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Abstract

Terrestrial ecosystems sequester roughly 30% of anthropogenic carbon emission. However this estimate has not been directly deduced from studies of terrestrial ecosystems themselves, but inferred from atmospheric and oceanic data. This raises a question: to what extent is the terrestrial carbon cycle intrinsically predictable? In this paper, we investigated fundamental properties of the terrestrial carbon cycle, examined its intrinsic predictability, and proposed a suite of future research directions to improve empirical understanding and model predictive ability. Specifically, we isolated endogenous internal processes of the terrestrial carbon cycle from exogenous forcing variables. The internal processes share five fundamental properties (i.e., compartmentalization, carbon input through photosynthesis, partitioning among pools, donor pool-dominant transfers, and the first-order decay) among all types of ecosystems on the Earth. The five properties together result in an emergent constraint on predictability of various carbon cycle components in response to five classes of exogenous forcing. Future observational and experimental research should be focused on those less predictive components while modeling research needs to improve model predictive ability for those highly predictive components. We argue that an understanding of predictability should provide guidance on future observational, experimental and modeling research.

The need to advance our predictive understanding of the terrestrial carbon cycle

Terrestrial ecosystems play a crucial role in the global carbon cycle and in the regulation of climate change. Anthropogenic CO_2 emissions increased from 2.4 Pg C in 1960 to 8.7 Pg C per year in 2008 while terrestrial ecosystems absorbed roughly 30% during that period (Le Quere *et al*., 2009). If that absorption capacity were to change, in either direction, it would have a large impact on atmospheric CO_2 concentrations, resulting in a strong feedback effect on climate (Friedlingstein *et al*., 2006; Denman *et al*., 2007). It is, therefore, imperative to accurately predict dynamics of the terrestrial carbon cycle in order to accurately predict future changes in the Earth's climate. Here, we examine the current state of the art of predictive modeling of the global carbon cycle, and outline how an understanding of the intrinsic predictability of its components can be used to guide future experimental research and develop the next generation of carbon cycle models.

To date, the magnitude of the terrestrial carbon sink has been deduced indirectly: combining analyses of atmospheric carbon dioxide concentrations with ocean observations to infer the net terrestrial carbon flux (Denman *et al*., 2007; Ballantyne *et al*., 2012). In contrast, when knowledge about the terrestrial carbon cycle is integrated into different terrestrial carbon models they make widely different predictions and fit observations poorly (Schaefer *et al*., 2012; Todd-Brown *et al*., 2013). For example, none of the 11 earth system models (ESM) participating in the 5th Climate Model Intercomparison Project (CMIP5) could accurately predict patterns of soil carbon (the largest terrestrial carbon pool) across the global land surface (Todd-Brown *et al*., 2013) (Fig. 1). Similarly regional evaluation of 26 models against estimated gross primary production (GPP) at 39 eddy covariance flux tower sites across the United States and Canada shows poor matches of modeled with estimated GPP within observed uncertainty (Schaefer *et al*., 2012). These problems have been known for more than a decade (Cramer *et al*., 2001; Mcguire *et al*., 2001) and obstruct our ability to adequately inform policy and decision makers about the probable consequences of anthropogenic emissions and land use change scenarios.

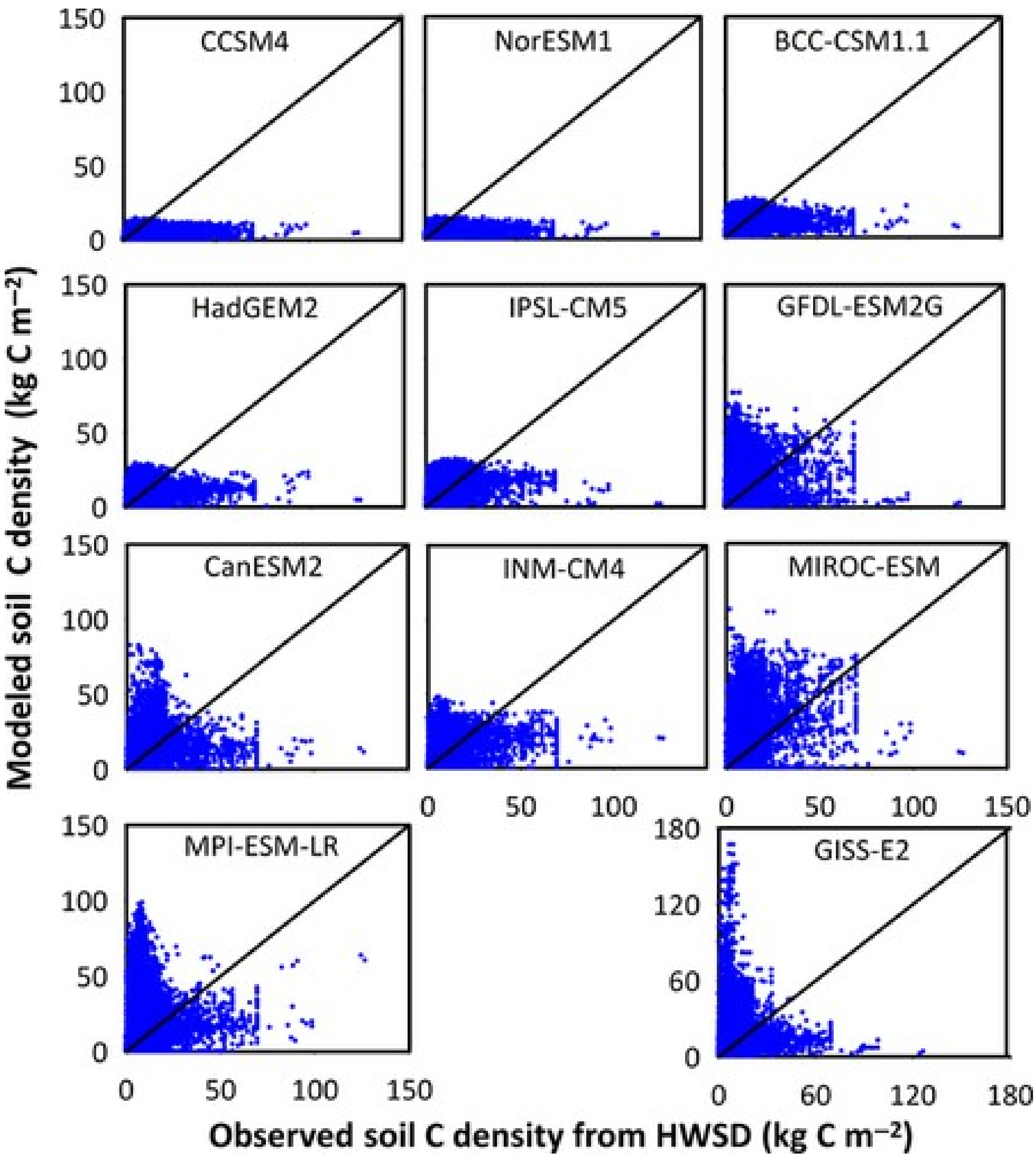

Figure 1

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Modeled vs. observation-based soil carbon densities. The modeled soil carbon densities (kg m^{-2}) represent 1995–2005 means from the historical simulations of the Climate Model Intercomparison Project 5 by 11 Earth system models. The observation-based soil carbon density in the top 1 m of soil from the Harmonized World Soil Database (HWSD). All of the models had difficulty representing soil carbon at the 1° scale. Despite similar overall structures, the models do not agree well among themselves or with empirical data on the global distribution of soil carbon although data themselves have great uncertainty. CCSM4 is US Community Climate System Model, NorESM1 is Norwegian Earth System Model, BCC-CSM1.1 is Beijing Climate

Center model, HadGEM2 is UK Met Office Climate model, IPSL-CM5 is French Institut Pierre Simon Laplace model, GFDL-ESM2 is US Geophysical Fluid Dynamics Laboratory model, CanESM2 is Canadian Earth System Model, INM-CM4 is Russian Institute for Numerical Mathematics model, MIROC-ESM is Japan Earth System Model, MPI-ESM-LR is Germany Max Plank Institute model, and GISS-E2 is US Goddard Institute for Space Studies model. (Replotted from data of Todd-Brown *et al*., 2013).

The modeling community has adopted a variety of different approaches to improve the terrestrial carbon models in ESMs, none of which, unfortunately, has led to significant reductions in the variation between model predictions. A common approach has been to incorporate an increasing number of processes known to influence the carbon cycle, to make the models as realistic as possible. However, the more processes the models incorporate, the more complex and less tractable the models are, making it practically impossible to understand why different models make different predictions. Model intercomparisons have been effective at revealing the extent of the differences between model predictions (Schwalm *et al*., 2010; Keenan *et al*., 2012; Kauwe *et al*., 2013) but have typically provided limited insights into its origins. Benchmark analyses have provided assessments of model performance against standard datasets (Luo *et al*., 2012), but so far been restricted to processes occurring over short time-scales (Randerson *et al*., 2009) (e.g. days to years). Data assimilation methods have been applied to directly constrain simple models or model components with observations (Smith *et al*., 2013) yet less extensively to global models (Hararuk *et al*., 2014).

Many research programs, involving observations and experiments, are underway to improve understanding of the terrestrial carbon cycle (Kao *et al*., 2012). Observations to characterize carbon cycle components over all continents on Earth are usually carried out by satellites or research networks (Baldocchi, 2008). These have generated various regional and global data products, such as global maps of gross and net primary production (GPP and NPP) (Running *et al*., 2004; Jung *et al*., 2011), and regional and global distributions of soil carbon content and soil respiration (Tarnocai *et al*., 2009). These data products have been extremely useful for improving of our understanding of the processes and properties underpinning patterns in terrestrial carbon cycle components (Zhou *et al*., 2009; Jung *et al*., 2010). Experimental studies are also implemented to manipulate factors that are expected to vary as a consequence of climate change, such as elevating CO_2 concentrations, increasing ambient temperature, and altering precipitation rates (Rustad, 2008). This enables direct insights into how ecosystems respond to such perturbations and have revealed some important new mechanisms, such as acclimation and adaptation of the carbon cycle to climate change (Niu *et al*., 2012). Nevertheless, they have yet to lead to better-constrained predictions of the terrestrial carbon cycle.

The lack of progress in improving the predictive ability of the models raises a question: to what extent is the terrestrial carbon cycle intrinsically predictable by its own nature? By intrinsic predictability we mean the degree to which a system's state and dynamics can be predicted given knowledge about initial conditions, external forcing and internal properties. If the intrinsic predictability of the terrestrial carbon cycle is low, then we should expect further research to make limited improvements in the accuracy of model projections despite improving our understanding. However if its intrinsic predictability is high, then why do the projections from state of the art models continue to differ so widely? The concept of predictability has been studied in detail in other fields (Heisenberg & Maclachlan, 1958; Grace & Hütt, 2013). For example, intrinsic predictability is famously limited in chaotic systems, where an extreme sensitivity to differences in initial conditions and imperfect knowledge of the system state combine to fundamentally constrain how accurate future projections can be (Lorenz, 1969; Smith, 2007). In the case of terrestrial carbon cycling, the theoretical limits to predictability have yet to be addressed.

In this article, we investigate the predictability of the terrestrial carbon cycle. We first examine its internal properties, which largely determine and constrain its dynamics everywhere on the Earth. Those properties also form the basis upon which intrinsic predictability should be analyzed. We then identify five key classes of external forcing, and discuss how each influences the predictability of the terrestrial carbon cycle. Together, these classes encompass almost all possible scenarios that terrestrial ecosystems experience. We then present empirical and quantitative evidence to argue that some aspects of the terrestrial carbon cycle appear to be highly predictable while others less predictive. The key benefit from understanding predictability is allowing sources of uncertainty to be targeted for improvement through further research. With that, we then highlight key areas for empirical research to improve predictive understanding and outline strategies to realize the predictability in terrestrial carbon models. Our analysis here does not extend to assessing how confidently Earth System Models as a whole might be able to predict the terrestrial carbon sink, but we hope that it can provide guidance for where future carbon model development is needed to improve that confidence.

Fundamental properties of the terrestrial carbon cycle

Phenomenologically, the dynamics of the terrestrial carbon cycle appear very rich, exhibiting fluctuations, directional changes, and tipping points (Scheffer *et al*., 2001; Cox *et al*., 2004; Hirota *et al*., 2011; Baudena & Rietkerk, 2012). These occur because multiple environmental forcing variables interact with internal carbon cycle processes to cause diverse dynamics over different temporal and spatial scales. However, the internal processes are in fact relatively simple, and their responses to external forcing variables, as described in the next section, can be highly predictable once the forcing variables are sufficiently well-characterized.

The internal processes of the terrestrial carbon cycle are compartmentalized into distinct pools. The dynamics of carbon within each pool can be largely characterized by the differences between the rates of carbon input and output. The vast majority of the input of carbon into an ecosystem is through photosynthesis (Schlesinger & Bernhardt, 2013) (Fig. 2a) while we usually ignore minor inputs from migratory heterotrophs, lateral flows and carbonate exchange. Carbon is then partitioned among pools, principally leaves, stems and roots. Subsequent carbon transfers are then donor-pool dominated, with input rates to litter and soil pools being dependent on the output rates of their donor pools. The output rates from these pools, predominantly the decay of organic matter in litter and soils, are well-approximated using simple first-order kinetics (Olson, 1963; Meentemeyer, 1978; Adair *et al*., 2008; Zhang *et al*., 2008): in the absence of inputs, the pool size of litter or soil organic carbon decays exponentially through time. Carbon in the ecosystem is then, ultimately, released back into the atmosphere through respiration. These internal carbon processes are universal although their rates vary with ecosystems and environments over space and time. Some processes, such as photodegradation in arid and semi-arid lands (Austin & Vivanco, 2006) and anaerobic decomposition in peatlands (Bridgham & Richardson, 1992), may be ecosystem-specific but ultimately result in modifications to the rates of output processes. Overall, understanding common characteristics of these processes is central to predicting carbon cycling in any ecosystem.

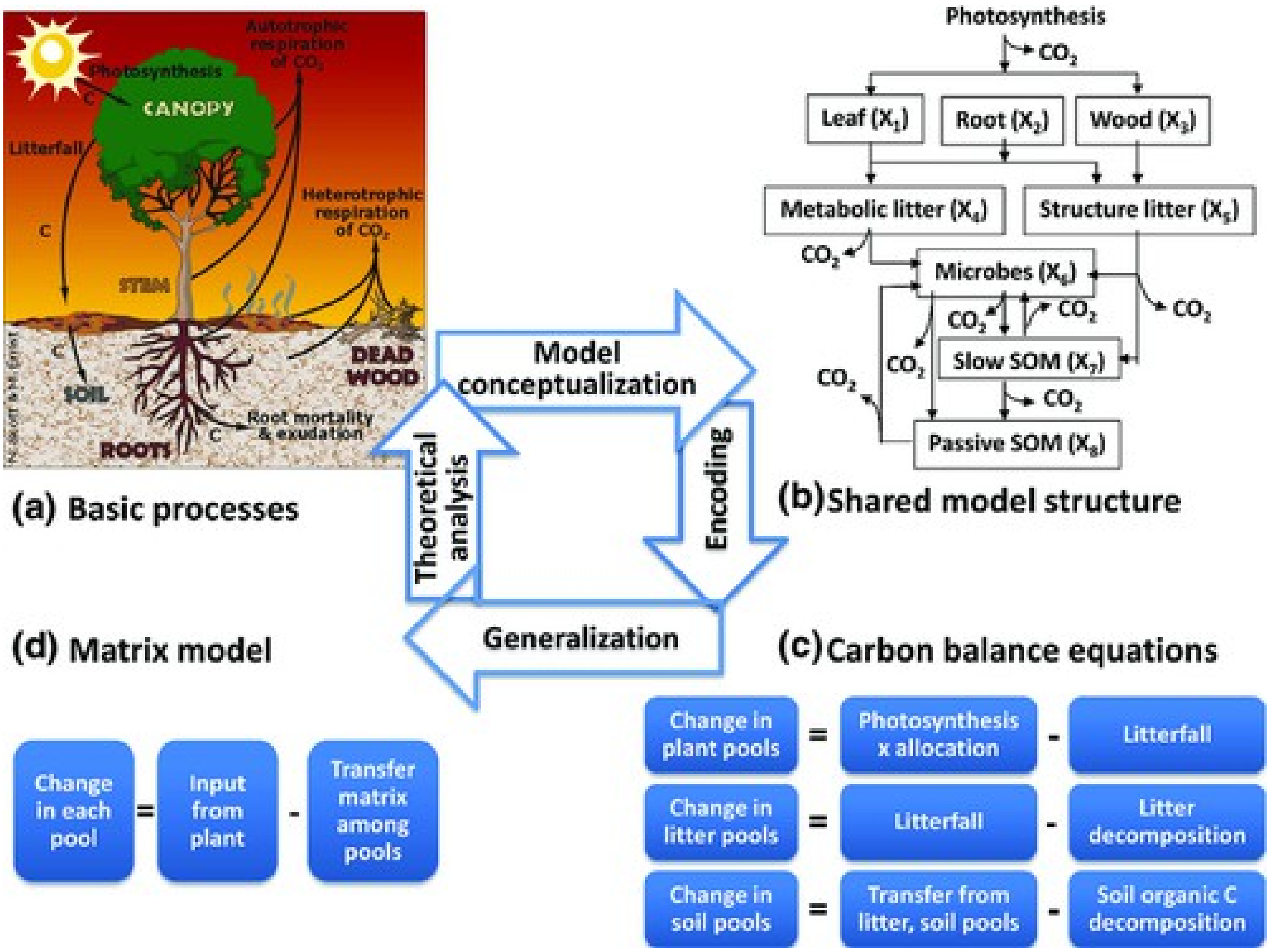

Figure 2

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A generalized model for predictability analysis of the terrestrial carbon cycle The basic carbon cycle processes are represented by five fundamental properties for all terrestrial ecosystems (see text) (a). The five properties have been incorporated into all terrestrial carbon cycle models with a pool-and-flux structure (b). The structure is typically encoded using very similar sets of balance equations with carbon input into and output from each pool [Eqn 1] (c). The balance equations in all terrestrial carbon cycle models can be converted to a matrix equation [Eqn 2] (d). Thus, the matrix equation can be considered as a general system of equations for the terrestrial carbon cycle and has a specific structure that restricts the set of possible behaviors and thus offers insights into its intrinsic predictability under different environments.

The internal carbon cycle processes can thus be characterized by five fundamental properties: (i) compartmentalization of carbon within distinct pools; (ii) photosynthesis as the dominant carbon input; (iii) partitioning of that photosynthetic input between the various pools; (iv) donor pool-dominated carbon transfers between pools; and (v) the first-order decay of litter and soil organic matter to release CO_2 via respiration (Zhang *et al*., 2008; Harmon *et al*., 2009; Luo & Weng, 2011; Davidson *et al*., 2012; Schädel *et al*., 2013). These fundamental properties are common to all ecosystems on Earth, although their rates vary. This representation of the terrestrial carbon cycle has been utilized for decades in models and still forms the backbone to the structure of most terrestrial carbon models (Luo & Weng, 2011; Todd-Brown *et al*., 2013; Xia *et al*., 2013).

Over time, many elaborations to this structure have been investigated, most notably assessing the importance of various internal feedbacks. Examples include nitrogen and phosphorus cycling (Domingues *et al*., 2010; Wang *et al*., 2010; Zaehle *et al*., 2010), which modify the rates of processes but do not change dynamic patterns of the terrestrial carbon cycle over different space and timescales. Positive feedbacks between leaf biomass and photosynthesis rate can occur when leaf area index (LAI) is relatively low: LAI increases with leaf biomass allowing more photosynthesis per unit ground area (Williams *et al*., 2005). However, over timescales of years to decades this feedback is of minor importance because LAI reaches maximum potential relatively fast. Recently, various nonlinear microbial models have been developed (Weintraub & Schimel, 2003; Allison *et al*., 2010; Wieder *et al*., 2013). These models introduce various feedbacks that could theoretically generate more complex dynamics (e.g. oscillations) than just first order decay of carbon (Wang *et al*., 2014), but there is no evidence for such complex behavior in empirical data from natural ecosystems.

What has been missing to date is an understanding of how the structure of the terrestrial carbon cycle itself determines our ability to predict it in the first place given various sources of uncertainty in external forcing and initial conditions. Such understanding can be obtained through studies focused on analysis of intrinsic predictability.

The intrinsic predictability of the terrestrial carbon cycle

We evaluate the predictability of the terrestrial carbon cycle primarily based on empirical evidence and constraints from its five fundamental properties. One of the most widely observed properties of terrestrial carbon dynamics is that the total carbon tends to converge over time to some form of equilibrium, if it starts from a carbon content distant to that equilibrium (e.g. after disturbances) (Matamala *et al*., 2008; Yang *et al*., 2011). Carbon models conforming to the five fundamental properties always predict this behavior (Mcguire *et al*., 2001), which can be explained very simply: the rate of carbon input is relatively independent of the vegetation carbon content (there is typically a weak feedback between photosynthesis and foliage biomass carbon; Williams *et al*., 2005) whereas the rate of output increases with carbon content. Therefore, the carbon content adjusts until the rate of carbon losses becomes equal to the rate of carbon inputs.

This universal behavior implies that the rate of approach to equilibrium, and the equilibrium itself, is relatively predictable given knowledge about carbon input rates, loss rates, the initial conditions, and governing environmental constraints.

Intrinsic predictability under five classes of external forcing

Evaluation of the intrinsic predictability of the terrestrial carbon cycle requires an understanding of how sensitive carbon cycle components are to known sources of external forcing because a range of environmental factors perturb terrestrial ecosystems over different space and time scales. Below we discuss how five classes of forcing, encompassing almost all possible environmental change scenarios experienced by terrestrial ecosystems on the Earth, likely influence the intrinsic predictability of the carbon cycle (Table 1).

Table 1. Intrinsic predictability of response patterns of the terrestrial carbon cycle to five classes of external forcing. The predictability of the carbon cycle measures a degree to which the response pattern is predictable given one class of external forcing. The predictability is usually judged by the sensitivity (e.g., diverging vs. converging) of systems behavior in response to various classes of perturbation and external forcing. In general, carbon cycle responses *per se* are more predictable than external forcing, which causes much high uncertainty in predicting carbon cycle responses to climate change

External forcing		**Response of the terrestrial carbon cycle**		
Class	**Example**	**General pattern**	**Component**	**Intrinsic predictability**
Cyclic environment	Diurnal, seasonal, and interannual	Cyclic	Diurnal and seasonal	High
			Interannual	Less known
Disturbance event	Fire, land use, insect outbreak, and storms etc.	Pulse-recovery	Time of events happening	Low
			Immediate impacts of disturbance events on carbon	Medium

External forcing		Response of the terrestrial carbon cycle		
Class	**Example**	**General pattern**	**Component**	**Intrinsic predictability**
			cycle	
			Recovery	High
			Recovery to original or new equilibrium	Less known
Climate change	Rising $(CO_2)_a$, climate warming, altered precipitation	Gradual	Direct impacts	High
			Indirect impacts via induced changes in disturbance regimes and ecosystem states	Less known
Shifts in Disturbance regimes	Regional, long-term patterns of fire, land use, insect outbreak, and storm etc.	Disequilibrium	Joint probability to describe disturbance regimes and their shifts	Unknown
			Impacts of shifted disturbance regimes on mean carbon storage	High

External forcing		Response of the terrestrial carbon cycle		
Class	**Example**	**General pattern**	**Component**	**Intrinsic predictability**
Ecosystem state change	Forest to cropland, grassland to cropland, reforestation, etc.	Abrupt changes	When and where ecosystem states change	Less known
			Carbon cycle change with ecosystem states	High

First, some external variables exhibit cyclic changes; most important are the daily and seasonal cycles of light, temperature, and other environmental factors. These typically cause the carbon flux rates, such as photosynthesis and respiration, to vary with the same period as the forcing (Table 1). The magnitude of the carbon response in different pools depends on the residence times – the duration of carbon staying in an ecosystem from entrance via photosynthesis to release via respiration. Pools with residence times of the same order as the cycle of the forcing (e.g. leaf carbon and seasonal cycles) tend to have larger amplitudes of responses than those with residence times much longer than the cyclic period of the forcing. The cyclic patterns of photosynthesis have long been well-predicted using a commonly used set of equations that capture leaf-level responses to light, temperature, and water status (Farquhar *et al*., 1980). Similarly, most carbon cycle models can adequately simulate the response of respiration to short-term environmental variability if the model parameters are well-calibrated (Fox *et al*., 2009). This implies that the responses of terrestrial carbon to daily and seasonal cyclic forcing should be highly predictable. However, interannual variability in the terrestrial carbon cycle, as reflected in eddy-flux measurement (Yuan *et al*., 2009) and variations in the growth rate of atmospheric CO_2 (Keeling *et al*., 1995), is less known for its underpinning mechanisms (Zeng *et al*., 2005; Keenan *et al*., 2012; Wang *et al*., 2013), making it difficult at present to evaluate its predictability.

The second class of forcing is disturbance events, such as wildfire and climate extremes (Foley *et al*., 2005; Running, 2008; Bowman *et al*., 2009; Mack *et al*., 2011;

Reichstein *et al*., 2013). During such events, relatively large amounts of carbon are removed rapidly, mostly from the aboveground biomass and organic layers of litter (Mack & D'antonio, 1998). Recovery then occurs over the subsequent years and decades following the monotonic response pattern described above (Odum, 1969; Yang *et al*., 2011; Williams *et al*., 2012). Simple pulse-recovery response patterns such as these are general phenomena having been observed in hundreds of studies on carbon dynamics during the secondary forest succession (Yang *et al*., 2011) and grassland restoration (Matamala *et al*., 2008). The recovery dynamics following a disturbance then appear to be highly predictable given adequate knowledge of the carbon influx rates, the residence times, and the pool sizes following disturbance (Weng *et al*., 2012) (Table 1). Moreover, these three sets of parameters can be estimated by analysis of time series data, either by direct calibration or though data-assimilation (Luo *et al*., 2003). The disturbance events themselves, however, have an inherent random component (e.g. chances of a hurricane) making the precise predictability of individual events relatively low. Likewise, the severity of disturbance impacts on carbon cycle is not very predictable, either. Even so, the typical frequency of disturbance events over a landscape can be used to constrain the probability of disturbance events themselves. Moreover, there is evidence that some ecosystems may recover to an alternative steady state following disturbance (Suding & Hobbs, 2009). Our lack of understanding of why this occurs limits our assessment of its consequences for carbon cycle predictability.

The third class of external forcing is directional trends in environmental variables, including rising atmospheric CO_2 concentrations, climate warming, altered precipitation, and nitrogen deposition. These climate change factors cause disequilibrium in terrestrial carbon pools though their influences on carbon influx rates, residence times and pool sizes (Denman *et al*., 2007). For example, rising atmospheric CO_2 concentrations directly stimulate photosynthesis and thus increase ecosystem carbon influx (Franks *et al*., 2013). Most of the direct effects of climate changes on the terrestrial carbon cycle can be predicted via relatively simple response functions in ESMs (Reynolds & Acock, 1985; Burke *et al*., 2003). Those functions are usually based on experimental and observational studies and incorporated into models (e.g., environmental scalars) to translate environmental changes to changes in carbon processes. However, climate change also causes indirect effects on the terrestrial carbon cycle (Korner *et al*., 2005; Cernusak *et al*., 2013), such as changes in plant species composition (Higgins & Scheiter, 2012), microbial priming (Kuzyakov *et al*., 2000), and respiratory acclimation (Luo *et al*. 2001). The indirect effects are much less well-understood, making it currently unclear just how predictable they are (Table 1). Moreover, climate change may induce shifts in disturbance regimes and changes in ecosystem states as discussed below (Westerling *et al*., 2011).

The fourth class of external forcing is changes in disturbance regimes at decadal, centennial and longer time scales (Hu *et al*., 2010). Each region of the Earth naturally has its own disturbance regime, typically determined by stochastic processes such as hurricanes and fires (Arora & Boer, 2005; Frolking *et al*., 2009; Vanderwel *et al*., 2013). Disturbance regimes can be quantified by joint probabilistic distributions of disturbance frequency and severity (Weng *et al*., 2012). This can be used in modeling studies to investigate its consequences for terrestrial carbon dynamics (Mcguire *et al*., 2001). Long-term datasets are needed to characterize frequency and severity of the prevailing disturbance regime in a region (Grace *et al*., 2014), which, in turn, can be used to generate a probability distribution of ecosystem carbon storage. The mean of the probability distribution determines the realizable carbon storage capacity under a given regime, reflecting the mean carbon storage capacity over a sufficiently long-time period or over a sufficiently large area (Luo & Weng, 2011). This mean carbon storage capacity could thus be predictable. However, we do not have enough knowledge to predict when the disturbance regime changes by direct (e.g., slash and burn agricultural expansion) or indirect (e.g., climate change) anthropogenic forcing (Westerling *et al*., 2011). We need to understand how the conditional probability distributions of disturbance frequency and severity respond to such changes before the consequences for the carbon cycle can be characterized.

The fifth class comprises changes in ecosystem states, usually induced by shifts in climate and disturbance regimes (Scheffer *et al*., 2001; Hirota *et al*., 2011; Staver *et al*., 2011; Higgins & Scheiter, 2012). Ecosystem state change is usually considered as a response of ecosystems to external forcing but we treat it as type of external forcing here. This is because ecosystem state changes usually result from vegetation state and/or soil structure changes rather than the five fundamental properties of the terrestrial carbon cycle as described in section 2. For example, land use and land cover changes directly result in ecosystem state changes, such as from forests or grasslands to croplands, through human activities (Houghton *et al*., 2012). Woody encroachment into grassland usually results from shifted fire regimes, climate change, and human activities (Higgins & Scheiter, 2012). In certain arid ecosystems there can be multiple alternative equilibrium states, such as grasslands and woodlands, due to interactions among biomass accumulation, fire, and establishment (Baudena & Rietkerk, 2012; Higgins & Scheiter, 2012; Staver & Levin, 2012). When ecosystem states change, carbon cycle dynamics within and between the plant, litter, and soil carbon pools also change. Dynamic vegetation models usually simulate ecosystems state changes and quantitate their consequences on carbon cycle through different sets of carbon cycle parameters for vegetation types. Given the change in vegetation structures and corresponding parameters, a consequent change in carbon cycle is quantifiable. However, while vegetation state changes have been studied (Chapin *et al*., 1995;

Hirota *et al*., 2011), their relationships with those carbon cycle parameters remains poorly understood.

Overall, there is ample evidence to indicate that some components of the terrestrial carbon cycle are intrinsically predictable. However, the terrestrial carbon cycle becomes less predictable when climate change induces indirect effects via changes in species composition and disturbance regimes, leading to ecosystem state changes. Even within a stationary disturbance regime, individual disturbance events usually occur stochastically and thus their impacts on the carbon cycle are less predictable.

Mathematical analysis of predictability

The predictability of a system can be mathematically analyzed if the system model can be defined. We first highlight that the terrestrial carbon cycle can be represented by a matrix equation. Its mathematical properties restrict the set of possible behaviors the terrestrial carbon cycle can exhibit and, thus, defines its predictability.

All of the terrestrial carbon models embedded in ESMs adopt a pool-and-flux structure. The structure well-represents the five fundamental properties of the terrestrial carbon cycle (Fig. 2a and b) (Luo & Weng, 2011). Such structured models simulate the flow of carbon through different pools from its entrance via photosynthesis to its release via respiration, obeying the law of mass conservation. The majority of carbon flows in one direction, from entrance to release, with a relatively small fraction being recycled through microbial growth, death, and decomposition (Xia *et al*., 2013). The rate of input into the pool is normally independent of the pool size but its output rate depends, in part, on how much carbon it contains (Luo *et al*., 2003). This input-output relationship can be represented as a set of linked carbon balance equations (Fig. 2c). In reference to the model structure in Fig. 2b, the set of balance equations are:

$$
\begin{cases}
\frac{dx_1(t)}{dt} = b_1 U(t) - \xi(t) c_1 X_1(t) \\
\frac{dx_2(t)}{dt} = b_2 U(t) - \xi(t) c_2 X_2(t) \\
\frac{dx_3(t)}{dt} = b_3 U(t) - \xi(t) c_3 X_3(t) \\
\frac{dx_4(t)}{dt} = \xi(t)[c_1 a_{41} X_1(t) + c_3 a_{43} X_3(t) - c_4 X_4(t)] \\
\frac{dx_5(t)}{dt} = \xi(t)[c_1 a_{51} X_1(t) + c_2 X_2(t) + c_3 a_{53} X_3(t) \\
\qquad -c_5 X_5(t)] \\
\frac{dx_6(t)}{dt} = \xi(t)[c_4 a_{64} X_4(t) + c_5 a_{65} X_5(t) \\
\qquad +c_7 a_{67} X_7(t) + c_8 a_{68} X_8(t) - c_6 X_6(t)] \\
\frac{dx_7(t)}{dt} = \xi(t)[c_5 a_{75} X_5(t) + c_6 a_{76} X_6(t) - c_7 X_7(t)] \\
\frac{dx_8(t)}{dt} = \xi(t)[c_6 a_{86} X_6(t) + c_7 a_{87} X_7(t) - c_8 X_8(t)]
\end{cases}
\quad (1)
$$

where $X_i(t)$, $i = 1, 2, \ldots, 8$, is carbon stock at time t, respectively, in leaf, root, wood, metabolic litter, structural litter, active, slow, and passive pools; b_i, $i = 1, 2, 3$, is partitioning coefficients of photosynthetic carbon input to leaf, root and wood, respectively; $U(t)$ is photosynthetic carbon input; $\xi(t)$ is an environmental scalar to represent temperature and moisture effects on carbon processes; c_i, $i = 1, 2, \ldots, 8$, is carbon exit rate, respectively, from leaf, root, wood, metabolic litter, structural litter, active, slow, and passive pools; $a_{j,I}$ is transfer coefficient of exited carbon from ith pool to jth pool.

Similar carbon balance equations have been encoded in all ESMs despite variations in the number of equations. The set of balance equations can be summarized by a matrix equation (Luo *et al*., 2003; Luo & Weng, 2011) (Fig. 2d) as:

$$
\begin{cases}
\frac{dX(t)}{dt} = \mathbf{BU}(t) - \xi(t)\mathbf{ACX}(t) \\
X(t=0) = X_0
\end{cases}
\quad (2)
$$

where $X(t)$ is a vector of pool sizes, B is a vector of partitioning coefficients, U(t) is photosynthesis rate, $\xi(t)$ is an environmental scalar, A is a matrix of transfer coefficients, C is a diagonal matrix of exit rates, and X_0 is initial values of pool sizes. Thus, matrix Eqn 2 can describe carbon transfers among pools within all types of terrestrial ecosystems as described by balance Eqn 1.

The matrix equation has long been used to examine carbon balance in and transfers among pools (Bolin & Eriksson, 1958; Emanuel *et al*., 1981) and can be argued to represent internal processes that drive carbon cycle toward equilibrium for all types of terrestrial ecosystems on the Earth (Bolker *et al*., 1998; Luo & Weng, 2011). It has been recently used to derive a semi-analytic solution to accelerate the computationally expensive spin up of the land models (Xia *et al*., 2012) and to establish a traceability framework to facilitate model intercomparisons, benchmark analyses, and data assimilation (Xia *et al*., 2013).

As a general system of equations for the terrestrial carbon cycle, the matrix equation describes a system that, under constant environments, all pools converge monotonically toward their equilibriums through time, regardless of their initial states. This implies that equilibrium carbon pool sizes are highly predictable anywhere on the global land surface where carbon influx and residence times can be estimated. Initial states, even if unknown, influence the trajectory of convergence toward the equilibriums for the duration that is a function of residence time (Bolker *et al*., 1998; Luo & Weng, 2011).

The matrix equation can also be used to analyze the predictability of the terrestrial carbon cycle under the five classes of forcing as in Table 1 although these formal studies still need to be conducted. First, the cyclic environmental forcing directly influences photosynthetic carbon input, $U(t)$, and respiration through the environmental scalar, $\xi(t)$, in the matrix equation. Thus if the forcing can be known with confidence, then this implies that the carbon cycle responses to the cyclic environmental variation should be highly predictable. Second, disturbance events usually remove carbon in different pools, which corresponds to the reduction of pool sizes, $X\ (t = t_0)$, in the matrix equation. Once the initial pools after disturbance are known, the equation can be used to predict a recovery trajectory unless the system shifts to a new equilibrium state. Third, direct responses of the terrestrial carbon cycle to global change can be predicted by linking global change factors of temperature and precipitation to the carbon cycle via the scalar, $\xi(t)$, or atmospheric CO_2 concentrations via a photosynthesis model. Fourth, the impacts of shifts in disturbance regimes on carbon can be predicted by quantifying the joint probability densities of disturbance frequency and severity (Weng *et al*., 2012). Fifth, ecosystem state changes are usually simulated by dynamic vegetation models and linked to carbon cycle with different sets of parameters for different vegetation types to the carbon balance equations. Thus their impacts on carbon cycle could be predictable if those sets of parameters are known with sufficient confidence.

The terrestrial carbon cycle is one example of a complex system whose dominant dynamics can be explained using relatively simple principles. This is similar to a case famously revealed by Dr.

Robert May in a sense that simple models can lead to complex dynamics (May, 1976). However, the simplest nonlinear models in May's case can lead to chaotic population dynamics with low predictability. The terrestrial carbon cycle is different in that its internal processes imply it has much higher predictability, even given the effects of multiple environmental forcing variables. Unlike chaotic systems, where small perturbations to an initial state grow over time, the internal properties of the terrestrial carbon cycle cause any deviations from equilibrium to decay monotonically over time. From a dynamical systems perspective this may make the terrestrial carbon cycle seem rather uninspiring! However, from the perspective of those aiming to improve models of the terrestrial carbon cycle this is really important: it gives us the confidence that we should indeed be able to improve the models significantly.

Future research to improve predictive ability

Although the above analysis indicates that we should expect high intrinsic predictability for some components of the terrestrial carbon cycle, the accuracy of predictions of current ESMs is highly limited. Our analysis has also identified components of the terrestrial carbon cycle whose predictability we presently have limited or no knowledge about (Table 1). Future observational and experimental research should aim to improve predictive understanding of those less known components. For those components with high predictability, it is urgent to develop strategies to narrow the gaps between the expected and actual predictive ability of terrestrial carbon models. Below we highlight future research directions, for both empirical and theoretical research, to improve our ability to predict responses of the terrestrial carbon cycle to climate change (Table 2, Fig. 3).

Table 2. Proposed roadmap of improving terrestrial carbon cycle models

Roadmap	Description
State of the art	Many essential processes understood
	Understanding improvement through further observations, experiments and modeling
	Global models synthesizing current understanding make widely diverging predictions

Roadmap	Description
	Intrinsic predictability poorly understood
Research needs	Identify and fill critical understanding gaps
	Identify critical uncertainties
	Understand intrinsic predictability
	Improve predictive skill
Recommendations	Integrated analysis to identify critical traceable components and achieve systemic understanding
	Identify key sources of uncertainty in critical components through
	Data-model fusion
	Benchmark analyses
	Model intercomparisons
	Develop new generation of data, theory, and models
Future state of the art	Intrinsic and achieved predictability quantified

Roadmap	Description
	Key sources of uncertainty well-characterized
	Evolving holistic understanding of knowledge gaps
	Key data, model and understanding deficiencies targeted

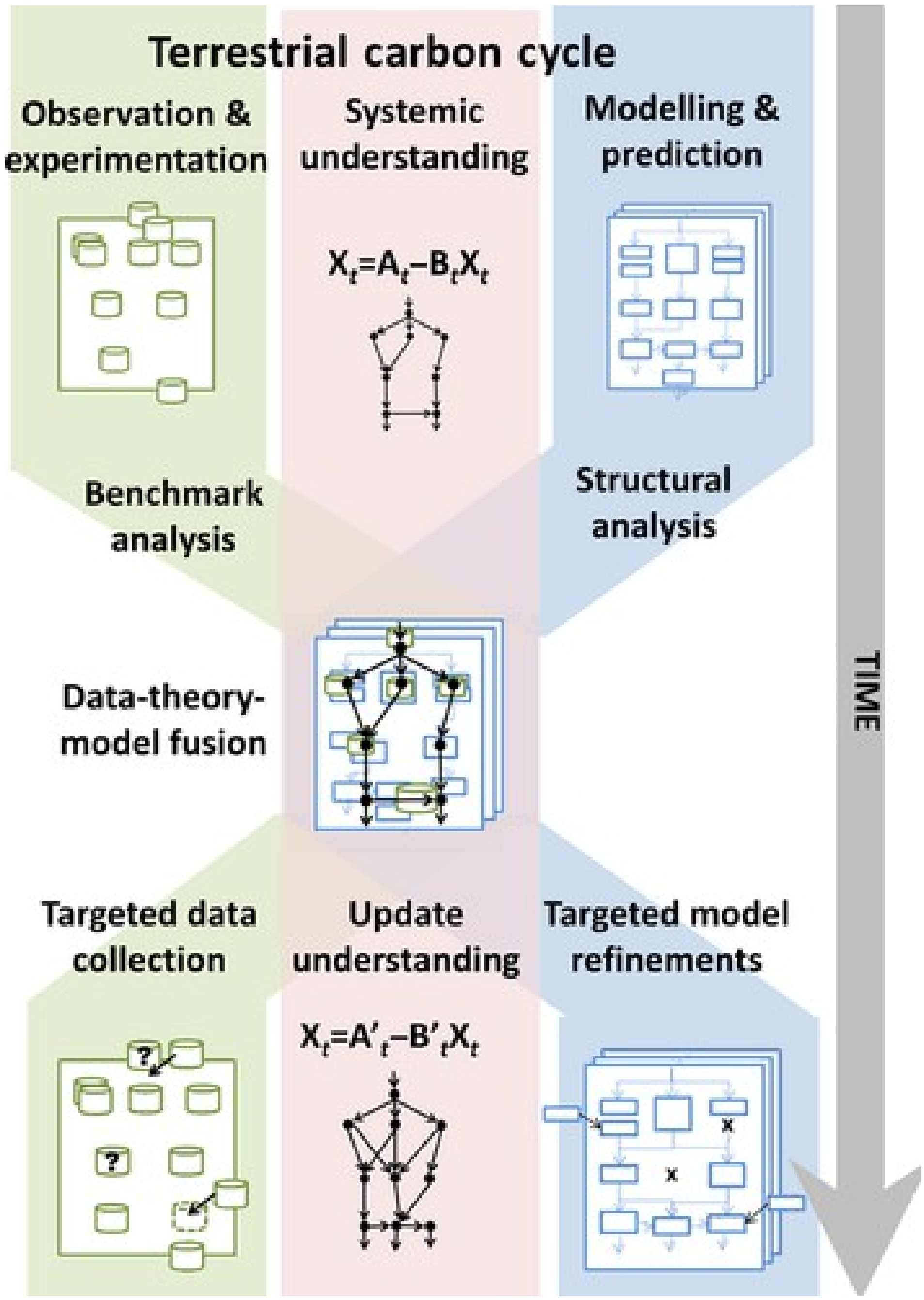

Figure 3

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Proposed roadmap for the future development of terrestrial carbon models. Terrestrial carbon cycle research is currently carried out through observation, experimentation, and modeling. Benchmark analysis should be promoted to measure model performance against data from observation and experiments. Theoretical understanding of the terrestrial carbon cycle has not been advanced but has the potential to evaluate essential structural components across all carbon models. Ideally, data, theory, and model need to be infused together to guide future data collection, theory development, and model improvement. Integrated analyses should eventually narrow the gap between the intrinsic and achieved predictability with major sources of uncertainty well-characterized.

Future empirical research directions

Ecosystem state and its transition

Ecosystem transitions are probably the least understood process in terrestrial carbon dynamics over decadal to centennial timescales but potentially have the most profound impacts on the global carbon cycle (Cox *et al*., 2000; Scheffer *et al*., 2001; Higgins & Scheiter, 2012). Examples include the respiration of vast stores of organic carbon from thawing permafrost, predominantly in polar regions (Schuur *et al*., 2009), the fixation of new carbon in such regions with vegetation transitions from shrublands to forests (Starfield & Chapin, 1996), and the dieback of the Amazon forests in response to changing precipitation which would release stores of carbon held in standing wood (Cox *et al*., 2000, 2004; Hirota *et al*., 2011). Such transitions can occur through progressive changes (e.g. warming) or stochastic events (e.g. sudden drought) (Chapin *et al*., 1995; Mack & D'antonio, 1998). Ecosystem transition redefines the expected equilibrium carbon state. That equilibrium is predictable if we know how carbon cycle parameters change with ecosystem states. Unfortunately, our knowledge is poor on ecosystem state changes, their predictability, and subsequent influences on carbon cycle processes. Future studies are therefore needed to address our critical knowledge gaps about how directional climate changes, stochastic events of disturbances, and internal mechanisms interact to influence the likelihood of ecosystem state change and its predictability.

States of and shifts in disturbance regimes

Disturbance regimes represent long-term and regional characteristics of disturbance frequency and severity (Pickett & White 1985) (Fig. 4). They largely determine the statistical probability for the degree of carbon-cycle disequilibrium in any ecosystem (Hu *et al*., 2010). A global understanding of different disturbance regimes is thus essential to quantitate the degrees of disequilibrium across the global land surface. Ideally, global terrestrial carbon models should be initialized (or spun up) to reflect the degrees of disequilibrium at prevailing disturbance regimes. Presently our understanding of disturbance regimes at the global scale is minimal and even less so for their conditional probability distributions on natural and anthropogenic variables to describe their shifts with climate change. Without characterization of states of disturbance regimes, both at a particular time and their shifts over time, it is impossible to accurately quantitate carbon dynamics in terrestrial ecosystems.

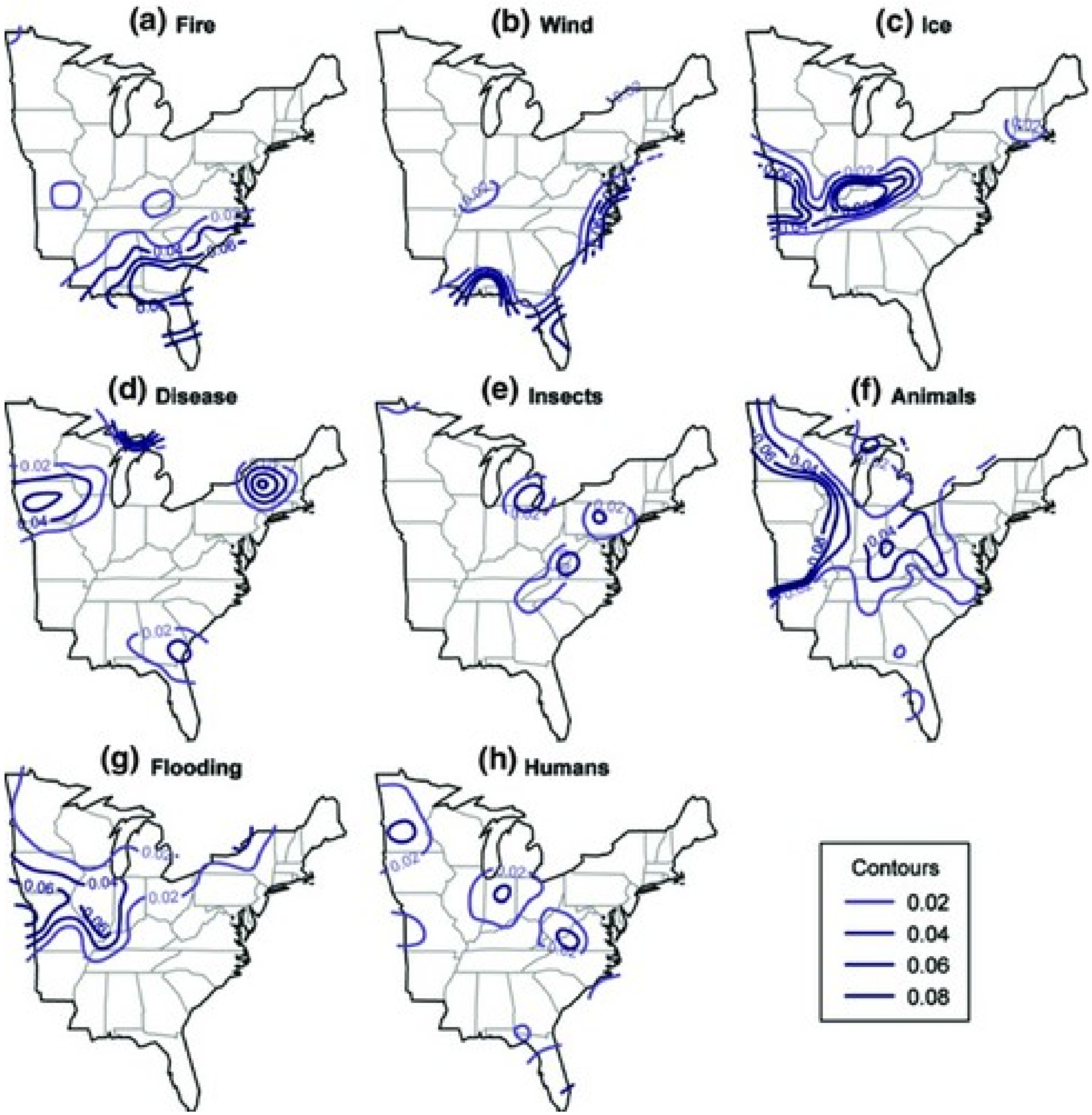

Figure 4

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Probability of occurrence for eight forest disturbance agents, across the eastern United States (1995–2011). Disturbances are defined according to the most recent census of 47 723 Forest Inventory and Analysis plots and as events that damage or kill at least 25% of trees across an area at least one acre (0.405 ha) in size since the last plot measurement (Vanderwel *et al*., 2013).

Disturbance events and recovery trajectories

Disturbance events can result in the direct emission of a large amount of carbon into the atmosphere (Mack *et al*., 2011). Following disturbance events, ecosystems typically recover to predisturbance states over time (Yang *et al*., 2011). Individual disturbance events alter the carbon cycle on yearly and decadal time scales but only have long-term effects if the ecosystem recovers to an alternative state. It is therefore critical to characterize the recovery trajectories of different ecosystems, and to examine whether they recover to initial or alternative states. In the former case, we need to quantitate initial values of carbon pools, carbon influx, and residence times to realize the potentially high predictability of carbon dynamics during the disturbance-recovery processes. In the latter case, we have to characterize the conditions under which ecosystems do not return to their initial state following disturbances.

Response functions

Response functions relate the rates of different carbon cycle processes to environmental variables and are thus crucial for predicting carbon cycle dynamics under global change (Burke *et al*., 2003). Presently, our knowledge of response functions is still insufficient to effectively improve our predictive ability. Terrestrial carbon models use a variety of response functions to predict ecosystem responses to various global change factors (Adams *et al*., 2004; Adair *et al*., 2008; Smith *et al*., 2013). New experiments and/or new analyses of existing observations are needed to characterize response functions and their variations under different conditions and over time so that they can realistically reflect ecosystem responses to environmental changes in the future. Highly nonlinear response functions, such as a sudden decrease in soil decomposition rates or sudden increase in tree mortality rates at high ambient temperatures, are likely to be especially important for understanding the predictability of the carbon cycle because small differences in environmental conditions could lead to large differences in carbon cycle responses (Adair *et al*., 2008; Smith *et al*., 2013). Understanding the variations of response functions among carbon processes, ecosystem types, and climate regimes, will help to characterize a range of possible dynamics the carbon cycle might exhibit under climate variation.

Improvements to the predictive ability of terrestrial carbon models

At present, the predictive ability of terrestrial carbon cycle models appears to fall far short of the intrinsic predictability (Fig. 1) for components for which we have plenty of data and knowledge. Transparent practices for model development, evaluation, and improvements are therefore needed if terrestrial carbon cycle models are to achieve high predictive ability. We therefore recommend the following measures to improve the predictive ability of terrestrial carbon models (Table 2; Fig. 3).

Model tractability

The biggest impediment to model evaluation and improvement at present is model intractability. The more processes incorporated, the more difficult it becomes to understand or evaluate model behavior. As a result, uncertainty in predictions among models cannot be easily diagnosed and attributed to its sources (Friedlingstein *et al*., 2006; Schwalm *et al*., 2010; Keenan *et al*., 2012; Raczka *et al*., 2013). It is essential to understand the common core elements among terrestrial carbon models (Fig. 2) and to identify and characterize those traceable components so as to improve model tractability (Xia *et al*., 2013) (Fig. 5a). Developing such a traceability framework would consequently help improve the comparability of models and data, evaluate impacts of additional model components (Fig. 5b), facilitate benchmark analyses, model intercomparisons (Fig. 5c), and data-model fusion (Fig. 5d); and improve model predictive power. The predictability of the core elements can then be clearly characterized under different sources of variation (e.g. external forcing and uncertainty in process understanding) (Fig. 5a) and compared to the achieved predictive ability. The traceability framework enables diagnosis of where carbon models are clearly lacking predictive ability and evaluation of the relative benefit of adding more components to the models.

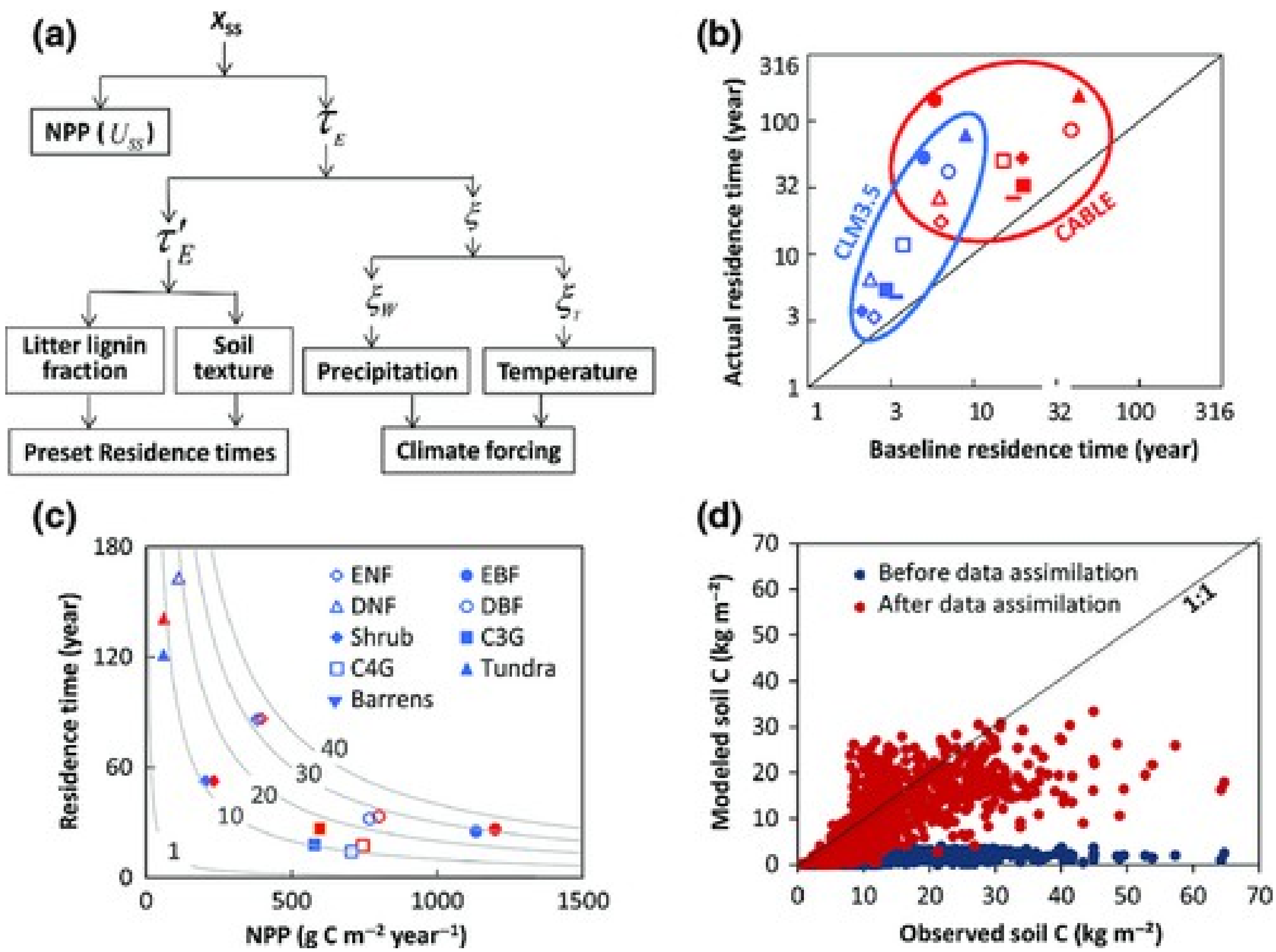

Figure 5

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Improvements to model predictive ability. The fundamental properties of the terrestrial carbon cycle, and their representation in shared structures among existing models, enable key traceable elements to be identified and characterized (a). This traceability will make all terrestrial carbon models more tractable and attribute model uncertainty in model intercomparison projects to its sources (b) and help evaluate impacts of adding new components into an ESM on carbon cycle (c) so as to pinpoint parts of models for improvement via model-data fusion (d). The traceability framework in panel A was developed to decompose modeled ecosystem carbon storage capacity (X_{ss}) to (i) a product of net primary productivity (NPP) and ecosystem residence time (τ_E). The latter τ_E can be further traced to (ii) baseline carbon residence times (τ'_E), which are usually preset in a model according to vegetation characteristics and soil types; (iii) environmental scalars (ξ), including temperature and water scalars; and (iv) environmental forcing (Xia *et al.*, 2013). Panel (b) shows that model intercomparison traced differences in ecosystem carbon storage capacity to differences in parameter settings in Community Land Model 3.5 (CLM3.5) and CABLE leading to substantial differences in baseline carbon residence times (τ'_E). Panel (c) shows the impacts of incorporating nitrogen processes into the Australian Community Atmosphere Biosphere Land Exchange (CABLE) model on the ecosystem carbon storage capacity (open symbols) as determined by NPP and the carbon residence time (τ_E) in comparison with carbon-only simulations (filled symbols). Panel (d) shows that parameter adjustment via data assimilation substantially improved data-model fitting for soil carbon density in CLM3.5 (Hararuk *et al*., 2014).

Origin of model uncertainty

We need to identify sources of uncertainty in model predictions so as to pinpoint those components most in need of improvement. The dynamics of the carbon cycle can be fully defined by Eqn 2 if parameters related to carbon influx, residence time, and initial values are specified. Inconsistency among model predictions must arise from uncertainty and discrepancy among those parameters and forcing given the fact that model structures are similar. Indeed, as shown by Todd-Brown *et al*. (2013), initial values of carbon pool sizes differ by 5.9-fold, carbon influx by 2.6-fold, and residence times by 3.6-fold among 11 terrestrial carbon models used in CMIP5. Those differences in initial pool sizes and parameter values all propagate in the forward modeling to generate considerable uncertainty in predicted carbon-climate feedbacks among models. The identification and improvement of processes that generate large differences in those parameters among models should substantially reduce uncertainty in model predictions.

Parameterization and model-data fusion

With similar carbon balance equations encoded in global land models (Fig. 2c and d), future trajectories of carbon dynamics can be fully defined at given forcing if the coefficients of the carbon balance equations are well-constrained by observations. However, it is still challenging to parameterize ESMs to capture the heterogeneity of global vegetation and soil carbon processes. It is therefore essential to identify processes, databases, and modeling techniques that can help substantially improve representation of carbon processes in the models. In particular, we need to examine variations of coefficients of the carbon balance equations and estimate them against best available observations via model-data fusion (Raupach *et al*., 2005; Keenan *et al*., 2013; Smith *et al*., 2013; Hararuk *et al*., 2014) (Fig. 5d). There are presently technical difficulties in applying model-data fusion techniques to large, complex models. By isolating model components under a framework of traceability, these techniques can be successfully applied (Hararuk *et al*., 2014). This will not only improve model predictive performance but will also allow the identification of aspects of the carbon cycle where more empirical data are needed.

A new generation of models

Our analysis indicates that some components of the terrestrial carbon cycle appear to be highly predictable whilst our knowledge is limited on predictability of interannual variability, disturbance regime shifts, and indirect effects of climate change. It is practically feasible to constrain structures and parameters of model components for which we have solid theoretical and empirical understanding (predictive ability meets our understanding of predictability), whilst allowing structural variations for those components for which we have limited understanding of their predictability. In the latter components, alternative hypotheses should be explored. For example, we have limited observations on changes in disturbance regimes, vegetation dynamics, and ecosystem states under climate change despite potentially important consequences for the terrestrial carbon balance (Running, 2008). In the absence of adequate knowledge, different hypotheses on the response of the carbon cycle to these changes have been postulated in models. The new generation of models must have the capacity to compare the relative influences of the alternative hypotheses in greater detail than can be done at present, thus allowing identification of the aspects of our understanding in need of improvement.

Conclusions

In this article, we investigated fundamental properties of the terrestrial carbon cycle, examined its intrinsic predictability, and proposed a suite of future research directions to improve empirical understanding and model predictive ability of the carbon cycle. Specifically, we isolated endogenous internal processes of the terrestrial carbon cycle from exogenous forcing variables. The internal processes share five fundamental properties among all types of ecosystems on the Earth, which are (i) compartmentalization of carbon with distinct pools in an ecosystem; (ii) photosynthesis as the dominant carbon input; (iii) partitioning of input carbon between the various pools; (iv) donor pool-dominated carbon transfers between pools; and (v) the first-order decay of litter and soil organic matter to release CO_2 via respiration. The five properties together result in an emergent constraint that carbon pools tend to converge monotonically over time to some form of equilibrium. We used this constraint to evaluate the predictability of various components of the terrestrial carbon cycle in response to five classes of exogenous forcing. We categorize these components into five groups of high, medium, low, less known, and unknown predictability.

Future observational and experimental research should be focused on those components for which we have a poor understanding of their predictability, such as ecosystem state and its transition, states of and shifts in disturbance regimes, disturbance events and recovery trajectories, and response functions. Modeling research also needs to improve model predictive ability for the highly predictable components. To achieve that, it is essential to cope with complexity and gain tractability of ESMs. Then we can effectively evaluate impacts of adding model components, facilitate benchmark analyses, empower model intercomparisons, and enable data-model fusion. Overall, we suggest that characterizing the intrinsic predictability of different components of the terrestrial carbon cycle can help identify the major priorities for the research community.

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