

6

Frontiers of Ecosystem Modeling and Large-Scale Experiments

Lifen Jiang, Jiang Jiang, Junyi Liang, Kevin R. Wilcox, Scott L. Collins,
Alan K. Knapp, William T. Pockman, Melinda D. Smith, and Yiqi Luo

CONTENTS

6.1	Introduction.....	138
6.2	Experiment–Model Integration: Needs, History, and Current Status	138
6.2.1	Experiment–Model Integration with Data from Global Change Experiments and Observational Networks.....	143
6.2.2	Experiment–Model Integration: A Case Study with the SPRUCE Project	145
6.2.2.1	Infrastructure Challenges in the SPRUCE Experiment.....	145
6.2.2.2	Informing Models Using the SPRUCE Experiment.....	147
6.2.2.3	Toward an Interactive Experiment–Model Approach.....	148
6.2.3	Experiment–Model Integration: A Case Study with EDGE Project	149
6.2.3.1	Coordinated Experiments across Space in the EDGE Project	150
6.2.3.2	Integrating Experimental Findings and Process- Based Models.....	151
6.3	Challenges and Strategies to Promote Integrated Experiment– Model Approaches.....	153
6.3.1	Data Set Development.....	153
6.3.2	Development of High-Fidelity Emulators and Traceability Analysis.....	154
6.3.3	Infrastructure Development	154
6.3.4	Communications between Experimentalists and Modelers.....	155
6.4	Conclusions.....	155
	References.....	156

6.1 Introduction

Observational studies, ecological experiments, and modeling are the three foundational approaches in ecological research. With increasing data availability from ecological observations and experiments, data–model integration becomes a critical tool to reduce model uncertainty and gain more reliable predictions of future ecosystem dynamics. In this chapter, we review the need, history, and current status of data–model integration to improve model simulations. Data from long-term manipulative experiments (e.g., free-air CO₂ enrichment experiments), observation networks of eddy covariance measurements (e.g., FLUXNET), and global databases (e.g., IGBP-DIS soil C database) have been successfully incorporated into ecosystem or global biogeochemical models to improve model projections. We also take two ongoing projects, Spruce and Peatland Responses Under Climatic and Environmental Change Experiment (SPRUCES) and Extreme Drought in Grasslands Experiment (EDGE), as examples to illustrate how experiment–model integration approaches are designed to achieve different research goals. In SPRUCES, the operational forecasting system is developed to assimilate data streams in real time to predict ecosystem responses to two global change factors, warming and elevated CO₂, whereas in EDGE, the application of data assimilation is designed to disentangle the role of environmental context versus ecosystem attributes in response to drought and eventually to scale findings obtained at distributed sites to regional scales. Finally, we review the challenges in data–model integration and propose a few strategies to move forward.

6.2 Experiment–Model Integration: Needs, History, and Current Status

In recent decades, tremendous efforts have been made to improve the predictability of ecosystem states and processes using three independent approaches: carefully designed long-term observational studies, ecological experimentation, and process-based modeling. The state of this knowledge is becoming increasingly important in light of global climate change. Ecological experiments, including in situ observations, have been conducted at many individual sites globally, and through these, we have obtained large amounts of observational and experimental data. Manipulative experiments, by creating novel conditions of projected climate, have improved our understanding of how ecosystems respond to climate change. While site-based experiments are still an important way to explore ecological patterns and underlying mechanisms, coordinated distributed experiments have become

an emerging tool to test hypotheses at the global scale (Fraser et al. 2012). More and more networks and cross-site studies at regional and global scales are generating huge amounts of data on daily or annual time scales such as FLUXNET, LTER Network, Nutrient Network, Drought-Net, NGEA-Arctic, NGEA-Tropics, and the National Ecological Observatory Network (NEON). Ecological research is now in a data-rich era (Luo et al. 2011b), and a major challenge is to know how to use those data in an efficient and appropriate manner to understand the ecological pattern and process and, based on that understanding, to forecast how ecosystems will change under global environmental change.

Empirical data from observational and experimental studies are useful in exploring general patterns of ecosystem phenomena and studying underlying mechanisms. However, ecological observations and experiments have inherent limitations to predict future changes, such as (1) difficulties in observing or measuring certain critical variables (e.g., turnover of different nutrient or carbon pools in soils), (2) large costs of conducting observations and manipulations at high temporal and spatial resolutions, (3) expense associated with conducting experiments over a time period long enough to detect changes in slow processes (Luo et al. 2011a), and (4) logistical constraints when conducting experiments across broad spatial scales; many difficulties remain for using empirical data to assess the impacts caused by changes in environmental conditions at multiple spatial and temporal scales. In addition, observational data and manipulative experiments with certain treatments alone lack power to forecast future dynamics of ecosystems in response to global change, which is challenging because we now live in a world that is undergoing rapid environmental change and highly altered disturbance regimes (Clark et al. 2001, Luo et al. 2011a,b, Niu et al. 2014).

Ecological models, particularly process-based models, can supplement limitations inherent in observations and experiments (Luo et al. 2011b). Process-based models have advanced quickly in recent years, which can partly be attributed to the dramatic increase of computational capability. Global models of the terrestrial carbon (C) cycle, developed about two decades ago, have been widely used to predict changes in terrestrial C storage under increasing atmospheric CO₂ concentration and climate change (IPCC 2013). Models have become increasingly complex due to the need for incorporating additional ecosystem processes, such as multiple vertical soil layers in the Community Land Model, CLM4.5 (Koven et al. 2013) and dynamic vegetation model (e.g., Sitch et al. 2003). However, with more processes added to models, models are more complex and generate larger uncertainties in their projections of terrestrial carbon storage and uptake, thus poorly fitting observations as shown in a number of Model Intercomparison Projects (MIP, Friedlingstein et al. 2006, Jones et al. 2013, Todd-Brown et al. 2013, 2014, Carvalhais et al. 2014, Jiang et al. 2015, Tian et al. 2015). On one hand, models need to include critical processes that predict future dynamics correctly; on the other hand,

models should lower their uncertainty in predictions. The large uncertainties associated with projections among different models as well as between models and observations strongly limit their usefulness for informing policy makers. This makes experiment–model integration improve model behaviors and forecasting an urgent task (Clark et al. 2001, Luo et al. 2011a,b). The research community is still struggling to improve predictability of models (Luo et al. 2016). Informed by empirical data, models can obtain more reliable projections (Niu et al. 2014).

Empirical data can help model development and improvement through a few pathways: providing mechanistic understanding behind ecosystem processes (e.g., photosynthesis and litter decomposition), generalizing patterns (e.g., vegetation distributions along temperature and precipitation gradients), identifying ranges and patterns of key model parameters, and constraining models. In practice, experiment–model integration can improve model performance by evaluating the goodness-of-fit of models using data (i.e., benchmarking, Luo et al. 2012, Walker et al. 2014), model parameterization with data, assimilating multiple streams of data to constrain models (Figure 6.1, Luo et al. 2011b, Niu et al. 2014), and representing unresolved processes with new algorithms supported by data (Williams et al. 2009).

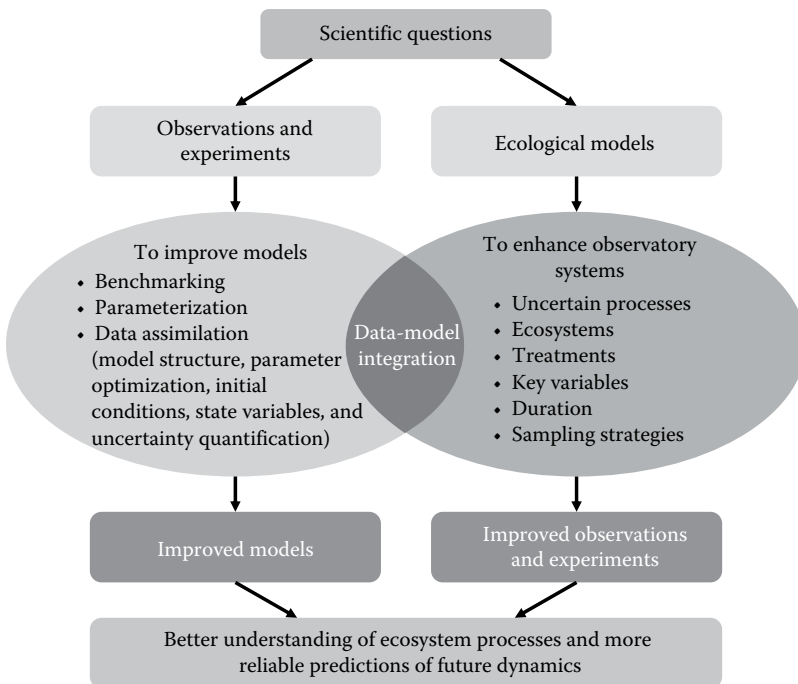


FIGURE 6.1

Conceptual flow of ecological research via experiment–model integration.

Modeling studies, on the other hand, can guide observations and experiments (e.g., Wang et al. 2009, Keenan et al. 2012). Modeling results may inform observational and experimental studies about the most uncertain processes that experiments should be conducted to explore, where or what ecosystems need more research, what treatments need to be considered, what measurements should be added (i.e., key variables needed to improve modeling), how long a manipulative experiment should last, and appropriate sampling strategies such as sampling frequency and spatial resolution for sampling (Figure 6.1).

Observational and experimental data have often been used for evaluating process-based models since the early stages of their development (e.g., Parton et al. 1987, 1993, Pacala et al. 1993, Luo et al. 2012). It is still common practice for modelers to tune their models to match specific data or reflect general patterns. However, multiple factors could result in bias between model simulations and data, and it becomes frustrating to tune models if a model has lots of interacting parameters. Experiment–model integration via rigorous statistical methods such as the Bayesian approaches provides a new way to enable simultaneous analysis of diverse sources of data to train a process-based model (Ogle 2009). Data assimilation is such a cyber-enabled process, which incorporates data into models to determine initial values and state variables, estimate model parameters (Richardson et al. 2010), and evaluate alternative model structures (Figure 6.1; Keenan et al. 2012, Liang et al. 2015b). As a result, data assimilation can substantially improve model simulations and gain more reliable predictions for future ecosystem dynamics (Raupach et al. 2005, Williams et al. 2005, 2009, Luo et al. 2011b, Peng et al. 2011, Niu et al. 2014). Indeed, data assimilation is recognized as a top priority for near-term modeling research to reduce systematic biases in modeling soil carbon dynamics by Earth system models, making data assimilation an essential tool in ecological research in a data-rich era (Luo et al. 2016). Also, data assimilation allows quantification of uncertainties stemming from data, model structures, parameters, boundary conditions, and statistical method selection (Luo et al. 2003, 2011b, Weng and Luo 2011, Dietze et al. 2013, LeBauer et al. 2013).

While data assimilation has been applied in biogeochemical cycles for a relatively short period, it has long been used in weather forecasts since the 1950s when the advances in computational power allowed data assimilation to be done within a reasonable time frame (LeBauer et al. 2013, Niu et al. 2014). The application of data assimilation in process-based models has been largely motivated by the need for ecological forecasting to inform decision-making processes toward better management of natural resources in a world undergoing rapid global change (Clark et al. 2001, 2003, Luo et al. 2011a,b). Since 2000, the application of data assimilation in process-based models has incorporated a variety of sources of data. For example, data from manipulative experiments (Luo et al. 2011a, Shi et al. 2015b,c), particularly those Free-Air CO₂ Enrichment Experiments (FACE, Luo and Reynolds 1999,

Parton et al. 2007, Weng and Luo 2011, Walker et al. 2014, Medlyn et al. 2015, Norby et al. 2016, Xu et al. 2016), have been frequently assimilated to constrain model parameters and state variables to improve predictions; data contributed by the observational networks such as FLUXNET and AmeriFlux have been used to train ecosystem or land surface models (e.g., White et al. 2006, Williams et al. 2009, Wu et al. 2009, Zhang et al. 2010, Kuppel et al. 2012); compiled continental and global data sets of biomass and soil C content were found to be useful in improving models (Zhou and Luo 2008, Zhou et al. 2009, 2013, 2015, Hararuk and Luo 2014, Hararuk et al. 2014, 2015); soil incubation data were collected and used to evaluate model structures and responses of soil C decomposition to warming and the factors regulating soil C decomposition (Li et al. 2013, Schädel et al. 2013, Liang et al. 2015a, Xu et al. 2016).

Many data assimilation techniques have been employed to constrain models. Usually, model parameters are specified and set a priori according to knowledge of processes. Optimal solutions and uncertainty analyses are determined by searching and selecting within realistic ranges of the chosen parameter values. The applied optimization techniques include the adjoint method (White and Luo 2002), the Levenberg–Marquardt method in combination with quasi-Monte Carlo algorithm (Luo et al. 2003), genetic algorithms (Zhou and Luo 2008), Markov chain Monte Carlo (MCMC) with the Metropolis–Hastings algorithm (Xu et al. 2006, Zhou et al. 2010, Hararuk et al. 2015, Shi et al. 2016), conditional inversion (Wu et al. 2009), and the ensemble Kalman filter (Gao et al. 2011). These optimization techniques identify sets of parameters, which result in model output that best fits the data. One of the most important applications of data assimilation is addressing the initial condition problems. Traditionally, Earth system models usually use spin-up cycles with preindustrial forcing to determine the initial condition (i.e., steady state), which may overestimate terrestrial C pools (Wutzler and Reichstein 2007). By relaxing the steady-state assumption, data assimilation can significantly increase model efficiency and reduce normalized average error (Carvalhais et al. 2008, Williams et al. 2009).

However, applications of data assimilation, even at a regional or global scale, have mostly been conducted with simplified models that had a limited number of parameters to be constrained by data, typically from several to less than 20 parameters (e.g., Braswell et al. 2005, Williams et al. 2009, Zhou et al. 2009, 2012). Data assimilation with complex models containing thousands of parameters are not feasible until a breakthrough in semi-analytic spin-up of global land model (Xia et al. 2012) and traceability analysis of model structures (Xia et al. 2013). High-fidelity emulators that reproduce original complex models are often used to make data assimilation computationally feasible. By assimilating a global soil carbon data set into an emulator of the Community Land Model coupled with Carnegie-Ames-Stanford Approach biogeochemistry submodel (CLM-CASA) to optimize the parameters, Hararuk et al. (2014) were able to substantially improve soil carbon

simulations, increasing the correlation between model simulations and the observations from an R^2 of 0.27 before calibration of parameters to an R^2 of 0.41. Using the emulator of CLM-CASA and a combination of global soil carbon and soil microbial biomass data sets, model simulations after parameter optimization via data assimilation detected stronger soil carbon responses to climate change (Hararuk et al. 2015).

6.2.1 Experiment–Model Integration with Data from Global Change Experiments and Observational Networks

As mentioned earlier, traditionally, process-based models are usually validated by comparing model simulations with data from ecological observations or experiments. This validation, however, can be biased by limited availability of observations or experiments. Recently, large-scale benchmarking, which includes as many available observations and experiments as possible, has been proposed and developed to evaluate the performance of models by scoring models based on how well the models reproduce data (Luo et al. 2012). While this approach provides comprehensive evaluations of model performance, benchmarking itself rarely leads to model improvement because reasons for model performance are not typically identified (Medlyn et al. 2015).

Over the past decades, an increasing number of global change experiments have been initiated due to the need for information concerning ecosystem responses to a rapidly changing climate. Data from these global change experiments are valuable in helping models identify ecosystem responses to long-term climate change. Enormous efforts have been made to elucidate ecosystem dynamics in response to elevated CO_2 and increased temperature. For example, a recent FACE Model-Data Synthesis (FACE-MDS) project was sponsored to assess terrestrial models by using observational data collected in two temperate forest FACE experiments in the United States (Walker et al. 2014, Medlyn et al. 2015). In this project, 11 terrestrial models were evaluated by comparing with data from the Oak Ridge National Laboratory FACE (ORNL FACE) and Duke FACE sites. In addition to comparing model simulations with direct measurements, they also focused on assumptions resulting in disagreement among models (Medlyn et al. 2015). For example, the 11 terrestrial models generally reproduced the responses of NPP to CO_2 enrichment in the early years of the experiment, but they were not able to predict NPP responses in later years. By further decomposing NPP to nitrogen (N) use efficiency (NUE) and N uptake, they found that even if correctly estimating the response of NPP to CO_2 enrichment in the early years, models achieved that by overestimating NUE response but underestimating the response of N uptake (Zaehle et al. 2014, Medlyn et al. 2015).

In addition to NPP, other processes and ecosystem properties, such as stomatal conductance, water use efficiency, NPP allocation, N cycling, stoichiometry, and leaf mass per area (LMA), were also studied in the FACE-MDS

project (De Kauwe et al. 2013, 2014, Walker et al. 2014, Zaehle et al. 2014, Medlyn et al. 2015). This project has identified specific aspects for improving model performance and experimental design. The identified aspects for model improvement include stomatal conductance, NPP allocation, LMA, plant stoichiometry, and priming (Medlyn et al. 2015). It is suggested that models should employ a proportional relationship between the ratio of photosynthetic C assimilation to stomatal conductance and atmospheric CO₂ concentration (De Kauwe et al. 2013, Medlyn et al. 2015). Dependence of NPP allocation to plant tissues (e.g., leaves, wood, and fine roots) on resource availability is necessary to match observations (De Kauwe et al. 2014, Medlyn et al. 2015). Moreover, priming of soil N release seems important to reproduce N transfer from soil organic matter to vegetation (Zaehle et al. 2014, Medlyn et al. 2015). In addition to these mechanisms on which clear suggestions have been proposed, there are some others on which new theories are needed. For example, LMA is usually set constant in models, leading to a stronger response of leaf area index (LAI)—a key property that determines photosynthetic C assimilation in both models and reality—to CO₂ enrichment in models than identified in observations (Medlyn et al. 2015). Additionally, new theory of flexibility of plant stoichiometry is needed to better simulate the balance of N supply and demand (Zaehle et al. 2014, Medlyn et al. 2015).

Aspects of improvement of experimental design have also been identified based on findings in the FACE-MDS project. First, more empirical evidence is needed to determine the relative importance of electron transport and Rubisco limitations to photosynthetic C assimilation on the leaf and canopy scales (Medlyn et al. 2015). Additionally, observations of sensitivity of transpiration to stomatal conductance, precipitation interception by canopy, the interactive effect of drought, turnover of plant tissues, and ecosystem's N losses (e.g., leaching) are also needed to provide a scientific basis for model assumptions. However, one potential limitation of the FACE-MDS project is that only two FACE experiments, both located in temperate regions, are involved. Extensive meta-analyses (e.g., Liang et al. 2015b) and experiments in other regions, such as boreal and tropical systems, are necessary to help evaluate and improve the performance of Earth system models on the global scale (Norby et al. 2016).

In addition to site-level manipulative experiments, observations at larger scales are valuable resources that can be used to improve model performance. One of the successful data set networks that has been assimilated to improve terrestrial model performance is the FLUXNET observations (Williams et al. 2009). FLUXNET is an international observation network based on the eddy covariance (EC) technique, which can provide continuous measurements of land surface–atmosphere exchanges of C, water, and energy (Verma 1990). There are many regional EC networks across the globe, such as AmeriFlux (<http://ameriflux.ornl.gov/>), ChinaFlux (<http://www.chinaflux.org/>), JapanFlux (<http://www.japanflux.org/>), and Swiss Fluxnet

(<http://www.swissfluxnet.ch/>). Each of the regional networks consists of a number of EC observation sites. These regional networks then form the global network FLUXNET (<http://fluxnet.ornl.gov/>), which provides rich collection of information concerning the exchanges of C, water, and energy between land surface and the atmosphere across spatial and temporal scales. FLUXNET observations have been widely used in data assimilation techniques to improve model performance. For example, Zhu and Zhuang (2015) assimilated five sites of AmeriFlux carbon flux data to Terrestrial Ecosystem Model (TEM) to reduce uncertainty of 10 posterior parameters and improve simulations of regional carbon dynamics.

Those global change experiments and observational networks are usually designed for examining patterns of ecosystem responses to environmental changes and underlying mechanisms. The resulting data sets are then found useful for model improvements. Recently, a number of projects have been designed and initiated to conduct both experiment and data–model integration for forecasting or upscaling site-level knowledge to a regional scale. In the following text, we take two ongoing projects, SPRUCE and EDGE, as examples to illustrate how data assimilation is designed to achieve different research goals.

6.2.2 Experiment–Model Integration: A Case Study with the SPRUCE Project

SPRUCE is a climate change manipulative experiment supported by Terrestrial Ecosystem Science Scientific Focus Area of ORNL's Climate Change Program. The experiment aimed toward integration of experiments with ecosystem modeling, data assimilation, and model structure evaluation to yield reliable model projections. Although the SPRUCE experiment only initiated the Deep Peatland Heating treatments in June of 2014 and the whole-ecosystem warming and elevated CO₂ treatments will not start until June 2016, the integrated model-experiment approach based on pretreatment data sets and modeling activities have promoted an interactive and mutually beneficial engagement between modelers and experimentalists to advance predictions from experiments and models.

6.2.2.1 Infrastructure Challenges in the SPRUCE Experiment

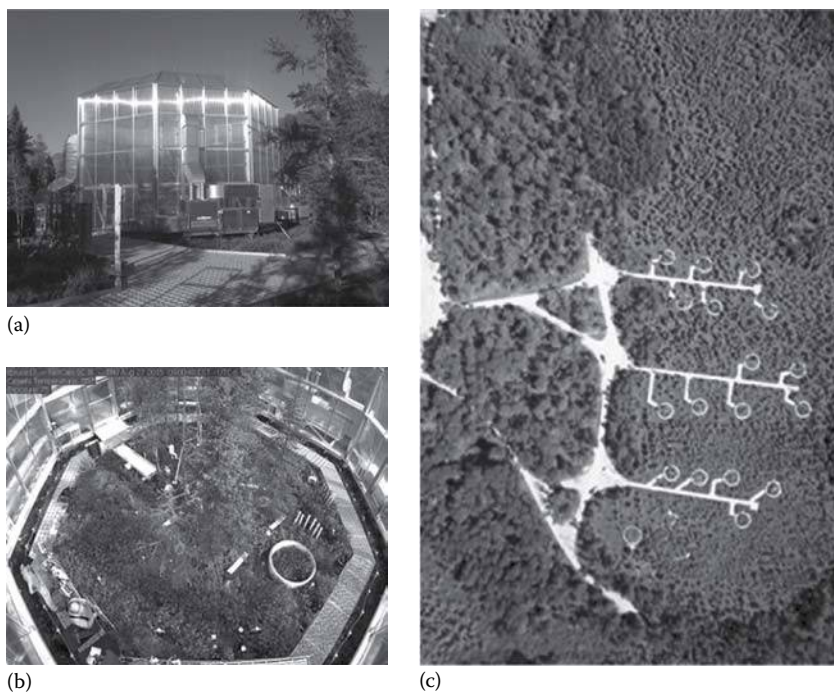
The SPRUCE experiment is being operated as the first whole-ecosystem, forest-scale experiment to increase temperature and CO₂ concentrations from deep soil to the tops of tree canopies. This decade-long experiment is conducted in a weakly ombrotrophic peatland with a perched water table that has little regional groundwater influence and is located in northern Minnesota in the USDA Forest Service Marcell Experimental Forest (MEF). The 8.1 ha experimental site (S1-Bog) is dominated by *Picea mariana* (black spruce), regenerated from strip cuts in 1969 and 1974. Located at the southern

margin of the boreal peatland, this ecosystem is anticipated to be approaching its tipping point with high vulnerability in response to climate change. Shifts of plant communities at the southern margin of boreal ecosystems under climate change is not fully understood, so large-scale long-term experiments like SPRUCE are needed to improve mechanistic representation of unresolved processes in understudied ecosystems in Earth system models.

To achieve the overall goal of assessing ecosystem-level biological responses of vulnerable, high carbon terrestrial ecosystems to climate change, the SPRUCE experiment faces many infrastructure challenges including, but not limiting to, plot facilities, sensors and instruments, data acquisition and control system, automated data monitoring system, data management, model–data integration, and synthesis of model outputs. In this section, we do not attempt to describe all the research infrastructure challenges facing large-scale experiments like SPRUCE, but we highlight those key elements necessary for model–data integration.

Long-term monitoring of ecosystem dynamics is an important data source for data–model integration. But more powerful manipulative ecosystem experiments are needed to distinguish future climate change impacts from those inherent responses to natural variability. Climate change–caused warming scenarios predicted by the Intergovernmental Panel on Climate Change (IPCC 2013) are much higher than observed variation in mean annual temperatures ($\pm 2^\circ\text{C}$) under current climate. The SPRUCE experiment provides a platform to understand physiological and biogeochemical processes under future climate through a combination of multiple levels of warming up to $+9^\circ\text{C}$ at ambient or elevated CO_2 levels. Air warming is achieved with heating infrastructures enclosed in 10 plots of 12 m diameter by 8 m high open-top enclosures (Figure 6.2). The open-top enclosures can keep warming air around the enclosed plots by limiting air turnover, while still allowing natural precipitation to fall on experimental plots. The design also enables maintenance of high concentration of CO_2 (800–900 ppm) in the elevated CO_2 treatment. One unprecedented data set that the SPRUCE experiment can provide for modeling activities is the Deep Peat Heating (DPH, -2 m) with belowground temperatures being consistent with future aboveground warming scenarios (Hanson et al. 2011). Belowground deep warming evaluates responses of deep peat C stocks, microbial communities, and biogeochemical cycling processes, which can be used for evaluating model projections.

The SPRUCE program also provides data from real-time automated monitoring systems, which advance data–model integration approach in an interactive fashion. All data collected from sensors or instruments are recorded by dataloggers and then transferred to a data storage server every 30 min. Data are then published via a web server and used for remote monitoring and control (Krassovski et al. 2015). The standardized data streams are then immediately available to feed and inform models.

**FIGURE 6.2**

(See color insert.) View of SPRUCE experiment infrastructure with (a) exterior view of experimental chamber, (b) interior view of experimental chamber, and (c) aerial view of the S1 Bog site. (Pictures a and c are Oak Ridge National Laboratory Images from: <http://mnspruce.ornl.gov>. Image b is a PHENOCAM network SPRUCE image from <http://phenocam.sr.unh.edu/webcam/gallery/>.)

6.2.2.2 Informing Models Using the SPRUCE Experiment

Current Earth system models predict high variability of terrestrial carbon uptake with uncertainty in the direction and magnitude of global carbon cycling under future climate change (Friedlingstein et al. 2006, Arora et al. 2013). Northern peatlands contain 200–400 Pg of carbon, about 30% of that contained in the global soil carbon pool. These peat carbon pools are sensitive to climate change due to their tight dependence on hydrology and temperature (Frolking et al. 2013). In spite of the importance of peat carbon, the dynamics are still less represented in most Earth system models. Current models often change parameter values related to wetland and peatland regions assuming the same formulation as other regions (Luo et al. 2016), and therefore underestimate peat carbon storage (Limpens et al. 2008).

Manipulative experiments are needed to improve the unresolved processes in terrestrial carbon cycle models to refine projections of the net

carbon balance of the northern peatlands in the face of a warming global environment. The SPRUCE experiment interacts with multiple modeling activities to improve the representation of terrestrial C processes required to reduce uncertainty in forecasting from ESMs. For example, the Community Land Model currently has poor representations of vegetated peatlands, where the carbon fluxes are strongly influenced by water table height. Future warming could drop the water table due to increased evapotranspiration, thus influencing the stability of carbon stocks. To improve the representations of peatland water tables, Shi et al. (2015a) modified CLM to include fully prognostic water table algorithms to improve projections of peatland responses to future climate change. The model was parameterized and evaluated against half-hourly measurements of daily water table levels for 3 years from the SPRUCE experiment. Those observations include pretreatment data sets and long-term peatland hydrology studies on the MEF, where the SPRUCE site located. To further quantify how warming may influence water table and carbon fluxes, however, we need data sets from manipulative experiments to validate models, and further refine related processes.

6.2.2.3 *Toward an Interactive Experiment–Model Approach*

With more realistic representations of ecosystem processes, models become more complex and more parameters are required to be constrained. Developing an operational forecasting system is an interactive way to integrate experiments and models to accomplish this. The forecasting system would assimilate various data streams into models so as to improve model predictions. Forecasting outcomes can provide feedback to experiments from which data sets are needed to further improve model predictions. In turn, new data sets can then be fed back into models further constraining and improving model predictions.

In the SPRUCE project, we are developing a data assimilation and operational ecological forecasting system called ECOlogical Platform for Assimilation of Data (ECOPAD). Pretreatment data sets from different field campaigns are compiled, including large-collar in situ CO₂ flux measurements across 4 years, aboveground NPP and carbon pool sizes from sampled vegetation, phenological data derived from PhenoCam imagery, and peat carbon from core samples. The data sets are then assimilated into the Terrestrial ECOsystem (TECO) model using a Markov chain Monte Carlo technique to constrain parameters. The TECO model is used because it simulates processes of canopy photosynthesis, plant growth, carbon transfer among compartments, and soil water dynamics. Unlike Earth system models, the TECO model is simple enough to overcome computational cost. With data assimilation, we can quantify how much uncertainty of forecasting could be reduced as more data become available. The relative contributions of external forcing versus model parameters to the uncertainty of

forecasting can also be estimated. The projections of carbon cycles will be compared to future data streams to refine model structure, update model parameters, generate new scientific questions, and test competing hypotheses. The new data sets are then assimilated to enable new projections. This flow of work should be done regularly and automated in an operational system such as ECOPAD.

Although researchers have collected enormous amounts of data to understand various ecosystem processes over past decades, a major challenge is to combine understanding of multiple processes together to form a complete picture of how ecosystems will respond as a whole. Usually, empirical data from observations and manipulative experiments are scattered among individual teams and a significant proportion of them is not published in a timely manner, or is not available to modelers even after published. In the SPRUCE experiment, while individual teams collect data to answer questions related to specific ecosystem processes, they also work as a large group to confront models with data. ORNL is developing and deploying data and information management, and integration capability required for the collection, storage, processing, discovery, access, and delivery of data, including experimental data and model outputs. These capabilities and systems are designed to facilitate uncertainty associated with characterization and quantification. The systems will also be developed for assimilation of available measurements, synthetic analysis of results, model forcing and boundary condition data sets, and model results. Such an information system facilitates data–model integration and provides accessibility to model output, benchmarking analysis, visualization, and synthesis activities.

6.2.3 Experiment–Model Integration: A Case Study with EDGE Project

Site-level studies (e.g., a temperature manipulative experiment in a forest or measurements made in a grassland across years with different precipitation) can provide excellent information concerning ecological responses to climate change on small spatial scales. However, substantial limitations exist when trying to scale up to form regional and global predictions. Indeed, we know much more about how climate drivers are likely to be altered at various spatial scales (Murphy 2000, Schoof et al. 2010) than how the resulting impacts on ecosystem processes will play out to affect ecosystem services.

There are a number of major challenges associated with extending field-based findings to larger spatial scales. Two major ones are (1) understanding the mechanisms driving ecosystem responses to alterations in environmental variables and (2) obtaining knowledge about how these mechanisms vary across ecosystems. These challenges lead to an important overarching question: what are the relative strengths of climatic context (e.g., wet versus dry systems) versus ecosystem attributes (e.g., types of plant community) in driving how sensitive an ecosystem will be to changes in climate? For example,

an arid system may have high sensitivity to drought because conditions are already dry and water is highly limiting. Yet on the other hand, xeric plant species may buffer primary production due to their having plant traits enabling growth even under stressful conditions. Indeed, empirical evidence has been shown for both increased sensitivity in drier systems (Huxman et al. 2004) and ecosystem attributes moderating responses to altered precipitation (Wilcox et al. 2015), yet methodological differences among studies obscure the relative strengths of these drivers in controlling ecosystem responses to climate change.

6.2.3.1 Coordinated Experiments across Space in the EDGE Project

EDGE is a multisite study being conducted in six grasslands spanning climate gradients but also varying in their ecosystem attributes (Figure 6.3). The approach of this experiment solves three major problems typically confronting single-site studies, meta-analyses, and data synthesis approaches

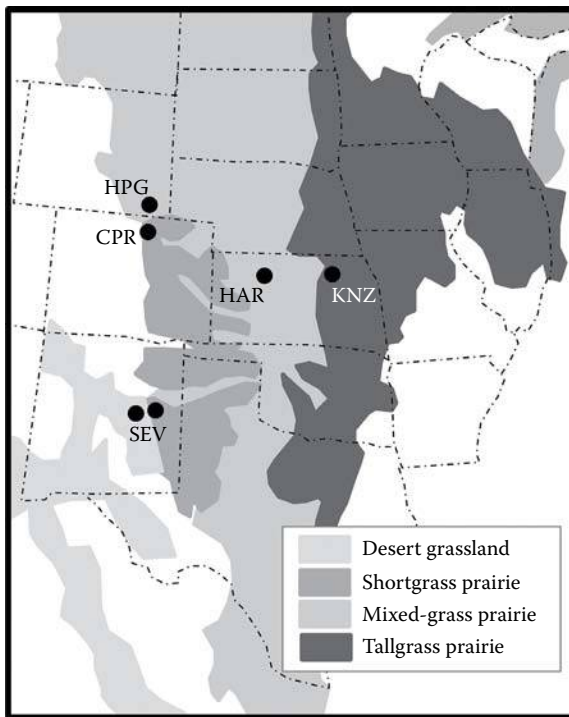


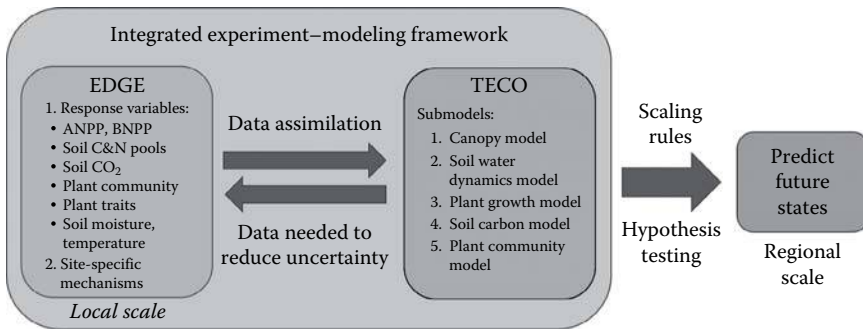
FIGURE 6.3

(See color insert.) Map of the Midwest United States showing locations of the six experimental sites of the EDGE project. SEV, Sevilleta National Wildlife Refuge, NM; CPR, Central Plains Experimental range; HPG, High Plains Grassland Research Center; HAR, Hays Agricultural Research Center; KNZ, Konza Prairie Biological Center.

to predict large-scale responses to climate change. First, consistent methodology among sites removes the uncertainty associated with meta-analyses that often compare experiments having different techniques for measuring ecosystem responses or implementing treatments; this allows for better detection of patterns of sensitivity across sites. For example, if a researcher has to compare results from two experiments, both simulating drought by removing 50% of ambient rainfall, but one study did this by removing rainfall from May to September and the other by removing rainfall from April to August, the researcher would not be able to know how much of the difference in responses was due to differential sensitivities of the systems and how much was due to the differences of drought timing. Second, the EDGE study is conducting extensive monitoring and sampling of ecosystem attributes at each site before and during the experiment. Meta-analyses or data syntheses usually get partial information from each single study. This provides mechanistic understanding into why sensitivity differs across ecosystems and tracks changes in ecosystem attributes as well as overall responses. Third, the EDGE experiment is designed to have three pairs of sites (Figure 6.3), with each pair existing along a precipitation gradient ranging from ~240 to 860 mm of mean annual rainfall and a temperature gradient ranging from 7.6°C to 13.3°C of mean annual temperature. Yet each pair represents two different plant community types existing within a particular climate envelope. For example, the two arid sites at SEV; both receive ~250 mm of precipitation on average and are quite close in space. However, one is a Chihuahuan Desert grassland dominated by *Bouteloua eriopoda* (black grama) while the other is more like the shortgrass steppe dominated by *Bouteloua gracilis* (blue grama). Comparison of differential responses between these two sites versus responses across the broad climate gradient will provide insight into how plant communities drive sensitivity of ecosystems to drought within the context of climate.

6.2.3.2 Integrating Experimental Findings and Process-Based Models

In EDGE, modelers and experimental ecologists are working in close collaboration to incorporate field data into an integrated experiment–modeling framework (Figure 6.4), where data are used to estimate parameters of the process-based model, TECO. In turn, this process identifies information gaps, for which additional sampling efforts can be conducted within the experiment. For example, some variables being measured in EDGE concerning C cycling processes are aboveground and belowground standing crop biomass, aboveground litter, soil respiration, and total soil C content. By mapping and comparing TECO output to these measured variables using a Markov chain Monte Carlo technique (Metropolis–Hastings algorithm; Hastings 1970), multiple model parameters are able to be estimated for each site. Additionally, model parameters not well constrained using the current level of data inform where additional sampling efforts should be applied.

**FIGURE 6.4**

Conceptual representation of the integrated experiment-modeling framework employed by EDGE to assess mechanisms behind differential ecosystem sensitivity to drought across grasslands spanning climatic gradients and having various ecosystem attributes. Data obtained from the multisite experiment are integrated into the process-based model, TECO, to identify scaling rules for model parameters. These, in turn, are incorporated into regional-scale projections that allow for broader testing of hypotheses related to future ecosystem status under altered climate regimes.

Once parameters are able to be properly estimated, they can then be linked with the climatic conditions across sites to provide insight into how ecosystem processes as represented by model parameters and climate should covary. Second, examination of parameter estimates in different sites, but within the same climate envelope, gives insight into how parameters should be assigned based on ecosystem attributes separate from climatic context. For example, despite both having mean annual precipitation close to 350 mm and mean annual temperature around 9°C, paired sites in northern Colorado and southern Wyoming have very different functional composition with one site being dominated by C₄ warm-season grasses and the other by C₃ cool-season grasses. These different functional groups have very different growth strategies and water use efficiencies, which will impact how these grasslands respond to alterations in rainfall. Variation of estimated parameters in these grasslands provides insight into how mechanisms driving ecosystem responses to drought may differ along with plant functional types and how model projections should be scaled across ecosystems varying in plant functional types. Using the information about how model parameters vary across space due to environmental context and ecosystem attributes allows for model projections to be scaled up from single-sites to the regional level. Once scaling rules are established and incorporated into process-based models, hypotheses are then able to be tested at larger spatial scales.

Both the design of the EDGE study and integration of experiment and process-based models are extremely important for this study's success. We suggest that, to provide much needed predictive power under altered climate regimes at regional scales, future studies examining ecosystem sensitivity to

environmental drivers should consider implementing consistent methodology across study sites at least when experimental sites exist within the same biome. Assimilating data across those regional sites would improve model performance upscaling from distributed experiments.

6.3 Challenges and Strategies to Promote Integrated Experiment–Model Approaches

Integrated experiment–model approaches will continue to serve a critical role for better understanding the natural world and more reliable predictions of future ecosystem states. Despite that experiment–model integration has the potential to significantly improve both model performance and experimental design, several challenges need to be addressed when conducting experiment–model integration. To move the experiment–model integration approach forward, some key actions need to be considered and stimulated.

6.3.1 Data Set Development

Incomplete use of empirical data in model parameterization is a major cause of model–model differences (Luo et al. 2016). More observational and experimental data are needed to constrain model parameters (Bonan 2008, Luo et al. 2015, 2016), potentially helping address equifinality, an issue that models yield similar outputs with different combinations of parameters (Williams et al. 2009). Therefore, it is necessary to evaluate whether model parameters can be well constrained by the available data. Different types of observations and experiments may be helpful to reduce equifinality. Including various types of observational and experimental data, instead of a single database, can lead to more accurate and efficient data assimilation.

An enormous amount of site-level ecological data has been generated over many decades, and ongoing projects and research networks will increasingly produce even more high-quality, high-resolution data. These data need to be synthesized, compiled, and often transformed before they can be used in model–data integration. To facilitate this process, it is vital that data are saved in a usable format, appropriately archived and well documented, and easily discoverable for use in synthesis and modeling.

Another challenge related to data set development is to fully address measurement uncertainty when documenting data set contents and protocols. It is critically important to identify data bias due to techniques and/or spatial-temporal distributions. Larger-scale data sets are essential to improve land surface models (Williams et al. 2009, Luo et al. 2016). A big challenge in compiling regional and global data sets is to harmonize data processing.

The schemes to process data should be documented clearly in the literature (Williams et al. 2009). Scaling site measurements to represent the whole grid is also problematic and the uncertainty related to scaling should be well specified. More well-designed experiments like EDGE could help to solve the scaling issue.

Moreover, new observations and experiments need to be designed to reveal mechanisms behind observed patterns and to discover some unresolved or missing processes. From the perspective of model improvements, future observational and experimental research should be focused on those model components whose predictability is poorly understood (Luo et al. 2015). These components may include ecosystem state transitions, changes in disturbance regimes, disturbance events and recovery trajectories, and ecosystem response functions.

6.3.2 Development of High-Fidelity Emulators and Traceability Analysis

Technical challenges of experiment–model integration impede the widespread use of models (LeBauer et al. 2013). Models are becoming more and more complex, such as land surface models in Earth system models. It is infeasible for the complex models to assimilate multiple data streams with traditional data assimilation techniques due to computational cost. High-fidelity emulators of complex models provide new ways to solve the problem. For a complex C model, an emulator is a simplified version of the model to describe the carbon flows and pools exactly as in simulations with the original model (Luo et al. 2016). For example, built upon the traceability framework proposed by Xia et al. (2013), Hararuk et al. (2014) developed an emulator of CLM-CASA, which enabled data assimilation with a global soil C data set. They first extracted the C cycle component of CLM-CASA into a set of C input–output equations that described C transfer among pools and then the set of equations was encoded into MATLAB® to perform data assimilation. The steady-state soil C produced by the MATLAB version matched closely to that simulated by the original CLM-CASA despite that the former used the semi-analytic spin-up approach developed by Xia et al. (2012).

As model complexity increases, traceability becomes more and more difficult. It is still a big challenge to explain differences among models in model intercomparisons (Friedlingstein et al. 2006, Jones et al. 2013, Luo et al. 2015, 2016). A clear traceability framework allows modelers to trace uncertainty back to each key component of a complex model (Xia et al. 2013, Ahlström et al. 2015) and thus lead to more practical strategies for model improvement.

6.3.3 Infrastructure Development

Both data processing and archiving require significant computing resources. The demand for computing resources will increase as more data become available for public access through repositories such as DataONE

(<https://www.dataone.org/>). The computational costs of data assimilation are already high and will become more so as data availability increases. The requirements for computational power to develop new data assimilation techniques might even be higher. In addition, we need to develop online tools to assimilate real-time data streams including model outputs and to visualize data assimilation for forecasting as illustrated by SPRUCE, so more researchers can easily use the online tools to employ data assimilation even though they do not have much technical training. The online tools for forecasting may also help policy makers and land managers to make decisions. Both computational costs and development of online tools require improvements of existing cyber infrastructure or building of new cyber infrastructure.

On the other hand, new experiments that simultaneously manipulate multiple global change factors are critically needed to determine how interactions among factors shape ecosystem responses to global change, to explore synergisms among variables and resolve complex processes, or to study highly sensitive ecosystems such as tundra and tropical forests (Seddon et al. 2016). Multifactor experiments are complicated to design and expensive to implement building and maintaining the required cyber infrastructure. Therefore, development of cyber infrastructure will be a key determinant for the success of experiment–model integration.

6.3.4 Communications between Experimentalists and Modelers

Due to the strengths and limitations of both models and experiments, the advance of experiment–model integration depends on the effectiveness of communication between experimentalists and modelers. Opportunities should be created and funded to facilitate interactions among these research communities to design useful and appropriate sampling regimes (also see Luo et al. 2011b) to provide useful parameters for models and for modelers to improve their models. This will not only maximize the efficiency of monetary investment into research but will also allow for rapid advancement and improvement of projections concerning future states of ecosystem services on a dynamic planet.

6.4 Conclusions

We are living in a world that is undergoing rapid environmental changes. Ecological research is now in a data-rich era, with massive amounts of accumulated data distributed globally and large volumes of incoming data produced by many ongoing research projects and networks. Fortunately, advances in computational capacity continue to develop at an unprecedented rate. However, our ability to predict future states still remains limited, as

indicated by large uncertainties in current model projections. Enhancing the accuracy of predictions of future ecosystem states under global change remains a challenge that must be resolved to better manage resources for sustainable development.

Ecological observations, experiments, and models remain the three foundational approaches for ecologists to tackling scientific problems. Field research, no matter how complex, only provides partial information about the system under study, whereas models, no matter how comprehensive, are always imperfect. To maximize gain from imperfect data and models, integrated experiment–model approaches are becoming a high priority. In the next a few decades, data–model integration to enhance observatory systems and to improve model projections will be critical to advance ecological understanding of dynamic systems. Closer collaborations between experimentalists and modelers will likely enhance data collection while new data assimilation techniques will improve model projections, resulting in better decisions for sustainable management of natural resources.

References

- Ahlström, A., J. Xia, A. Arneth, Y. Luo, and B. Smith. 2015. Importance of vegetation dynamics for future terrestrial carbon cycling. *Environmental Research Letters* **10**:054019.
- Arora, V. K., G. J. Boer, P. Friedlingstein, M. Eby, C. D. Jones, J. R. Christian, G. Bonan et al. 2013. Carbon–concentration and carbon–climate feedbacks in CMIP5 earth system models. *Journal of Climate* **26**:5289–5314.
- Bonan, G. B. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* **320**:1444–1449.
- Braswell, B. H., W. J. Sacks, E. Linder, and D. S. Schimel. 2005. Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. *Global Change Biology* **11**:335–355.
- Carvalhais, N., M. Forkel, M. Khomik, J. Bellarby, M. Jung, M. Migliavacca, M. Mu, S. Saatchi, M. Santoro, and M. Thurner. 2014. Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature* **514**:213–217.
- Carvalhais, N., M. Reichstein, J. Seixas, G. J. Collatz, J. S. Pereira, P. Berbigier, A. Carrara et al. 2008. Implications of the carbon cycle steady state assumption for biogeochemical modeling performance and inverse parameter retrieval. *Global Biogeochemical Cycles* **22**:GB2007.
- Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge et al. 2001. Ecological forecasts: An emerging imperative. *Science* **293**:657–660.
- Clark, J. S., M. Lewis, J. S. McLachlan, and J. HilleRisLambers. 2003. Estimating population spread: What can we forecast and how well? *Ecology* **84**:1979–1988.

- De Kauwe, M. G., B. E. Medlyn, S. Zaehle, A. P. Walker, M. C. Dietze, T. Hickler, A. K. Jain et al. 2013. Forest water use and water use efficiency at elevated CO₂: A model-data intercomparison at two contrasting temperate forest FACE sites. *Global Change Biology* **19**:1759–1779.
- De Kauwe, M. G., B. E. Medlyn, S. Zaehle, A. P. Walker, M. C. Dietze, Y.-P. Wang, Y. Luo et al. 2014. Where does the carbon go? A model–data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO₂ enrichment sites. *New Phytologist* **203**:883–899.
- Dietze, M. C., D. S. Lebauer, and R. O. B. Kooper. 2013. On improving the communication between models and data. *Plant, Cell and Environment* **36**:1575–1585.
- Fraser, L. H., H. A. Henry, C. N. Carlyle, S. R. White, C. Beierkuhnlein, J. F. Cahill Jr., B. B. Casper, E. Cleland, S. L. Collins, and J. S. Dukes. 2012. Coordinated distributed experiments: An emerging tool for testing global hypotheses in ecology and environmental science. *Frontiers in Ecology and the Environment* **11**:147–155.
- Friedlingstein, P., P. Cox, R. Betts, L. Bopp, W. von Bloh, V. Brovkin, P. Cadule et al. 2006. Climate–carbon cycle feedback analysis: Results from the C4MIP model intercomparison. *Journal of Climate* **19**:3337–3353.
- Frolking, S., N. Roulet, and D. Lawrence. 2013. Issues related to incorporating northern peatlands into global climate models. In A. J. Baird, L. R. Belyea, X. Comas, A. S. Reeve, and L. D. Slater, eds., *Carbon Cycling in Northern Peatlands*, pp. 19–35. American Geophysical Union, Washington, DC.
- Gao, C., H. Wang, E. Weng, S. Lakshminarayanan, Y. Zhang, and Y. Luo. 2011. Assimilation of multiple data sets with the ensemble Kalman filter to improve forecasts of forest carbon dynamics. *Ecological Applications* **21**:1461–1473.
- Hanson, P. J., K. W. Childs, S. D. Wullschleger, J. S. Riggs, W. K. Thomas, D. E. Todd, and J. M. Warren. 2011. A method for experimental heating of intact soil profiles for application to climate change experiments. *Global Change Biology* **17**:1083–1096.
- Hararuk, O. and Y. Luo. 2014. Improvement of global litter turnover rate predictions using a Bayesian MCMC approach. *Ecosphere* **5**:1–13.
- Hararuk, O., M. J. Smith, and Y. Luo. 2015. Microbial models with data-driven parameters predict stronger soil carbon responses to climate change. *Global Change Biology* **21**:2439–2453.
- Hararuk, O., J. Xia, and Y. Luo. 2014. Evaluation and improvement of a global land model against soil carbon data using a Bayesian Markov chain Monte Carlo method. *Journal of Geophysical Research: Biogeosciences* **119**:403–417.
- Hastings, W. K. 1970. Monte Carlo sampling methods using Markov chains and their applications. *Biometrika* **57**:97–109.
- Huxman, T. E., M. D. Smith, P. A. Fay, A. K. Knapp, M. R. Shaw, M. E. Loik, S. D. Smith et al. 2004. Convergence across biomes to a common rain-use efficiency. *Nature* **429**:651–654.
- IPCC. 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, U.K.
- Jiang, L., Y. Yan, O. Hararuk, N. Mickle, J. Xia, Z. Shi, J. Tjiputra, T. Wu, and Y. Luo. 2015. Scale-dependent performance of CMIP5 earth system models in simulating terrestrial vegetation carbon. *Journal of Climate* **28**:5217–5232.

- Jones, C., E. Robertson, V. Arora, P. Friedlingstein, E. Shevliakova, L. Bopp, V. Brovkin, T. Hajima, E. Kato, and M. Kawamiya. 2013. Twenty-first-century compatible CO₂ emissions and airborne fraction simulated by CMIP5 earth system models under four representative concentration pathways. *Journal of Climate* **26**:4398–4413.
- Keenan, T. F., E. A. Davidson, J. W. Munger, and A. D. Richardson. 2012. Rate my data: Quantifying the value of ecological data for the development of models of the terrestrial carbon cycle. *Ecological Applications* **23**:273–286.
- Koven, C., W. Riley, Z. Subin, J. Tang, M. Torn, W. Collins, G. Bonan, D. Lawrence, and S. Swenson. 2013. The effect of vertically resolved soil biogeochemistry and alternate soil C and N models on C dynamics of CLM4. *Biogeosciences* **10**:7109–7131.
- Krassovski, M. B., J. S. Riggs, L. A. Hook, W. R. Nettles, P. J. Hanson, and T. A. Boden. 2015. A comprehensive data acquisition and management system for an ecosystem-scale peatland warming and elevated CO₂ experiment. *Geoscientific Instrumentation, Methods and Data Systems* **4**:203–213.
- Kuppel, S., P. Peylin, F. Chevallier, C. Bacour, F. Maignan, and A. Richardson. 2012. Constraining a global ecosystem model with multi-site eddy-covariance data. *Biogeosciences* **9**:3757–3776.
- LeBauer, D. S., D. Wang, K. T. Richter, C. C. Davidson, and M. C. Dietze. 2013. Facilitating feedbacks between field measurements and ecosystem models. *Ecological Monographs* **83**:133–154.
- Li, D., C. Schädel, M. L. Haddix, E. A. Paul, R. Conant, J. Li, J. Zhou, and Y. Luo. 2013. Differential responses of soil organic carbon fractions to warming: Results from an analysis with data assimilation. *Soil Biology and Biochemistry* **67**:24–30.
- Liang, J., D. Li, Z. Shi, J. M. Tiedje, J. Zhou, E. A. Schuur, K. T. Konstantinidis, and Y. Luo. 2015a. Methods for estimating temperature sensitivity of soil organic matter based on incubation data: A comparative evaluation. *Soil Biology and Biochemistry* **80**:127–135.
- Liang, J., X. Qi, L. Souza, and Y. Luo. 2015b. Processes regulating progressive nitrogen limitation under elevated carbon dioxide: A meta-analysis. *Biogeosciences Discussions* **12**:16953–16977.
- Limpens, J., F. Berendse, C. Blodau, J. G. Canadell, C. Freeman, J. Holden, N. Roulet, H. Rydin, and G. Schaepman-Strub. 2008. Peatlands and the carbon cycle: From local processes to global implications—A synthesis. *Biogeosciences* **5**:1475–1491.
- Luo, Y., A. Ahlström, S. D. Allison, N. H. Batjes, V. Brovkin, N. Carvalhais, A. Chappell et al. 2016. Toward more realistic projections of soil carbon dynamics by Earth system models. *Global Biogeochemical Cycles* **30**:40–56.
- Luo, Y., T. F. Keenan, and M. Smith. 2015. Predictability of the terrestrial carbon cycle. *Global Change Biology* **21**:1737–1751.
- Luo, Y., J. Melillo, S. Niu, C. Beier, J. S. Clark, A. T. Classen, E. Davidson et al. 2011a. Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Global Change Biology* **17**:843–854.
- Luo, Y., K. Ogle, C. Tucker, S. Fei, C. Gao, S. LaDeau, J. S. Clark, and D. S. Schimel. 2011b. Ecological forecasting and data assimilation in a data-rich era. *Ecological Applications* **21**:1429–1442.
- Luo, Y., J. T. Randerson, G. Abramowitz, C. Bacour, E. Blyth, N. Carvalhais, P. Ciais, D. Dalmonch, J. B. Fisher, and R. Fisher. 2012. A framework for benchmarking land models. *Biogeosciences* **9**:3857–3874.

- Luo, Y. and J. F. Reynolds. 1999. Validity of extrapolating field CO₂ experiments to predict carbon sequestration in natural ecosystems. *Ecology* **80**: 1568–1583.
- Luo, Y., L. W. White, J. G. Canadell, E. H. DeLucia, D. S. Ellsworth, A. Finzi, J. Lichter, and W. H. Schlesinger. 2003. Sustainability of terrestrial carbon sequestration: A case study in Duke Forest with inversion approach. *Global Biogeochemical Cycles* **17**:1021.
- Medlyn, B. E., S. Zaehle, M. G. De Kauwe, A. P. Walker, M. C. Dietze, P. J. Hanson, T. Hickler et al. 2015. Using ecosystem experiments to improve vegetation models. *Nature Climate Change* **5**:528–534.
- Murphy, J. 2000. Predictions of climate change over Europe using statistical and dynamical downscaling techniques. *International Journal of Climatology* **20**:489–501.
- Niu, S., Y. Luo, M. C. Dietze, T. F. Keenan, Z. Shi, and J. Li. 2014. The role of data assimilation in predictive ecology. *Ecosphere* **5**:1–16.
- Norby, R. J., M. G. De Kauwe, T. F. Domingues, R. A. Duursma, D. S. Ellsworth, D. S. Goll, D. M. Lapola, K. A. Luus, A. R. MacKenzie, and B. E. Medlyn. 2016. Model–data synthesis for the next generation of forest free-air CO₂ enrichment (FACE) experiments. *New Phytologist* **209**:17–28.
- Ogle, K. 2009. Hierarchical Bayesian statistics: Merging experimental and modeling approaches in ecology. *Ecological Applications* **19**:577–581.
- Pacala, S. W., C. D. Canham, and J. Silander Jr. 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. *Canadian Journal of Forest Research* **23**:1980–1988.
- Parton, W. J., J. A. Morgan, G. Wang, and S. Del Grosso. 2007. Projected ecosystem impact of the Prairie Heating and CO₂ enrichment experiment. *New Phytologist* **174**:823–834.
- Parton, W. J., D. S. Schimel, C. Cole, and D. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* **51**:1173–1179.
- Parton, W., J. Scurlock, D. Ojima, T. Gilmanov, R. Scholes, D. S. Schimel, T. Kirchner, J. C. Menaut, T. Seastedt, and E. Garcia Moya. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles* **7**:785–809.
- Peng, C., J. Guiot, H. Wu, H. Jiang, and Y. Luo. 2011. Integrating models with data in ecology and palaeoecology: Advances towards a model–data fusion approach. *Ecology Letters* **14**:522–536.
- Raupach, M., P. Rayner, D. Barrett, R. DeFries, M. Heimann, D. Ojima, S. Quegan, and C. Schimmlus. 2005. Model–data synthesis in terrestrial carbon observation: Methods, data requirements and data uncertainty specifications. *Global Change Biology* **11**:378–397.
- Richardson, A. D., M. Williams, D. Y. Hollinger, D. J. Moore, D. B. Dail, E. A. Davidson, N. A. Scott, R. S. Evans, H. Hughes, and J. T. Lee. 2010. Estimating parameters of a forest ecosystem C model with measurements of stocks and fluxes as joint constraints. *Oecologia* **164**:25–40.
- Schädel, C., Y. Luo, R. D. Evans, S. Fei, and S. M. Schaeffer. 2013. Separating soil CO₂ efflux into C-pool-specific decay rates via inverse analysis of soil incubation data. *Oecologia* **171**:721–732.

- Schoof, J. T., S. C. Pryor, and J. Surprenant. 2010. Development of daily precipitation projections for the United States based on probabilistic downscaling. *Journal of Geophysical Research: Atmospheres* **115**:D13106.
- Seddon, A. W. R., M. Macias-Fauria, P. R. Long, D. Benz, and K. J. Willis. 2016. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* **531**:229–232.
- Shi, X., P. E. Thornton, D. M. Ricciuto, P. J. Hanson, J. Mao, S. D. Sebestyen, N. A. Griffiths, and G. Bisht. 2015a. Representing northern peatland microtopography and hydrology within the Community Land Model. *Biogeosciences* **12**:6463–6477.
- Shi, Z., X. Xu, O. Hararuk, L. Jiang, J. Xia, J. Liang, D. Li, and Y. Luo. 2015b. Experimental warming altered rates of carbon processes, allocation, and carbon storage in a tallgrass prairie. *Ecosphere* **6**:1–16.
- Shi, Z., Y. Yang, X. Zhou, E. Weng, A. C. Finzi, and Y. Luo. 2016. Inverse analysis of coupled carbon–nitrogen cycles against multiple datasets at ambient and elevated CO₂. *Journal of Plant Ecology*. **9**:285–295.
- Sitch, S., B. Smith, I. C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J. Kaplan, S. Levis, W. Lucht, and M. T. Sykes. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* **9**:161–185.
- Tian, H., C. Lu, J. Yang, K. Banger, D. N. Huntzinger, C. R. Schwalm, A. M. Michalak, R. Cook, P. Ciais, and D. Hayes. 2015. Global patterns and controls of soil organic carbon dynamics as simulated by multiple terrestrial biosphere models: Current status and future directions. *Global Biogeochemical Cycles* **29**:775–792.
- Todd-Brown, K. E. O., J. T. Randerson, F. Hopkins, V. Arora, T. Hajima, C. Jones, E. Shevliakova, J. Tjiputra, E. Volodin, T. Wu, Q. Zhang, and S. D. Allison. 2014. Changes in soil organic carbon storage predicted by Earth system models during the 21st century. *Biogeosciences* **11**:2341–2356
- Todd-Brown, K., J. Randerson, W. Post, F. Hoffman, C. Tarnocai, E. Schuur, and S. Allison. 2013. Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. *Biogeosciences* **10**:1717–1736.
- Verma, S. B. 1990. Micrometeorological methods for measuring surface fluxes of mass and energy. *Remote sensing reviews* **5**:99–115.
- Walker, A. P., P. J. Hanson, M. G. De Kauwe, B. E. Medlyn, S. Zaehle, S. Asao, M. Dietze, T. Hickler, C. Huntingford, and C. M. Iversen. 2014. Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate forest free-air CO₂ enrichment experiments: Model performance at ambient CO₂ concentration. *Journal of Geophysical Research: Biogeosciences* **119**:937–964.
- Wang, Y.-P., C. M. Trudinger, and I. G. Enting. 2009. A review of applications of model–data fusion to studies of terrestrial carbon fluxes at different scales. *Agricultural and Forest Meteorology* **149**:1829–1842.
- Weng, E. and Y. Luo. 2011. Relative information contributions of model vs. data to short- and long-term forecasts of forest carbon dynamics. *Ecological Applications* **21**:1490–1505.
- White, L. and Y. Luo. 2002. Estimation of carbon transfer coefficients using Duke Forest free-air CO₂ enrichment data. *Applied Mathematics and Computation* **130**:101–120.
- White, L., F. White, Y. Luo, and T. Xu. 2006. Estimation of parameters in carbon sequestration models from net ecosystem exchange data. *Applied Mathematics and Computation* **181**:864–879.

- Wilcox, K. R., J. C. Fischer, J. M. Muscha, M. K. Petersen, and A. K. Knapp. 2015. Contrasting above- and belowground sensitivity of three Great Plains grasslands to altered rainfall regimes. *Global Change Biology* **21**:335–344.
- Williams, M., A. Richardson, M. Reichstein, P. Stoy, P. Peylin, H. Verbeeck, N. Carvalhais, M. Jung, D. Hollinger, and J. Kattge. 2009. Improving land surface models with FLUXNET data. *Biogeosciences* **6**:1341–1359.
- Williams, M., P. A. Schwarz, B. E. Law, J. Irvine, and M. R. Kurpius. 2005. An improved analysis of forest carbon dynamics using data assimilation. *Global Change Biology* **11**:89–105.
- Wu, X., Y. Luo, E. Weng, L. White, Y. Ma, and X. Zhou. 2009. Conditional inversion to estimate parameters from eddy-flux observations. *Journal of Plant Ecology* **2**:55–68.
- Wutzler, T. and M. Reichstein. 2007. Soils apart from equilibrium? consequences for soil carbon balance modelling. *Biogeosciences* **4**:125–136.
- Xia, J., Y. Luo, Y.-P. Wang, and O. Hararuk. 2013. Traceable components of terrestrial carbon storage capacity in biogeochemical models. *Global Change Biology* **19**:2104–2116.
- Xia, J., Y. Luo, Y.-P. Wang, E. Weng, and O. Hararuk. 2012. A semi-analytical solution to accelerate spin-up of a coupled carbon and nitrogen land model to steady state. *Geoscientific Model Development* **5**:1259–1271.
- Xu, X., Z. Shi, D. Li, A. Rey, H. Ruan, J. M. Craine, J. Liang, J. Zhou, and Y. Luo. 2016. Soil properties control decomposition of soil organic carbon: Results from data-assimilation analysis. *Geoderma* **262**:235–242.
- Xu, T., L. White, D. Hui, and Y. Luo. 2006. Probabilistic inversion of a terrestrial ecosystem model: Analysis of uncertainty in parameter estimation and model prediction. *Global Biogeochemical Cycles* **20**:1–15. GB2007.
- Zaehle, S., B. E. Medlyn, M. G. De Kauwe, A. P. Walker, M. C. Dietze, T. Hickler, Y. Luo et al. 2014. Evaluation of 11 terrestrial carbon–nitrogen cycle models against observations from two temperate free-air CO₂ enrichment studies. *New Phytologist* **202**:803–822.
- Zhang, L., Y. Luo, G. Yu, and L. Zhang. 2010. Estimated carbon residence times in three forest ecosystems of eastern China: Applications of probabilistic inversion. *Journal of Geophysical Research: Biogeosciences* **115**:G01010.
- Zhou, T. and Y. Luo. 2008. Spatial patterns of ecosystem carbon residence time and NPP-driven carbon uptake in the conterminous United States. *Global Biogeochemical Cycles* **22**:1–15. GB3032
- Zhou, X., Y. Luo, C. Gao, P. S. J. Verburg, J. A. Arnone, A. Darrouzet-Nardi, and D. S. Schimel. 2010. Concurrent and lagged impacts of an anomalously warm year on autotrophic and heterotrophic components of soil respiration: A deconvolution analysis. *New Phytologist* **187**:184–198.
- Zhou, T., P. Shi, D. Hui, and Y. Luo. 2009. Global pattern of temperature sensitivity of soil heterotrophic respiration (Q₁₀) and its implications for carbon-climate feedback. *Journal of Geophysical Research: Biogeosciences* **114**:1–9. G02016.
- Zhou, T., P. Shi, G. Jia, Y. Dai, X. Zhao, W. Shangguan, L. Du, H. Wu, and Y. Luo. 2015. Age-dependent forest carbon sink: Estimation via inverse modeling. *Journal of Geophysical Research: Biogeosciences* **120**:2473–2492.
- Zhou, T., P. Shi, G. Jia, and Y. Luo. 2013. Nonsteady state carbon sequestration in forest ecosystems of China estimated by data assimilation. *Journal of Geophysical Research: Biogeosciences* **118**:1369–1384.

- Zhou, X., T. Zhou, and Y. Luo. 2012. Uncertainties in carbon residence time and NPP-driven carbon uptake in terrestrial ecosystems of the conterminous USA: A Bayesian approach. *Tellus B* 64:17223.
- Zhu, Q. and Q. Zhuang. 2015. Ecosystem biogeochemistry model parameterization: Do more flux data result in a better model in predicting carbon flux? *Ecosphere* 6:art283.