, C management, and ecosystem sustainability.

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Competing interests The authors declare that they have no competing interests.

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