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Dynamic disequilibrium of the terrestrial carbon cycle under global change

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In this review, we propose a new framework, dynamic disequilibrium of the carbon cycles, to assess future land carbon-sink dynamics. The framework recognizes internal ecosystem processes that drive the carbon cycle toward equilibrium, such as donor pool-dominated transfer; and external forces that create disequilibrium, such as disturbances and global change. Dynamic disequilibrium within one disturbance–recovery episode causes temporal changes in the carbon source and sink at yearly and decadal scales, but has no impacts on longer-term carbon sequestration unless disturbance regimes shift. Such shifts can result in long-term regional carbon loss or gain and be quantified by stochastic statistics for use in prognostic modeling. If the regime shifts result in ecosystem state changes in regions with large carbon reserves at risk, the global carbon cycle might be destabilized.

The need for a unified concept for carbon research

Nearly 30% of carbon (C) released by anthropogenic activities has been sequestered by terrestrial ecosystems during a period in which fossil-fuel CO_2 emissions increased from 2.4 Pg C per year in 1960 to 8.7 Pg C per year in 2008 [1–3]. These figures suggest that the rate of land C sequestration has accelerated over time. Recent research has identified various causes of future instability of the land C sink in response to global change. For example, it is suggested that forest dieback would trigger a massive C release from Amazonian forests [4]. As permafrost regions store significant amounts of C [5], climate warming could also accelerate the release of old C stored in such regions [6]. In addition, disturbances such as fires [7], storms [8], insect outbreaks [9] and land-use change [10,11] have been estimated by many researchers to release huge amounts of C. These processes and events have to be evaluated in a cohesive framework to guide future research into the stability of terrestrial C storage.

In this review, we develop a conceptual framework, dynamic disequilibrium of C cycles, to gain insights into terrestrial C sink dynamics. We first define the dynamic disequilibrium framework based on two opposite forces: (i) internal ecosystem processes; and (ii) external forcing variables; and then examine each of the three major elements of the framework (internal processes, disturbances and global change). We focus on the properties of internal processes that gradually equalize C efflux to influx and

thus diminish the C sink over time. Disturbances create disequilibrium in the C cycle by both individual events and regime shifts. Global change affects both internal processes and disturbances, potentially leading to complex system dynamics. Among all types of dynamic disequilibrium created by disturbances and global change, the state change in the C cycle could potentially have the most profound impacts on future terrestrial C sink stability.

The dynamic disequilibrium of C cycling

We propose the dynamic disequilibrium as a central concept to quantify the C sink and assess its stability in response to global change (Box 1). The dynamic disequilibrium framework is built upon two opposing forces: the internal equilibration processes versus external forcing variables, which act against each other to maintain dynamic disequilibrium. The internal processes involve organic C metabolism from photosynthetic fixation to respiratory releases by plants, animals and microbes. They include C transfers among pools and the growth and decomposition of litter and soil organic matter. The external forcing variables include both disturbances and global changes. Disturbances include anthropogenic land use and land-use change (e.g. forest cleaning, urbanization, cropping, pasture management and forestry), natural events (e.g. insect outbreaks, fire and volcanic eruptions) and extreme weather conditions (e.g. floods, droughts and storms). Global change includes increasing atmospheric $[CO_2]$, climate warming, altered precipitation, nitrogen (N) deposition and plant invasion.

External forcing variables influence internal C processes to create dynamic disequilibrium in several ways (Table 1). Some disturbances (e.g. clearing harvests and fires), for example, result in reduced C stocks in plant and soil pools (Figure 1). Other disturbances, such as hurricanes and insect outbreaks, increase the C stock in litter pools, but decrease it in plant pools [8,9]. All of these disturbances cause C cycling at disequilibrium, from which the internal processes facilitate ecosystem recovery toward equilibrium. After the disturbances, the plant canopy is usually restored within a few years and so the plant biomass pool size gradually increases. C pool sizes in the litter and soil might initially decline following a disturbance, but then increase over time to a level of stabilized equilibrium [12]. Some disturbances, such as invasive species, can change the ecosystem structure, enhance C influx and increase pool sizes [13].

Box 1. Elements and predictions of the dynamic disequilibrium framework

Elements

- C sequestration (or release) occurs only when the C influx is larger (or smaller) than the C efflux (i.e. there is disequilibrium).
- Ecosystems have internal processes that, without disturbances and global changes, gradually equalize C efflux to influx and thus diminish the C sink or source over time to reach equilibrium (i.e. recovery force).
- External forces, such as disturbances and global change, create disequilibrium by altering internal C processes and pool sizes.
- The internal C processes and external forces are opposite and act against each other to maintain dynamic disequilibrium.

Predictions

- Disturbance causes temporal changes in the C sink and source within one disturbance–recovery episode, but has no impact on long-term C sink dynamics unless its regime changes.
- The realizable C storage is smaller than the equilibrium level when disturbances occur frequently enough to prevent the ecosystem from recovering fully under a prevailing regime (Figure 2d–f).
- Ecosystem C storage capacity decreases if global change and disturbance reduce canopy photosynthetic C influx and residence times, and vice versa.
- Terrestrial C storage capacity decreases, leading to positive feedback on climate change, if climate change causes more frequent, severe and extensive disturbances.
- Instability of the terrestrial C sink becomes globally significant when global change and disturbances trigger state changes in regions where vast C reserves are at risk.

Global change affects both internal C processes and external disturbance regimes, inducing dynamic disequilibrium. Climate warming, for example, can not only accelerate the microbial decomposition of litter and soil organic C [14], but also alter fire regimes [15]. Changes in precipitation not only affect plant growth [16], but can also be conducive to fire and insect outbreaks [9]. Thus, global change can induce dynamic disequilibrium via direct effects on internal C processes or indirectly via altered disturbance regimes. In short, the dynamic disequilibrium concept refers to a time-variant magnitude of the C-cycle disequilibrium. While the disequilibrium is created by disturbances and global change, its varying magnitude with time is driven by internal C processes.

Internal processes driving ecosystem C cycles towards equilibrium

The C cycle in an ecosystem is usually initiated when plants fix CO_2 via photosynthesis. Photosynthate is used partially for plant growth and partially for plant respiration, releasing CO_2 to the atmosphere. Plant tissues can live for several months (e.g. leaves and fine roots) up to hundreds of years (e.g. wood). Dead plant material (i.e. litter) is partially decomposed by microbes to release CO_2 and partially incorporated into soil organic matter (SOM). SOM can store C in the soil for up to hundreds or thousands of years before it is oxidized [17,18]. This C cycle in an

Table 1. Applications of the dynamic disequilibrium concept to assess properties of C sink dynamics in five cases

| Case	Equilibrium	Disequilibrium	Methods of quantification	Note
Ecosystem over 1 day and 1 year	Annual averages of C influx and efflux are balanced unless the ecosystem is at disequilibrium owing to disturbance or global change	Diel and seasonal imbalances of C influx and efflux are driven by cyclic environmental change	Diel and seasonal imbalances of C influx and efflux can generally be simulated successfully by models without changes in parameterization	No need to apply the dynamic disequilibrium concept for understanding diel and seasonal dynamics of the C cycle
Global change	An original equilibrium can be defined at a reference condition (e.g. pre-industrial [CO_2]) and a new equilibrium at the given set of changed conditions	Dynamic disequilibrium occurs as the C cycle shifts from the original to a new equilibrium. Global change factors gradually alter over time, leading to continuous dynamic disequilibrium	Direct effects of global change on the C cycle can be modeled via environmental scalars to estimate dynamic disequilibrium explicitly	Dynamic disequilibrium diminishes with acclimation and adaptation, but amplifies with changes in ecosystem structure to new states of the C cycle
Ecosystem within one disturbance–recovery episode	C cycle is at equilibrium if the ecosystem fully recovers after a disturbance. The equilibrium C storage equals the product of C influx and residence time	C cycle is at dynamic disequilibrium and an ecosystem sequesters or releases C before the ecosystem fully recovers to the equilibrium level	C sequestration or release under dynamic disequilibrium can be fully quantified by three sets of parameters related to C influx, residence time and initial pool size	Data assimilation and other techniques are needed to estimate the three sets of parameters simultaneously
Regions with multiple disturbances over time	C cycle is at dynamic equilibrium in a region when the disturbance regime does not shift (i.e. is stationary). The realizable C storage under a stationary regime is smaller than that at the equilibrium level (Figure 2d–f, main text)	C cycle is at dynamic disequilibrium and the region sequesters or releases C when the disturbance regime in the region shifts (i.e. is non-stationary)	Disturbance regime shifts can be characterized by a joint probability distribution of disturbance frequency and severity over space and time. The joint distribution can be combined with C cycle models to estimate regional C sink dynamics over time	Single disturbance events offer no information on regional C sequestration. Probability distribution can be used for prognostic C modeling by generating stochastic forcings of disturbance
Multiple states	C cycle can be at equilibrium at the original and alternative states	Dynamic disequilibrium occurs as an ecosystem changes from the original to alternative states	State changes usually result from changed ecosystem structures to require changes in structures and parameters of C models	State changes can be the major mechanisms for instability of future terrestrial C storage
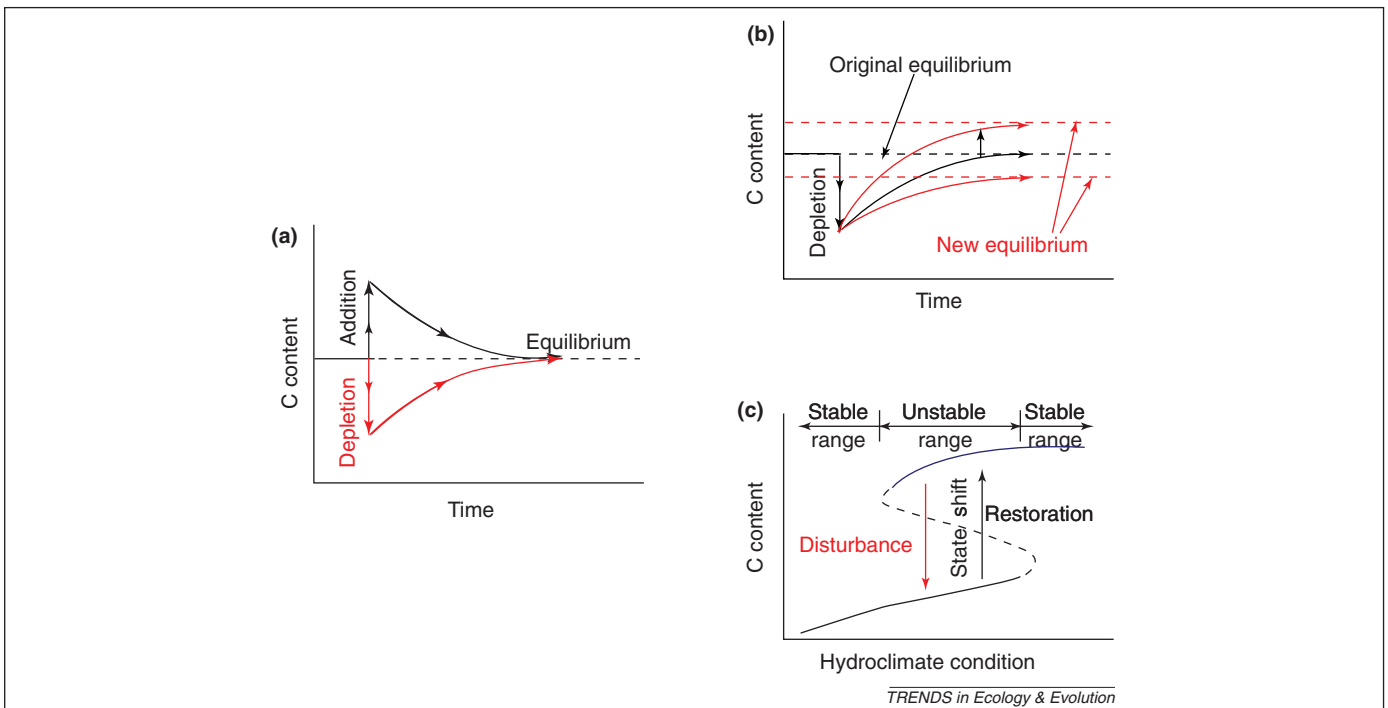
Figure 1. The forces shaping the dynamic disequilibrium of C cycling. **(a)** Disturbances usually create disequilibrium by: either depleting or adding C to plant, litter and soil pools; changing photosynthetic capacity; and altering residence times. Internal ecosystem processes, such as donor pool-dominated transfer, drive the recovery of the ecosystem towards equilibrium. The rate of recovery is determined by the photosynthetic capacity and C residence time. **(b)** Changes in the recovery trajectory if global change alters C influx and residence time. If elevated CO_2 increases photosynthetic C influx or residence time, for example, ecosystem C content might recover to a new equilibrium level (red dashed lines) that is higher than the original equilibrium level (black dashed line). If climate warming increases decomposition and decreases the C residence time or reduced precipitation decreases C influx, ecosystem C content might recover to an equilibrium level that is lower (red dashed line) than the original. **(c)** State changes of the ecosystem C cycle, which are determined by hydroclimate condition and triggered by disturbance or restoration. When global change and human activities substantially alter hydroclimate condition in a region, the ecosystem C cycle might change from a stable to an unstable state or vice versa. Along the moisture gradient in the USA, for example, ecosystems change from a relatively stable state of forest in the east to multiple states on the Great Plains to another relatively stable state of desert in the west. If climate change causes shifts in precipitation regimes, boundaries move between the relatively stable and unstable states of ecosystems. Human activities in terms of fire suppression have resulted in state changes from grasslands to woodlands on the Great Plains. Restoration of natural fire can reverse the state change.

ecosystem can be mathematically expressed [19] by Equation 1:

$$\begin{cases} \dfrac{dX(t)}{dt} = \xi(t)AX(t) + BU(t) \\ X(0) = X_0 \end{cases} \tag{1}$$

where $X(t)$ is the C pool size, A is the C transfer matrix, U is the photosynthetic input, B is a vector of partitioning coefficients, $X(0)$ is the initial value of the C pool and ξ is an environmental scalar. Equation 1 adequately describes most observed C processes, such as litter decomposition [20,21] and soil C dynamics, and has been repre-

sented in most ecosystem models [22,23] as well as being integrated into Earth system models [4,24].

The C cycle can be characterized by five properties (Box 2), of which the donor pool-dominated transfer is the most fundamental mechanism that drives C processes towards equilibrium. (In comparison, prey and predator populations are each regulated by both donor and recipient populations, causing complex dynamics of a predation system [25].) The equilibration mechanism of the C cycle was originally described by Odum [26] and can be verified by using mathematical analysis and empirical evidence. Mathematically, Equation 1 satisfies the Lyapunov stability

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Box 2. Properties of the internal C processes of an ecosystem

- Photosynthesis as the primary pathway of C entering an ecosystem and described by parameter U in Equation 1 (main text).
- Compartmentalization with clear physical boundaries of different pools of C in leaf, root, wood, litter and soil. Soil C has been further compartmentalized into a few conceptual pools in some models to describe adequately its short- and long-term dynamics. Pools are represented by vector $X(t)$ with their initial values by $X(0)$ in Equation 1 (main text).
- Partitioning of C from photosynthesis to various pools as described by vector B for plant C partitioning and matrix A for C transfer among plant, litter and soil pools (Equation 1, main text). Each of the pools has a different residence time, which is the inverse of its transfer coefficient (i.e. the diagonal element of A). The capacity of an ecosystem to sequester C is higher if more C is partitioned to pools with long residence times, such as wood and soil.

- Donor pool-dominated C transfers. C transfer from a plant to litter pool, for example, is dominated by the amount of C in the plant pool and not the litter pool. In this transfer, the plant is a donor, whereas the litter pool is a recipient. Although SOM decomposition is mediated primarily by microorganisms [98,99], C transfer among soil pools can be modeled effectively in proportion to donor-pool sizes and not to recipient pool sizes.
- The first-order decay of litter and SOM to release CO_2. A first-order decay function as described by the first term on the right side of Equation 1 (main text) can adequately describe the mass remaining of litter with time lapsed based on data from litter decomposition studies, and SOM decomposition from soil incubation experiments. The combined property of the donor pool-dominated transfers and first-order decay function is the fundamental mechanism that drives the C cycle toward equilibrium.

conditions with negative eigenvalues of the C transfer matrix *A* linearized near the equilibrium [27] see supplementary material online). Empirically, many studies have shown that C stocks in plant and soil pools recover towards equilibrium during secondary forest succession and grassland restoration following disturbances [28,29].

At equilibrium, C influx equals efflux, C pools are stabilized without any further change and the net ecosystem C exchange becomes zero (i.e. there is no C sink or source). The equilibrated size of C storage in an ecosystem equals the product of C influx and residence time [19]. C influx at the ecosystem scale is equals to canopy photosynthesis. The ecosystem residence time of C is determined by partitioning coefficients in vector *b* and the transfer matrix *A* of Equation 1 [30]. A tropical forest, for example, has longer residence times, and thus a larger C sink capacity, than does a tropical savanna, even though both have high C influx. By contrast, C pool sizes in tundra soil are large primarily because C residence times in these regions are long [5,6].

When the C pool size is smaller than the equilibrium size, respiratory CO_2 release is less than the photosynthetic influx, leading to C sequestration and an increase in the C pool size over time. When the C pool size is larger than the equilibrium pool size, the ecosystem becomes a net C source and the pool size diminishes over time, toward equilibrium. This dynamic disequilibrium can be quantified by three sets of parameters related to: (i) C influx; (ii) C residence time; and (iii) the initial pool size (Figure 2a–c). Traditionally, C cycle models were spun up to equilibrium before being used to study C sequestration in response to global change [25]. Such an assumption on equilibrium

could result in major discrepancies between observed and modeled C fluxes and pools [31]. Recently, data assimilation techniques have been used to estimate all three sets of parameters to account for disequilibrium [32].

At least three aspects of the internal C processes can be affected by disturbance and global change: (i) the pool sizes altered by disturbances; (ii) the equilibrium levels of C storage altered by global change; and (iii) ecosystem structure changed to different states of the C cycle (Table 1). For example, fire depletes C in plant and litter pools but might not affect the equilibrium level of C storage. Thus, fire effects can be modeled by resetting initial pool sizes without changes in parameters related to C influx and residence time. Increasing atmospheric $[CO_2]$ increases C influx so that the equilibrium C storage increases (Figure 1b). Climate warming might increase decomposition and decrease residence time so that the equilibrium C storage decreases. Most models have environmental scalars to simulate these direct effects of global change on C processes. If global change and disturbances result in changes in vegetation structure and soil properties, the state of the C cycle also might have changed. The C state change can be simulated by adjusting the parameter values in and modifying model structures of Equation 1.

Disturbances leading to disequilibrium

An ecosystem is subject to natural and anthropogenic disturbances, causing ecosystem C cycling processes to be at disequilibrium. Disturbances create disequilibrium of the C cycle by: (i) either depleting or adding C in pools; (ii) either decreasing or increasing canopy photosynthesis; and (iii)
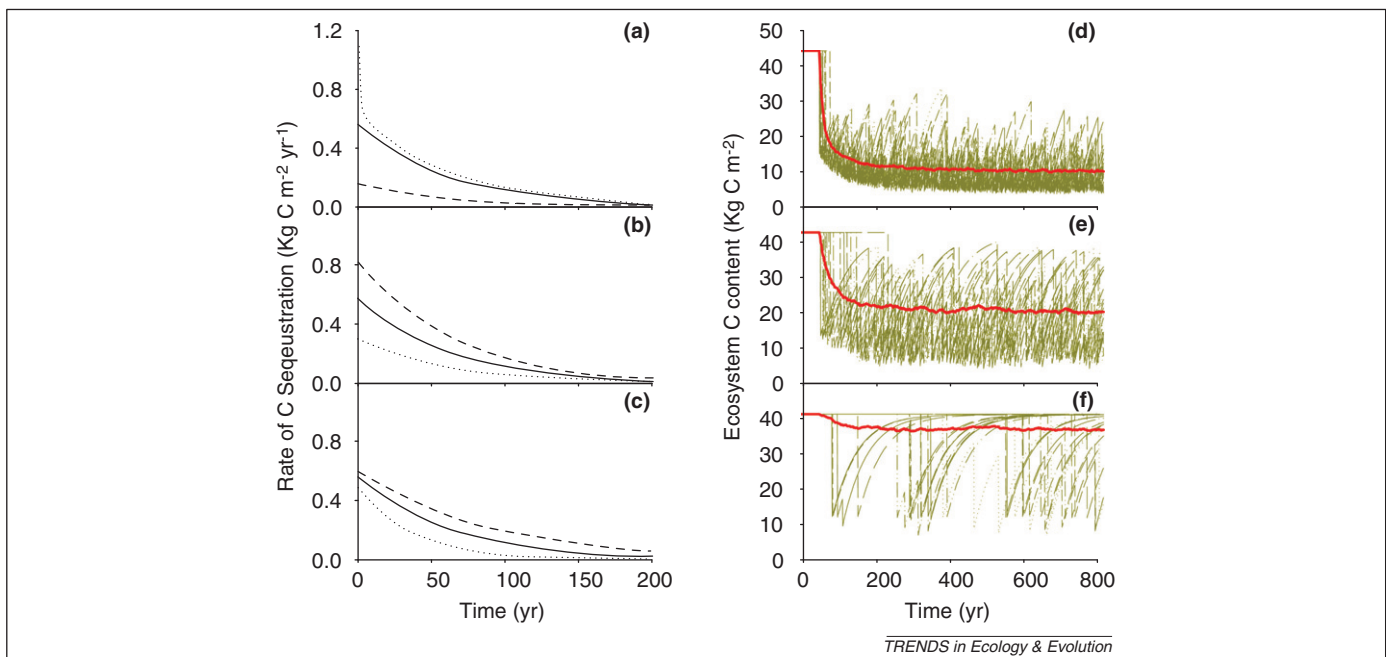

Figure 2. Simulated rate of C sequestration as affected by initial values of pool sizes **(a)**, C influx **(b)**, C residence time **(c)** and ecosystem C storage under disturbance frequency of once every 10 **(d)**, 40 **(e)** and 400 **(f)** years. The simulation was performed by using an eight-pool model with three levels of initial ecosystem C content, C influx and residence time. The baseline values of these parameters were 6.80 Kg C m^{-2}, 1.23 Kg C m^{-2} per year and 34.7 years, respectively. These values were obtained from an inverse analysis of data collected at the Duke Forest Free Air Free-Air CO_2 Enrichment site [28]. The baseline results are indicated by solid lines of (a–c), whereas the dotted and dashed lines indicate simulation results with low and high values of the three parameters, respectively. The low and high initial pool sizes were zero and five times of the base value, respectively. The low and high C influx and residence time were 40% lower and higher than the base values, respectively. The disturbance events were assumed to be Poisson events and to remove all biomass. The 20 dark-yellow lines in (d–f) are individual simulations of the eight-pool model with the baseline parameter values, whereas the red lines are the mean of 200 simulations. The figure shows that the realizable C storage in an ecosystem decreases with increasing disturbance frequency.

altering C residence times via changes in respiration and decomposition. Each disturbance creates disequilibrium at a different magnitude, spatial scale and frequency.

Land use and land-use change

Of all types of disturbance, land use is probably most significant in its effect because it affects the C cycle in at least two ways, through land-use change and continuous land use. Land-use change converts forests and native grasslands to croplands, pastures and urban areas. Conversion of forests not only results in the release of C to the atmosphere, but also shortens the C residence time owing to the elimination of C pools in plant wood biomass and coarse wood debris, and the physical disturbance of long-term soil C pools [33]. In the case of urban development in forests, canopy photosynthesis is all but stopped and no C flows into impermeable areas. Conversion of native grasslands leads to reduced C residence times in soil pools when the land is plowed. Continuous use after land conversion disturbs the C cycle on a regular basis. For example, in annual cropping systems with tillage, soil is disturbed at least once a year. In commercial plantations, forests are usually harvested once every 10–20 years. Once the land is released from human use, the C storage capacity usually recovers. For example, grassland restoration in North America increased C storage by 43 g C m^{-2}·per year during the first 26 years [29].

Spatially, humans use nearly 50% of the land surface of the Earth and 23% of net primary production for agriculture and domestic animal grazing [10,34]. From 1850 to 2000, land-use conversion resulted in net C emissions that accounted for ~35% of the total global anthropogenic emissions [11,35]. Currently, human land-use activities result in a net release of 1–2 Pg C per year to the atmosphere [11]. By contrast, reforestation, recovery and improved management of forests and croplands result in C sequestration [36].

Fire

Fire burns live and dead plants, litter, and sometimes C in the top soil layers, resulting in the removal of C from these pools to below equilibrium levels. Fire usually reduces ecosystem photosynthetic capacity and also alters its physical and chemical properties to influence the decomposition of litter and SOM [37]. Hence, C residence time can also be affected. Globally, wildfires burn 3.5–4.5 million km^2 of land per year (~4% of the vegetated land surface) and emit 2–3 Pg C per year into the atmosphere [38]. From 1997 to 2001, fire-induced CO_2 emissions ranged from 1.74 to 3.53 Pg C per year [39].

Other disturbances

Other episodic events, such as windstorms or insect epidemics, occur on a less extensive spatial scale than do fires and anthropogenic land use. Windstorms and insect outbreaks both reduce canopy photosynthesis and transfer C from plant to litter pools. Hurricane Katrina in the Gulf of Mexico in 2005 transferred C from trees so that they became a net source of ~0.1 Pg C in the years that followed [8,40]. A pine beetle epidemic that occurred in an estimated 374 000 km^2 of western North American forest killed trees and transferred C to litter pools, releasing C over tens of years [9]. Tornados, volcanic eruptions and floods all result in tree mortality and, therefore, release C [41]. A Europe-wide drought during 2003 resulted in a strong anomalous net release of CO_2 to the atmosphere [42]. Drought has also increased tree mortality (and thus decreased C residence times) in the USA and Amazon [43,44].

Disturbance regime

Disturbances occur at different frequencies with varying severity on diverse spatial scales in different regions. For example, fire disturbs the land C cycle relatively frequently in dry regions, but rarely occurs in wet regions [45]. Repeated disturbances not only affect C cycles during the events themselves, but also substantially reduce the realizable capacity of an ecosystem to store C owing to the short recovery time [46,47]. Indeed, the realizable C storage is lower than the potential capacity at the equilibrium level as the disturbance frequency and severity increases (Figure 2d–f). Thus, it is crucial to quantify the nonstationarity of disturbance regimes to estimate a regional C sink capacity. To this end, satellite data have been used to describe land-use patterns, fire regimes and other disturbances [48,49]. Eddy flux towers [50], forest inventories [51] and long-term observations [52] have been used to measure disturbance effects on C processes.

Impacts of global change on the terrestrial C cycle

Global change affects C sink dynamics via direct influences on C influx and residence time, indirect effects via induced changes in ecosystem structure and shifts in disturbance regimes.

Direct and indirect effects of global change on C processes

Increasing levels of atmospheric [CO_2], for example, primarily stimulate photosynthetic C influx, and usually result in increases in plant biomass growth and, possibly, in soil C storage [53] (Table 2). Instantaneous increases in C influx in response to increasing [CO_2] can be estimated from an invariant function [54,55]. However, the long-term sustainability of C sequestration depends on N availability [56], which regulates CO_2 stimulation of plant growth [57,58] and net soil C accumulation [59]. Changes in long-term N availability in terrestrial ecosystems have not been well quantified.

Temperature affects both C influx and residence time. It is usually assumed that C release is accelerated more (i.e. has a reduced residence time) by climate warming than is photosynthesis. As a consequence, climate warming would result in a net C release, leading to additional warming via positive feedback [25]. Experimental evidence has shown that temperature also indirectly affects ecosystem C processes via changes in phenology and the length of growing seasons, nutrient availability, ecosystem water dynamics and species composition, with complex effects on C influx and residence time [14].

Increased precipitation usually stimulates C influx into ecosystems as well as increasing decomposition rates (i.e.

Table 2. Kknowledge base, major gaps, and future needs on responses of C processes to global change

Factors	Knowledge base	Knowledge gaps	Future research needs
Increasing atmospheric [CO_2]	Elevated [CO_2] primarily stimulates C influx into ecosystems and creates potentials for C sequestration unless N and water strongly limit plant growth	N regulation of long-term C sequestration Partitioning of additional C to pools with different residence times	C partitioning to different pools C sink vs. N relationships as modified by water availability, clay content, and temperature regimes CO_2 effects on residence times
Climate warming	Warming affects all chemical, physical and biological processes Warming extends growing seasons, increases nutrient availability, alters species composition and water cycling Variable responses of photosynthesis and respiration to warming	Relative sensitivities of various C processes to temperature change Relative importance of various C processes in different ecosystems	Temperature response functions and acclimation of photosynthesis, respiration, SOM decomposition, species composition, phenology, nutrient availability and soil water availability Spatial and temporal variability of key parameters, such as Q_{10}
Altered precipitation	Increases in NPP, respiration and decomposition with increased precipitation and vice versa Increased variability in NPP and respiration with increased variability of precipitation in terms of amounts, intensity and frequency	Difficult to summarize ecosystem responses because of the many ways that their amounts, intensity, frequency and spatial distributions can be altered Changes in belowground C dynamics with precipitation	Response functions of NPP, respiration, species composition and decomposition rates with precipitation or moisture content Temporal and spatial variability in major C processes as related to variability in precipitation amount, intensity and frequency
Nitrogen deposition	Stimulates plant growth and NPP Litter produced under high N is of high quality and is easily decomposed Soil C can decrease or increase depending on the ecosystem type	Relative effects of N on NPP versus decomposition N-induced changes in C partitioning	N effects on relative C allocation to belowground Contribution of aboveground litter production to soil C storage Decomposition of litter produced under high levels of N

decreased C residence time) [16]. Precipitation as a forcing variable could change in its frequency, intensity and amount, each of which has different effects on ecosystem C processes. Increases in rainfall variability, for example, decreased soil respiration and aboveground net primary production [60,61]. Precipitation also influences species composition, soil development, nutrient availability and other processes, all of which could indirectly affect ecosystem C processes [62].

N fertilization and deposition usually stimulate C influx and result in C storage in plant pools [63,64]. Whether the increased plant growth can lead to net C storage in soil (the largest pool in terrestrial ecosystems) is controversial [65]. N fertilization significantly stimulated soil C gain in some ecosystems [66,67], but its loss in other ecosystems [68,69]. N usually stimulates litter and SOM decomposition [70] and more aboveground than belowground growth, reducing C input into the soil.

Effects of global change on disturbance regimes
Global change can also regulate disturbance regimes. Occurrences of large wildfires in forests in the western USA, for example, increased markedly during the mid-1980 s, owing largely to unusually warmer springs and longer summer dry seasons [15]. Tight coupling between fire activities and climate oscillations has been revealed by dendrochronological and observational analyses [71] and sedimentary charcoal records [72]. The projected global warming of 1.5–5.8 °C during the current century could increase extreme fire events [73], leading to significant C loss from affected ecosystems.

Episodic disturbances, such as forest dieback and insect outbreaks, are also influenced by global change [74]. Mortality rates of old forests in the western USA, for example, have increased rapidly in recent decades, attributable to regional warming and subsequent increases in water deficits [75]. Warming and drought stress can contribute directly to tree mortality [76] and enhance insect and pathogen attacks of trees [77] and wildfires. Yet it is still challenging to project future disturbance regimes in response to global change.

Future C sink dynamics and state changes
Future C sink dynamics in terrestrial ecosystems will be still governed by these internal processes as described by Equation 1 but also regulated by disturbances and global change in at least four ways: (i) temporal changes in pool sizes by disturbances; (ii) altered disturbance regimes; (iii) altered C influx and residence time directly by global change; and (iv) state changes in the C cycle caused by disturbances and global change (Table 1). Of these, the state change is least understood but has the most profound impact on future C stability in the terrestrial ecosystems [78–84].

The multiple states of ecosystem equilibrium have long been documented in ecology [85,86]. The state change might be primarily determined by hydroclimate conditions (Figure 1c), regulated by climate–land surface feedback, and triggered by natural disturbances and human intervention. When an ecosystem changes to a new state with a low C sink capacity, a net release of C from the ecosystem to the atmosphere occurs, leading to positive feedback on climate warming. Conversely, a change of an ecosystem to a state with a high sink capacity results in C sequestration. When the state change occurs in regions with huge amounts of C at stake, it can destabilize the global C cycle and enhance the positive C–climate feedback.

C storage in three regions of the world (Amazonian forests, African tropic forests and permafrost) could undergo

unstable state changes to become major C sources. The three regions contain a total of ~2000 Pg C, four to five times that in the atmosphere. Amazonian forests are currently the largest tropical forests on Earth and affect atmospheric circulation across continents and hemispheres [87]. The forests themselves contain ~86–140 Pg C [88] and an equivalent amount in their soils [87]. Climate change could alter moist convection, especially in the boundary between convecting and nonconvecting zones [89], leading to a reduction in dry-season rainfall in various parts of Amazonia [84] and triggering positive feedback, resulting in ecosystem state changes [90].

African tropical forests are distributed around the equator, away from which are savanna grasslands and deserts in a sequence to either the north or south. The Sahara was heavily vegetated 6000 years ago and experienced an abrupt change in its vegetation and climate 4000–5000 years ago [91]. The Sahel region of West Africa has also gone through state changes [92], resulting partially from interactions between the atmosphere and vegetation [93]. Changes in vegetation properties (e.g. rooting depth and leaf area index) or types (e.g. forest, grassland and desert) can alter the moisture gradient in the atmospheric boundary layer from the ocean to inland, leading to either positive or negative feedback, which then triggers ecosystem state changes.

Permafrost in the high latitude regions of the northern hemisphere contains 1672 Pg of organic C [94], ~50% of the estimated global belowground C pool. As land surface temperatures are projected to increase by up to 7–8 °C in these regions by the end of the current century [73], ecosystems will shift from permafrost to active layers via thawing. The state change will result in substantial C loss and become one of the most significant potential feedbacks from land ecosystems to the atmosphere [95]. The state changes from permafrost to active soil involve changes in physical, chemical, biological and ecological states. The instability of the land C sink could occur as a result of a vegetation shift between boreal forests and tundra [96], with different snow covers reflecting radiation and regulating temperature [97].

Concluding remarks

The dynamic disequilibrium framework provides guiding principles on the assessment of future land C sink dynamics in four cases. First, dynamic disequilibrium within one disturbance–recovery episode causes temporal changes in the C source and sink at yearly and decadal scales. Individual disturbance events might not have any impacts on longer-term C sequestration, unless the disturbance regimes shift. Dynamic disequilibrium within the episode can not be fully quantified until three sets of parameters related to C influx, residence time and initial pool sizes are estimated with data assimilation and other techniques. Second, shifts in disturbance regimes, which are usually caused by global change and human intervention, can result in long-term regional C loss or gain. Regime shifts can be quantified by joint probability distributions of disturbance frequency, severity and extensity over time and space. The probability distributions introduce stochastic approaches to the integration of disturbance

theory with biogeochemistry and can be used to generate disturbance events in prognostic modeling. Third, global change not only directly alters C influx and residence time, but also induces changes in ecosystem structure and disturbance regimes. Although direct effects of global change on the C cycle can be simulated by most Earth system models, it is still a major challenge to quantify future changes in disturbance regimes and ecosystem structure under global change. Fourth, when the ecosystem structure changes and disturbance regimes shift, the ecosystem C cycle might move to alternative states. State changes among multiple equilibriums can lead to global instability of future land C sink dynamics if they occur in regions with large C reserves at risk. Innovative methods are needed to examine the conditions and processes leading to state changes.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2010.11.003.

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