

LETTER • OPEN ACCESS

Recovery time and state change of terrestrial carbon cycle after disturbance

To cite this article: Zheng Fu *et al* 2017 *Environ. Res. Lett.* **12** 104004

View the [article online](#) for updates and enhancements.

Related content

- [Modeling Long-term Forest Carbon Spatiotemporal Dynamics With Historical Climate and Recent Remote Sensing Data](#)
Jing M. Chen
- [Warming-induced shift towards forbs and grasses and its relation to the carbon sequestration in an alpine meadow](#)
Fei Peng, Xian Xue, Manhou Xu *et al.*
- [Shifts in biomass and productivity for a subtropical dry forest in response to simulated elevated hurricane disturbances](#)
Jennifer A Holm, Skip J Van Bloem, Guy R Larocque *et al.*

Environmental Research Letters



LETTER

OPEN ACCESS

RECEIVED
6 May 2017

REVISED
4 September 2017

ACCEPTED FOR PUBLICATION
5 September 2017

PUBLISHED
3 October 2017

Original content from
this work may be used
under the terms of the
[Creative Commons
Attribution 3.0 licence](#).

Any further distribution
of this work must
maintain attribution to
the author(s) and the
title of the work, journal
citation and DOI.



Recovery time and state change of terrestrial carbon cycle after disturbance

Zheng Fu^{1,2}, Dejun Li³, Oleksandra Hararuk⁴, Christopher Schwalm⁵, Yiqi Luo⁶, Liming Yan⁷ and Shuli Niu^{1,2,8}

- ¹ Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, People's Republic of China
- ² University of Chinese Academy of Sciences, No.19A Yuquan Road, Beijing, 100049, People's Republic of China
- ³ Huanjiang Observation and Research Station for Karst Ecosystems, Key Laboratory of Agro-ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Changsha 410125, Hunan, People's Republic of China
- ⁴ Pacific Forestry Centre, Canadian Forest Service, Victoria, BC V8Z 1M5, Canada
- ⁵ Woods Hole Research Center, Falmouth MA 02540, United States of America
- ⁶ Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK 73019, United States of America
- ⁷ School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200062, People's Republic of China
- ⁸ Author to whom any correspondence should be addressed.

E-mail: sniu@igsnr.ac.cn

Keywords: state change, recovery time, carbon cycle, equilibrium state, global synthesis

Supplementary material for this article is available [online](#)

Abstract

Ecosystems usually recover from disturbance until a stable state, during which carbon (C) is accumulated to compensate for the C loss associated with disturbance events. However, it is not well understood how likely it is for an ecosystem to recover to an alternative state and how long it takes to recover toward a stable state. Here, we synthesized the results from 77 peer-reviewed case studies that examined ecosystem recovery following disturbances to quantify state change (relative changes between pre-disturbance and fully recovered states) and recovery times for various C cycle variables and disturbance types. We found that most ecosystem C pools and fluxes fully recovered to a stable state that was not significantly different from the pre-disturbance state, except for leaf area index and net primary productivity, which were 10% and 35% higher than the pre-disturbance value, respectively, in forest ecosystem. Recovery times varied largely among variables and disturbance types in the forest, with the longest recovery time required for total biomass (104 ± 33 years) and the shortest time required for C fluxes (23 ± 5 years). The longest and shortest recovery times for different disturbance types are deforestation (101 ± 28 years) and drought (10 ± 1 years), respectively. The recovery time was related to disturbance severity with severer disturbances requiring longer recovery times. However, in the long term, recovery had a strong tendency to drive ecosystem C accumulation towards an equilibrium state. Although we assumed disturbances are static, the recovery-related estimates and relationships revealed in this study are crucial for improving the estimates of disturbance impacts and long-term C balance in terrestrial ecosystems within a disturbance-recovery cycle.

1. Introduction

With the rapid growth of human population and acceleration of environment changes, disturbance events happen more frequently, which dramatically affects ecosystem carbon (C) cycle (Luo *et al* 2015, Villnäs *et al* 2013) and changes the C balance of terrestrial ecosystems (Mack *et al* 2011, Running 2008). For

example, the 2000–2004 droughts caused a $0.03\text{--}0.3$ Pg C year⁻¹ decline in the western North American C sink strength (Schwalm *et al* 2012) and the 2003 drought led to the loss of 0.5 Pg C from European ecosystems (Ciais *et al* 2005). Deforestation in the tropics caused an average annual C loss of 2.9 Pg C during 1990–2007 (Achard *et al* 2014, Pan *et al* 2011). Global fires burn around 348 Mha per year—about 4%

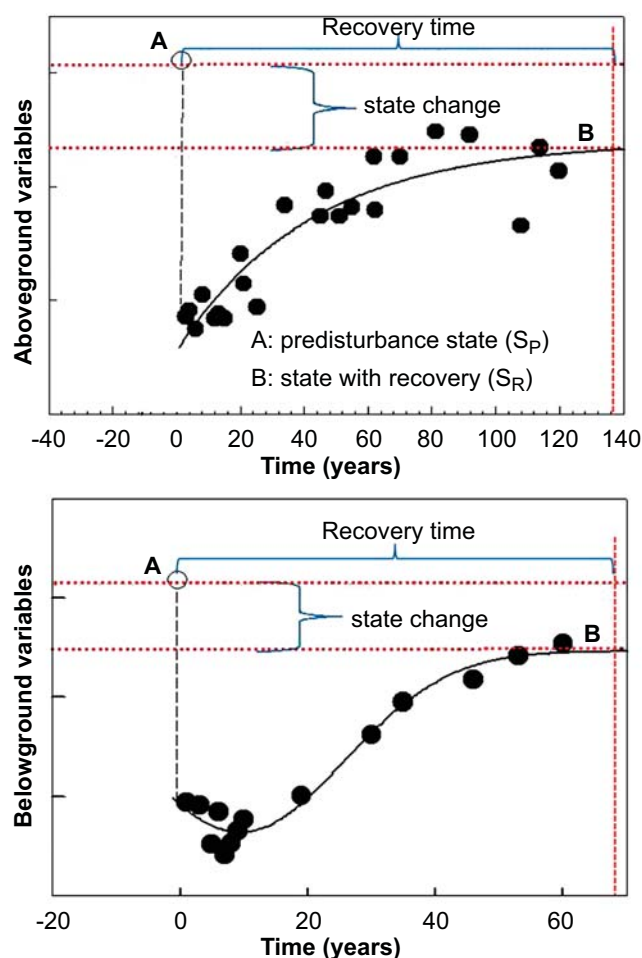


Figure 1. Conceptual figure for the recovery trajectory following a disturbance. The closed circles represent a variable measured along a chronosequence during recovery. We used the mono-exponential rise to maximum model (equations (1) and (4)) to fit the observations and extrapolate key parameters for each case study. A indicates a pre-disturbance state and B indicates the fully-recovered stable state. The relative differences between A and B were state change. The recovery time means the time it takes for a variable recover to a stable state. This conceptual figure refers to both carbon stocks and fluxes; the unit of y-axes is g C m^{-2} .

of vegetated land surfaces—and emit 4 Pg of C into the atmosphere annually (Chapin III *et al* 2011, Tansey *et al* 2008). Thus, disturbance is considered the primary driver to change ecosystems from C sinks to C sources (Baldocchi 2008, Le Quéré *et al* 2013). Despite numerous studies demonstrating critical impacts of disturbances on terrestrial ecosystem C cycle (Bowman *et al* 2009, Houghton 1995, Mack *et al* 2011, Reichstein *et al* 2013, Running 2008, Vanderwel *et al* 2013), a comprehensive analysis on the recovery of ecosystem C cycle from disturbance has drawn less attention.

Ecosystem recovery following disturbances usually absorbs C from the atmosphere to partially compensate the C losses caused by disturbance. It is documented that ecosystem recovery from disturbance contributes largely to the increasing C sink in forest ecosystems (Caspersen *et al* 2000, McMahon *et al* 2010, Raymond *et al* 2015) and the enlarging seasonal CO_2 amplitude in northern hemisphere (Graven *et al* 2013, Kasischke *et al* 2010, Zimov *et al* 1999). During recovery, ecosystem biomass usually accumulates in three stages: slow stage, followed by a fast stage and another slow stage, during which it reaches the maximum value

(Pare and Bergeron 1995, Preger *et al* 2010). Once the maximum value is reached biomass enters into a stable state (no change further with time) as conceptually depicted in the figure 1. Such patterns of biomass recovery have been detected in a wide range of ecosystems (Lichstein *et al* 2009). The carbon pool sizes in the litter and soil might initially decline right after a disturbance due to continued stimulation of C decomposition and no new C input, but then increase over time to a stable state (Sun *et al* 2004). So, a complete disturbance-recovery trajectory follows a monotonic response pattern with times, during which the ecosystem accumulates C (Odum 1969, Williams *et al* 2012, Yang *et al* 2011). Although the recovery trajectory is similar across ecosystem types and regions (Johnson *et al* 2000), the characteristics of recovery, like whether or not the ecosystems can recover to pre-disturbance states and how long it takes to fully recover, are not well quantified yet.

Theoretically, recovery would proceed toward a stable state after a disturbance (Luo *et al* 2015, Luo and Weng 2011, Scheffer *et al* 2001, Scheffer and Carpenter 2003, Villnäs *et al* 2013). This stable state might

be similar to the pre-disturbance state or it might approach alternative states (Turner 2010). Which state an ecosystem is likely to recover to may depend on disturbance severity and recovery time. The theory and concepts for state shift are rich (Barnosky *et al* 2012, Scheffer *et al* 2009), but real-world tests are rare (Carpenter *et al* 2011), especially for ecosystem properties in the terrestrial ecosystems. To our knowledge, there is little empirical evidence so far to illustrate the state changes of ecosystem C cycle after disturbances. The relationship between state changes, disturbance severity and recovery time is similarly poorly constrained and applied to C cycle, which lessens the predictability of the terrestrial C cycle (Luo *et al* 2015).

Recovery time, the period within which it takes an ecosystem to return to a stable state, usually considering years or decades, reflects the recovery dynamics of the ecosystem (Jones and Schmitz 2009, Sun *et al* 2004). It determines the long-term C cycle and budget of an ecosystem in response to disturbance (Luo *et al* 2015). A recent synthesis demonstrates that most ecosystems can recover on timescales from decades to half-centuries, with longer recovery times for ecosystem function and plant communities in terrestrial ecosystems (Jones and Schmitz 2009). However, previous studies rarely quantify and compare recovery time of different C processes under various disturbance types.

In this study, we compiled a global dataset of disturbance types, terrestrial C cycle variables, and pre-disturbance states from the peer-reviewed literatures to quantify disturbance severity, recovery time, and state change through synthesis of chronosequence studies on disturbance and recovery. The chronosequence approach is an effective research method on studying recovery process following a disturbance. In forest sciences, a chronosequence is a set of forested sites that share similar attributes but are of different ages, and chronosequence methods are used to represent and study the time-dependent development of a forest (Lichstein *et al* 2009, Sun *et al* 2004, Yang *et al* 2011). This synthesis focused on the general patterns of recovery properties and addressed the following specific questions: (1) How much do the ecosystem C cycle variables recover after a disturbance? (2) How long does it take for C cycle variables to recover to a stable state after various disturbances? (3) What's the relationship between state change and recovery time? We hypothesized that most C cycle processes would recover to a stable state that is not significantly different from the pre-disturbance state. The recovery time would vary largely for different C processes, which may be related to the state change. C pools could need longer recovery time than C fluxes.

2. Methods

2.1. Data compilation

We synthesized results from peer-reviewed papers that examined ecosystem recovery following disturbances.

The papers were searched from the datasets of 'Web of Science' with key words of disturbance, recovery, ecosystem C cycle, chronosequence, deforestation, fire, harvest, agriculture, mining, storm or drought. Studies with at least 6 chronosequence series that cover a complete disturbance-recovery trajectory were selected. For each study, the data points along the chronosequence series were extracted and then used to fit a model and calculate the parameters of recovery time and steady state. Data from the figures in the literatures were extracted using Engauge Digitizer (Free Software Foundation, Inc., Boston, MA, USA). In total, a database with 77 case studies was created in this synthesis (supplementary data available at stacks.iop.org/ERL/12/104004/mmedia). Information collected from the studies included background information of the studied area, ecosystem type, disturbance types, disturbance severity, C cycle variables, pre-disturbance values for C cycle variables, and the corresponding changes in variables along time series of a chronosequence. Terrestrial ecosystem C cycle or related variables examined in this study are ecosystem C fluxes (including net ecosystem C exchange, gross primary productivity, and ecosystem respiration), net primary productivity (NPP), leaf area index (LAI), aboveground biomass (AGB), belowground biomass (BGB), total biomass (TB), species richness (SR, including seedling density), microbial biomass C (MC), litter C pool (LCP), and soil C pool (SCP).

2.2. Parameter calculation

We used the data points along the time series of recovery trajectory in each case study to generate parameters of recovery time and state change. The recovery trajectory of C stocks was best described by a mono-exponential rise to the maximum model (figure 1). Such exponential models were originally developed based upon the concept of C saturation, which illustrates the changes in ecosystem C stocks with increasing C inputs (Gulde *et al* 2008, Six *et al* 2002, Stewart *et al* 2007). After an ecosystem is fully recovered, its pools and processes reach a stable state. Right after a disturbance, some belowground variables (e.g. soil C pool) first decline due to continued C decomposition and no new C input, and then increase over time in a similar pattern with aboveground variables (Sun *et al* 2004). Thus we used empirical equations to fit disturbance-recovery trajectories and to generate parameters of recovery time and state change for each variable in each case study (figure 1). For aboveground variables, we used the equation (1) (Preger *et al* 2010)

$$y = y_0 + a \times (1 - \exp(-bx)) \quad (1)$$

where y was the absolute value of a variable at a time x (in years) during the recovery; y_0 was the start value of a variable for recovery; a and b were constants. Based on the equation (1), recovery time (RT) (equation (2)) is derived by assuming that a variable like AGB is

recovered when it reached 95% of the maximum, which is defined as post-disturbance stable state (S_R) (equation (3), figure 1).

$$RT = \frac{\ln \left(1 - \left(0.95 - \frac{0.05y_0}{a} \right) \right)}{-b} \quad (2)$$

$$S_R = 0.95 \times (y_0 + a) \quad (3)$$

For the belowground variables, we used the equation (4) (Sun *et al* 2004),

$$y = y_1 + a \times \exp \left(-0.5 \times \left(\frac{x - x_0}{b} \right)^2 \right) \quad (4)$$

where x_0 was the duration of a decline in belowground variables after a disturbance; y_1 was the constant. Similarly, based on the equation (4), recovery time (equation (5)) is derived by assuming that a variable like soil C is recovered when it reached 95% of the maximum, which is defined as S_R (equation (6)).

$$RT = x_0 + b \times \sqrt{\frac{\ln \left(-0.05 \times \frac{y_1}{a} \right)}{-0.5}} \quad (5)$$

$$S_R = 0.95 \times y_1 \quad (6)$$

For pre-disturbance state (S_P) we used the values before disturbance or from undisturbed control or old-growth forests for each case study in forests. For grasslands, because most are annual grasses, we didn't consider age, just used the values before disturbance or from undisturbed control reported by the authors of a study. State change, the relative changes between the fully recovered state and the pre-disturbance state, was calculated as in equation (7). We also defined the absolute value of state change as the magnitude of state change (equation (8)).

$$\text{State change (\%)} = \frac{(S_R - S_P)}{S_P} \times 100\% \quad (7)$$

$$\begin{aligned} \text{Magnitude of state change (\%)} \\ = \left| \frac{(S_R - S_P)}{S_P} \times 100\% \right| \end{aligned} \quad (8)$$

Disturbance severity (equation (9)) was defined as the relative changes between pre-disturbance state and the minimum (S_0) based on equation (1) (y_0) or equation (4) ($y_1 + a$).

$$\text{Disturbance Severity (\%)} = \frac{(S_P - S_0)}{S_P} \times 100\% \quad (9)$$

The models were fitted to the data for each chronosequence using SigmaPlot 12.5 for Windows (Systat Software Inc., Richmond, CA, USA). The parameters a , b , x_0 , y_0 , and y_1 were estimated from the model fits. Totally 191 models were fitted, including 25 models with low R^2 ($R^2 < 0.4$).

2.3. Statistical analyses

The statistical analyses performed for state changes across disturbance types or all variables were done by comparing the means with zero to test their significance. We compared the recovery times among different C variables and disturbance types using analysis of variance (ANOVA) with post-hoc least significant difference (LSD) tests. The differences and variabilities of geographic and climate conditions for all studies were included in the ANOVA analysis as random factors. We calculated the mean and standard error for recovery time and state changes. The standard error reflected the variabilities of geographic and climate conditions for different studies. The differences were considered to be significant if $P < 0.05$. The relationships between recovery times and state changes or disturbance severity were tested using regression analysis and were considered significant if $P < 0.05$. The statistical analyses were conducted with the SPSS software (SPSS 20.0 for windows, SPSS Inc., Chicago, IL, USA), and the graphs were drawn with the SigmaPlot software (SigmaPlot 12.5 for windows).

3. Results

3.1. General patterns of state change and recovery time

The relative differences between the post-disturbance stable states and the pre-disturbance states were not significantly different from zero for most C cycle-related variables in either forest or grassland ecosystems, except for leaf area index (LAI) and net primary productivity (NPP) in forests (figure 2(a)), which were significantly increased by 10 and 35%, respectively (both $P < 0.05$, figure 2(a)). Across all variables post-disturbance stable states were significantly decreased by storm (28.2%) in forests, and increased by drought (26.7%) in grasslands (all $P < 0.05$, figure 2(b)).

Recovery time varied considerably between ecosystem types, variables (figure 3(a)), and disturbance types (figure 3(b)). In general, forests had longer recovery time than grasslands. In forests, ecosystem C fluxes needed the shortest time (23 ± 5 years) to get to the maximum values at the post-disturbance stable state (figure 3(a)), followed by NPP (32 ± 13 years), LAI (42 ± 17 years) and microbial C (52 ± 18 years), which needed three to five decades to recover to stable states. However, the recovery of belowground biomass (96 ± 25 years), aboveground biomass (104 ± 20 years) and total biomass (104 ± 33 years) took longer than 90 years (figure 3(a)). Both soil C pool and litter C pool required at least 60 years for the post-disturbance stable state in forest (figure 3(a)). In addition, species richness recovered to the stable state by 86 years (figure 3(a)). On average across all the variables, ecosystems needed one hundred years to fully recover from deforestation while only a few years was needed to recover from drought in both forests and grasslands (figure 3(b)). The recovery

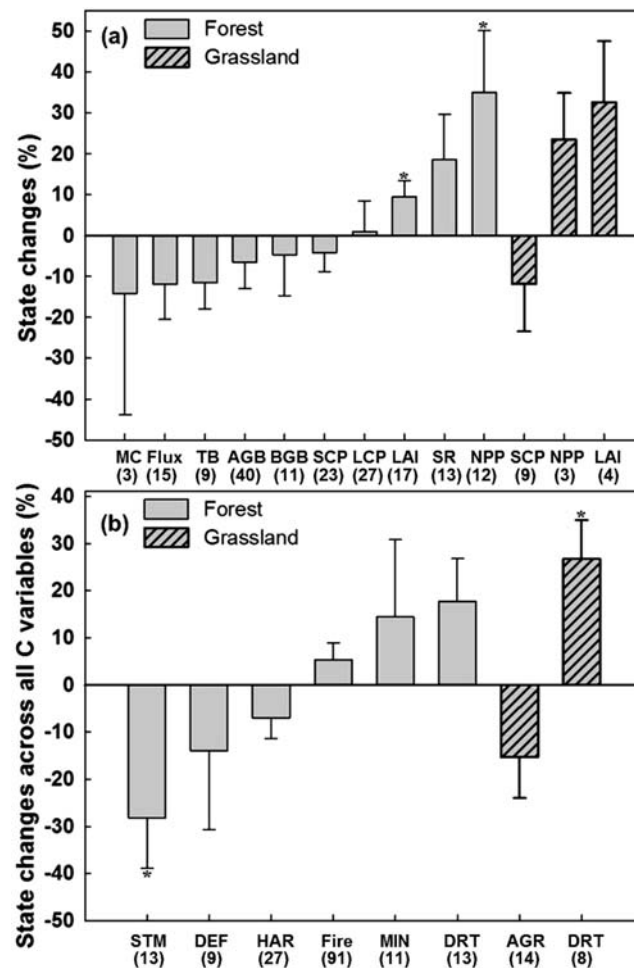


Figure 2. State changes (mean $\pm$ 1SE) of different variables (a) and disturbance types (b) in forest and grassland. The numbers beside the x-axis indicate the sample size for each variable or disturbance type. Abbreviations are MC, microbe carbon; Flux, ecosystem carbon flux; TB, total biomass; AGB, aboveground biomass; BGB, belowground biomass; SCP, soil carbon pool; LCP, litter carbon pool; LAI, leaf area index; SR, species richness; NPP, net primary production; STM, storm; DEF, deforestation; HAR, harvest; MIN, mining; DRT, drought; AGR, agriculture. * means the post-disturbance stable state was significantly different from the pre-disturbance state at the level of $P < 0.05$.

time for harvest and fire (more than eight decades) was nearly twice as long as that for mining (four decades) in forest ecosystems.

3.2. State change and recovery time for same disturbance type or variable

For a certain disturbance type, most C cycle-related variables showed the post-disturbance stable states were not significantly different from the pre-disturbance states. For example, after forest fire, LAI at the post-disturbance stable state exceeded the pre-disturbance value, while carbon flux, litter C pool (LCP), NPP, belowground biomass (BGB), aboveground biomass (AGB), species richness (SR), and soil C pool (SCP) at the post-disturbance stable states all showed non-significant changes compared to their pre-disturbance states (figure 4(a)). Recovery time varied with variables. Carbon flux and LCP recovered to a stable state in less than five decades. LAI and NPP fully recovered after six decades. BGB and SR recovered after eight decades, while SCP and AGB needed longer than 100 years for full recovery from fire (figure 4(b)). We didn't have

large enough sample size for other disturbance types to compare different variables' responses.

We used aboveground biomass (AGB) changes in forest to illustrate state change and recovery time of the same variable for different disturbance types because AGB was measured the most often in the studies selected and had the largest sample size. The post-disturbance stable state of AGB, after storm, harvest, fire or deforestation, all showed non-significant changes compared to their pre-disturbance states (all $P > 0.05$, figure 4(c)). Recovery time of AGB was not significantly different among deforestation, fire, storm and harvest (figure 4(d)).

3.3. Relationships between state change and recovery time

Both recovery times and magnitude of state changes were positively correlated with disturbance severity ($P < 0.01$) although the correlation coefficients were small that might be caused by the large variations between disturbance types and variables (figures 5(a) and (b)). The general patterns showed that the

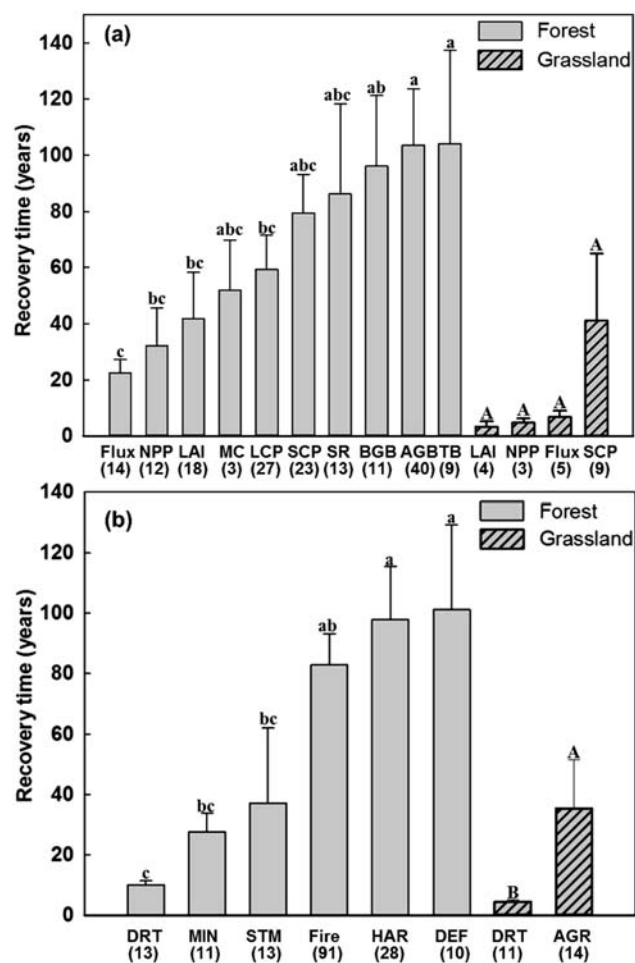


Figure 3. Recovery time (mean $\pm$ 1SE) of different variables (a) and disturbance types (b) in forest and grassland. The numbers beside the x-axis indicate the sample size for each variable or disturbance type. Different letters above the column indicate the significant difference ($P < 0.05$) between variables or disturbance types in forests (lowercase letters) or grasslands (capital letters). See figure 2 for abbreviations.

recovery time became longer and the absolute value of state change became larger with the increasing disturbance severity. Recovery times were also linked to state changes across different variables. The total C storage of an ecosystem had a strong tendency to be recovered towards an equilibrium state, in which C storage wasn't significantly different with the pre-disturbance states, in a long term (figures 5(c)). The general patterns of state change of terrestrial ecosystem C cycle with recovery time can be characterized as figure 5(d).

4. Discussion

4.1. State changes

The term 'state' has been commonly used to indicate the shifts of vegetation or dominant species (Beisner *et al* 2003, Scheffer *et al* 2001). In this study, we used 'state' to quantify the status of C fluxes or pools and provide an algorithmic approach to quantify changes in ecosystem C variables from disturbance to a fully recovered state. While most previous studies on state shifts

are conceptual, or supported only by paleoecological data (Beisner *et al* 2003, Scheffer and Carpenter 2003), this study provides empirical evidences on the state changes in ecosystem C cycle after recovery from disturbance. Specifically, we found that most C pool-related variables could eventually recover to a stable state that was similar to the pre-disturbance state in both forest and grassland (figures 2 and 4), whereas some C related variables, e.g. LAI and NPP, are likely to exceed the pre-disturbance state (figure 2(a)), which may be due to re-generation of new leaves during recovering.

Based on the disequilibrium theory (Luo and Weng 2011), the depletion of C due to disturbance drives the C cycle towards a disequilibrium stage. At disequilibrium stage 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. With the gradual increase of C accumulation, ecosystem will get to a new equilibrium state (Luo and Weng 2011). So, C losses triggered by the disturbance event can be compensated by C gain during recovery. For example, Amiro *et al* (2010) reported that the maximum

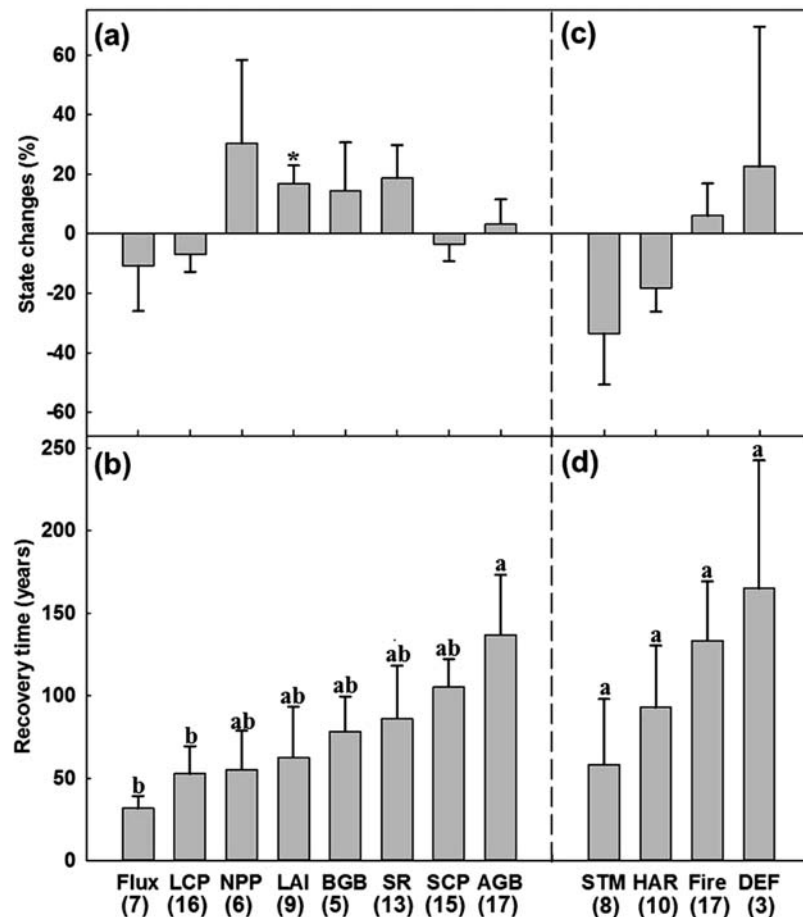


Figure 4. State changes (a) and recovery time (b) of different variables after fire. State changes (c) and recovery time (d) of aboveground biomass with different disturbance types. The numbers beside the x-axis indicate the sample size for each variable or disturbance type. Different letters above the column indicate the significant difference ($P < 0.05$) between variables or disturbance types. See figure 2 for abbreviations.

carbon losses following disturbance ($\text{g C m}^{-2} \text{y}^{-1}$) ranged from 1270 in Florida to 200 in boreal ecosystems, but the maximum uptake ($\text{g C m}^{-2} \text{y}^{-1}$) was 1180 in Florida mangroves and 210 in boreal ecosystems.

Theoretical models in restoration ecology predict that after restoration most ecosystems usually recover to an alternative stable state in terms of community structure changes (Suding and Hobbs 2009), owing to the loss of native species pools, shifts in species dominance, trophic interactions and invasion by exotics (Bakker and Berendse 1999). In reality it is difficult to quantify and characterize the state changes in plant community (Beisner *et al* 2003, Law and Morton 1993). Ecologists have not yet agreed on the definition of the alternate state in terms of changes in community structure, or on whether a biological or anthropomorphic metrics should be used to indicate state changes (Beisner *et al* 2003). In contrast, by quantifying the magnitude changes in ecosystem C cycle, this study provides one of the first attempts to characterize the state dynamics of ecosystem C cycle after disturbance. The trajectory-fitting algorithms used in this study provide an effective statistical approach to quantify C storage changes and capacity during disturbance-recovery.

4.2. Recovery time

Although ecosystem C cycle variables can eventually recover to a stable state, their recovery times vary largely, depending on the ecosystem types, variables, and disturbance types. Forest ecosystems generally recovered more slowly than grasslands, and forests took longer to recover from deforestation, fire, and harvest than from drought (figure 3(b)). This is probably due to that forest ecosystems need to absorb more C than grasslands to recover to the stable state after disturbance (Chapin *et al* 1994). For example, in *Fagus sylvatica* L. forests in southern England, NPP needs 16 years to recover to a maximum rate after drought (Power 1994). However, in a grassland, like northeastern Kansas, NPP only needs 3 years to recover to a stable state after drought (Nippert *et al* 2006).

In addition, our results showed that ecosystem C pools needed the longest time to recover (90–110 years) while NPP and leaf area index (30–60 years) recovered fast (figure 3(a)). This is mainly due to that ecosystem C uptake capacity is primarily controlled by leaf area index and photosynthetic rate (Chapin III *et al* 2011). LAI and NPP are first fully recovered and ecosystem can thus absorb more CO_2 , leading to more

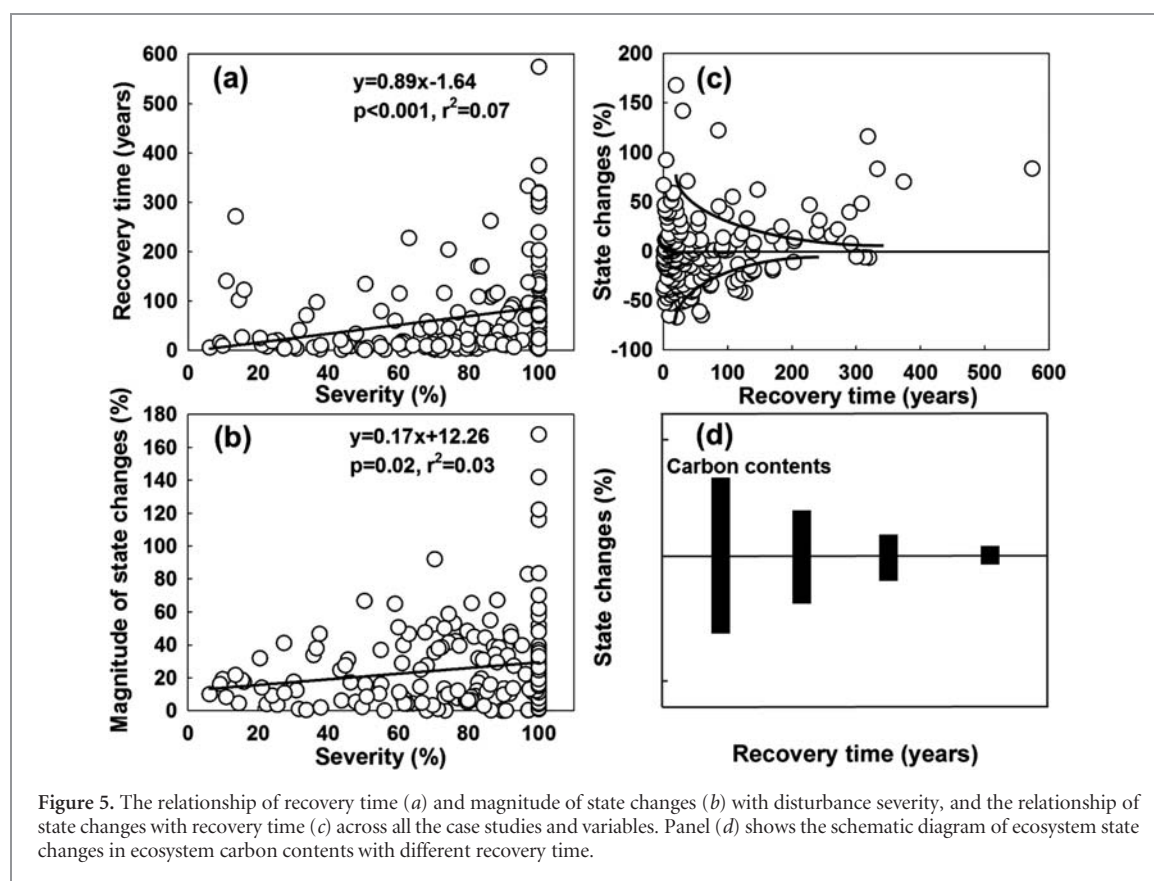


Figure 5. The relationship of recovery time (a) and magnitude of state changes (b) with disturbance severity, and the relationship of state changes with recovery time (c) across all the case studies and variables. Panel (d) shows the schematic diagram of ecosystem state changes in ecosystem carbon contents with different recovery time.

C accumulation in ecosystem, and then C pools get fully recovered. For example, Goulden *et al* (2011) found that LAI gets fully recovered around 40 years after fire in boreal forest ecosystems in central Manitoba, while AGB needs 239 years, and LCP needs 271 years, to recover to a stable state. Overall, the recovery of C cycle variables is frequently possible within a few decades. If human beings make some effort for restoration, ecosystem C cycle very likely recovers to a stable state quickly, compensating C loss associated with disturbance events.

Both recovery time and state change were positively correlated with disturbance severity (figures 5(a) and (b)). This may partly explain the large variations in recovery time and state change between different ecosystem types, variables and disturbance types. In general, across all disturbance types or variables, ecosystem C storage has the tendency to recover towards a stable state that was not significantly different from the pre-disturbance state given long enough time (figure 5(c)). At the early stage of recovery, some easily recovered variables (e.g. C fluxes) may recover to an alternative state, resulting in the net C loss or gain in a short-term. However, after long enough time, the entire ecosystem C storage can recover toward an equilibrium state, which is similar to the pre-disturbance state (figures 5(c) and (d)). The relationships between state change, recovery time, and disturbance severity are helpful to estimate long-term C balance and dynamics in terrestrial ecosystems within a disturbance-recovery cycle.

4.3. Implications

The findings in this study offer a better understanding of C cycle in response to disturbance. First, immediately after a disturbance an ecosystem has great C uptake potential, which may account for the large C sink in terrestrial ecosystems (Kasischke *et al* 2013, Kasischke *et al* 2010). In the long term, if disturbance regimes do not change over time, recovery processes after a disturbance event result in the net C uptake, which may fully compensate for C loss triggered by the disturbance event and lead to no net change in C balance over time. Similarly, over space, the C loss triggered by the disturbance event in one area can be compensated by C gain during recovery in other areas. Thus, disturbance impacts on biogeochemical cycles have to be interpreted in the context of disturbance regimes and their responses to global change.

Second, recovery time and state change depend on disturbance severity and the pre-disturbance state of an ecosystem (Kasischke and Johnstone 2005). As illustrated in figure 6, a disturbance that occurs at the point A, B, or C will result in different amounts of C loss and recovery times. If we do not know how severe a disturbance is, it is difficult to predict the recovery time and evaluate the impacts on ecosystem C cycle. Moreover, results from this study were obtained based on the assumption that the disturbance-recovery trajectory was under static disturbance regime. But disturbance regimes are dynamic in nature (Dale *et al* 2001, Hu *et al* 2010). This can be illustrated in figure 6 as the state one changes to state two under the changing

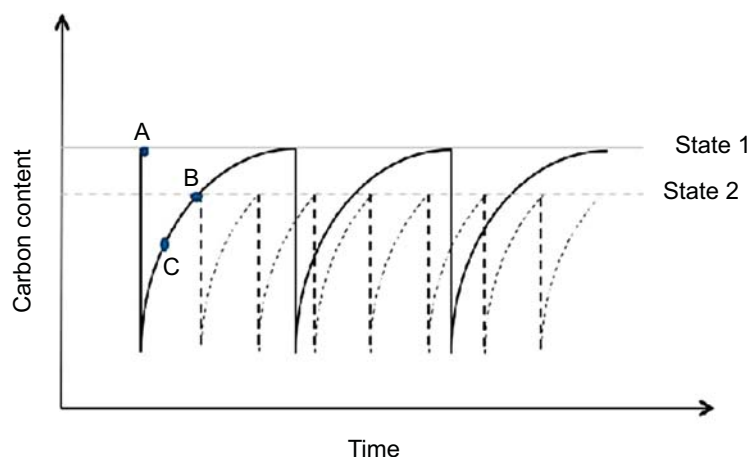


Figure 6. Conceptual figure of dynamic disequilibrium of ecosystem carbon cycling and disturbance regimes. Ecosystem carbon contents may shift from state 1 to state 2 and vice versa depending on various factors. The shift from state 2 to state 1 may happen when woody encroachment happens in grassland and herbaceous species are replaced by woody species with climate change. The shifts from state 1 to state 2 may occur when there is a shift in the disturbance regime and ecosystem does not have enough time to recover to previous equilibrium state.

disturbance regime. Because different C variables need different time scales to fully recover, the dynamic disturbances with varying frequency and severity may allow C fluxes to recover but may substantially reduce the capacity of an ecosystem to store C due to the short time of recovery (Balshi *et al* 2007, Gough *et al* 2008, Luo and Weng 2011).

5. Conclusions

This study comprehensively synthesized state change and recovery time of terrestrial C cycle components after various disturbances at global scale. We found that most ecosystem C cycle variables tended to eventually recover towards equilibrium states, which were not significantly different from the pre-disturbance states. Although different variables and disturbance types had substantially different recovery times, most of them could recover to a stable state within a few decades. Both state change and recovery time were related to disturbance severity. The severer the disturbance, the longer the recovery time was and the larger the state change was. These results indicate that we need to consider state change and recovery time when quantifying the disturbance impacts on ecosystems. Note that this study is assumed that disturbances are static, but they are dynamic in nature. Disturbance impacts on biogeochemical cycles need to be interpreted in the context of dynamic disturbance regimes. Nevertheless, the general patterns revealed in this study are important to better understand long-term C balance in terrestrial ecosystems within a disturbance-recovery cycle.

Acknowledgments

We thank Esther Ali and Xuecheng Chen for their help in collecting the data. This study was financially

supported by National Natural Science Foundation of China (31420103917, 31625006), the Ministry of Science and Technology of China (2013CB956300), the CAS STS project (KFJ-SW-ST-169) and the ‘Thousand Youth Talents Plan’.

ORCID iDS

Zheng Fu  <https://orcid.org/0000-0001-7627-8824>
Dejun Li  <https://orcid.org/0000-0002-6376-5786>

References

- Achard F *et al* 2014 Determination of tropical deforestation rates and related carbon losses from 1990 to 2010 *Glob. Change Biol.* **20** 2540–54
- Amiro B *et al* 2010 Ecosystem carbon dioxide fluxes after disturbance in forests of North America *J. Geophys. Res.: Biogeosci.* **115** G00K02
- Bakker J P and Berendse F 1999 Constraints in the restoration of ecological diversity in grassland and heathland communities *Trends Ecol. Evol.* **14** 63–8
- Baldocchi D 2008 TURNER REVIEW No. 15 Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems *Aust. J. Bot.* **56** 1–26
- Balshi M *et al* 2007 The role of historical fire disturbance in the carbon dynamics of the pan-boreal region: a process-based analysis *J. Geophys. Res.: Biogeosci.* **112** G02029
- Barnosky A D *et al* 2012 Approaching a state shift in Earth’s biosphere *Nature* **486** 52–8
- Beisner B E *et al* 2003 Alternative stable states in ecology *Front. Ecol. Environ.* **1** 376–82
- Bowman D M *et al* 2009 Fire in the Earth system *Science* **324** 481–4
- Carpenter S R *et al* 2011 Early warnings of regime shifts: a whole-ecosystem experiment *Science* **332** 1079–82
- Caspersen J P *et al* 2000 Contributions of land-use history to carbon accumulation in US forests *Science* **290** 1148–51
- Chapin F S *et al* 1994 Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska *Ecol. Monogr.* **64** 149–75

- Chapin III F S *et al* 2011 *Principles of Terrestrial Ecosystem Ecology* (New York: Springer)
- Ciais P *et al* 2005 Europe-wide reduction in primary productivity caused by the heat and drought in 2003 *Nature* **437** 529–33
- Dale V H *et al* 2001 Climate change and forest disturbances *Bioscience* **51** 723–34
- Gough C M *et al* 2008 Controls on annual forest carbon storage: lessons from the past and predictions for the future *Bioscience* **58** 609–22
- Goulden M L *et al* 2011 Patterns of NPP, GPP, respiration, and NEP during boreal forest succession *Glob. Change Biol.* **17** 855–71
- Graven H D *et al* 2013 Enhanced seasonal exchange of CO₂ by northern ecosystems since 1960 *Science* **341** 1085–9
- Gulde S *et al* 2008 Soil carbon saturation controls labile and stable carbon pool dynamics *Soil Sci. Soc. Am. J.* **72** 605–12
- Houghton R A 1995 Land-use change and the carbon cycle *Glob. Change Biol.* **1** 275–87
- Hu F S *et al* 2010 Tundra burning in Alaska: linkages to climatic change and sea ice retreat *J. Geophys. Res.-Biogeosci.* **115** G04002
- Johnson C M *et al* 2000 Post-disturbance aboveground biomass accumulation in global secondary forests *Ecology* **81** 1395–401
- Jones H P and Schmitz O J 2009 Rapid recovery of damaged ecosystems *PLoS One.* **4** e5653
- Kasischke E S *et al* 2013 Impacts of disturbance on the terrestrial carbon budget of North America *J. Geophys. Res.: Biogeosci.* **118** 303–16
- Kasischke E S and Johnstone J F 2005 Variation in postfire organic layer thickness in a black spruce forest complex in interior Alaska and its effects on soil temperature and moisture *Can. J. Forest Res.* **35** 2164–77
- Kasischke E S *et al* 2010 Alaska's changing fire regime-implications for the vulnerability of its boreal forests *Can. J. Forest Res.* **40** 1313–24
- Law R and Morton R D 1993 Alternative permanent states of ecological communities *Ecology* **74** 1347–61
- Le Quéré C *et al* 2013 The global carbon budget 1959–2011 *Earth Syst. Sci. Data* **5** 165–85
- Lichstein J W *et al* 2009 Biomass chronosequences of United States forests: implications for carbon storage and forest management *Old-Growth Forests* (Berlin: Springer) pp 301–41 (https://doi.org/10.1007/978-3-540-92706-8_14)
- Luo Y *et al* 2015 Predictability of the terrestrial carbon cycle *Glob. Change Biol.* **21** 1737–51
- Luo Y and Weng E 2011 Dynamic disequilibrium of the terrestrial carbon cycle under global change *Trends Ecol. Evol.* **26** 96–104
- Mack M C *et al* 2011 Carbon loss from an unprecedented Arctic tundra wildfire *Nature* **475** 489–92
- McMahon S M *et al* 2010 Evidence for a recent increase in forest growth *Proc. Natl Acad. Sci.* **107** 3611–5
- Nippert J B *et al* 2006 Intra-annual rainfall variability and grassland productivity: can the past predict the future? *Plant Ecol.* **184** 65–74
- Odum E P 1969 The strategy of ecosystem development *Science* **164** 262–70
- Pan Y *et al* 2011 A large and persistent carbon sink in the world's forests *Science* **333** 988–93
- Pare D and Bergeron Y 1995 Above-ground biomass accumulation along a 230 year chronosequence in the southern portion of the Canadian boreal forest *J. Ecol.* **83** 1001–7
- Power S 1994 Temporal trends in twig growth of *Fagus sylvatica* L. and their relationships with environmental factors *Forestry* **67** 13–30
- Preger A C *et al* 2010 Carbon sequestration in secondary pasture soils: a chronosequence study in the South African Highveld *Eur. J. Soil Sci.* **61** 551–62
- Raymond C L *et al* 2015 Representative regional models of post-disturbance forest carbon accumulation: integrating inventory data and a growth and yield model *Forest Ecol. Manage.* **336** 21–34
- Reichstein M *et al* 2013 Climate extremes and the carbon cycle *Nature* **500** 287–95
- Running S W 2008 Ecosystem disturbance, carbon, and climate *Science* **321** 652–3
- Scheffer M *et al* 2009 Early-warning signals for critical transitions *Nature* **461** 53–9
- Scheffer M *et al* 2001 Catastrophic shifts in ecosystems *Nature* **413** 591–6
- Scheffer M and Carpenter S R 2003 Catastrophic regime shifts in ecosystems: linking theory to observation *Trends Ecol. Evol.* **18** 648–56
- Schwalm C R *et al* 2012 Reduction in carbon uptake during turn of the century drought in western North America *Nat. Geosci.* **5** 551–6
- Six J *et al* 2002 Stabilization mechanisms of soil organic matter: implications for C-saturation of soils *Plant Soil* **241** 155–76
- Stewart C E *et al* 2007 Soil carbon saturation: concept, evidence and evaluation *Biogeochemistry* **86** 19–31
- Suding K N and Hobbs R J 2009 Threshold models in restoration and conservation: a developing framework *Trends Ecol. Evol.* **24** 271–9
- Sun O J *et al* 2004 Dynamics of carbon stocks in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA *Glob. Change Biol.* **10** 1470–81
- Tansey K *et al* 2008 A new, global, multi-annual (2000–2007) burnt area product at 1 km resolution *Geophys. Res. Lett.* **35** L01401
- Turner M G 2010 Disturbance and landscape dynamics in a changing world *Ecology* **91** 2833–49
- Vanderwel M C *et al* 2013 Quantifying variation in forest disturbance, and its effects on aboveground biomass dynamics, across the eastern United States *Glob. Change Biol.* **19** 1504–17
- Villnäs A *et al* 2013 The role of recurrent disturbances for ecosystem multifunctionality *Ecology* **94** 2275–87
- Williams C A *et al* 2012 Carbon consequences of forest disturbance and recovery across the conterminous United States *Glob. Biogeochem. Cycles* **26** GB1005
- Yang Y *et al* 2011 Carbon and nitrogen dynamics during forest stand development: a global synthesis *New Phytol.* **190** 977–89
- Zimov S *et al* 1999 Contribution of disturbance to increasing seasonal amplitude of atmospheric CO₂ *Science* **284** 1973–6