



## Invited review article

# Disturbance and the carbon balance of US forests: A quantitative review of impacts from harvests, fires, insects, and droughts



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## ABSTRACT

Disturbances are a major determinant of forest carbon stocks and uptake. They generally reduce land carbon stocks but also initiate a regrowth legacy that contributes substantially to the contemporary rate of carbon stock increase in US forestlands. As managers and policy makers increasingly look to forests for climate protection and mitigation, and because of increasing concern about changes in disturbance intensity and frequency, there is a need for synthesis and integration of current understanding about the role of disturbances and other processes in governing forest carbon cycle dynamics, and the likely future of this and other sinks for atmospheric carbon. This paper aims to address that need by providing a quantitative review of the distribution, extent and carbon impacts of the major disturbances active in the US. We also review recent trends in disturbances, climate, and other global environmental changes and consider their individual and collective contributions to the US carbon budget now and in the likely future. Lastly, we identify some key challenges and opportunities for future research needed to improve current understanding, advance predictive capabilities, and inform forest management in the face of these pressures.

Harvest is found to be the most extensive disturbance both in terms of area and carbon impacts, followed by fire, windthrow and bark beetles, and lastly droughts. Collectively these lead to the gross loss of about 200 Tg C y<sup>−1</sup> in live biomass annually across the conterminous US. At the same time, the net change in forest carbon stocks is positive (190 Tg C y<sup>−1</sup>), indicating not only forest resilience but also an apparently large response to growth enhancements such as fertilization by CO<sub>2</sub> and nitrogen. Uncertainty about disturbance legacies, disturbance interactions, likely trends, and global change factors make the future of the US forest carbon sink unclear. While there is scope for management to enhance carbon sinks in US forests, tradeoffs with other values and uses are likely to significantly limit practical implementation. Continued and expanded remote sensing and field-based monitoring capabilities and manipulative experimentation are needed to improve understanding of the US forest carbon sink, and assess how disturbance processes are responding to the pressures of global environmental change. In addition, continued development and application of holistic, decision support tools that consider a range of forest values are needed to enable managers and policy makers to use the best available information for guiding forest resources now and into the future.

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## 1. Introduction

Ecological disturbances strongly influence local to global land carbon storage (Chapin et al., 2012). They affect ecosystem metabolism (productivity and respiration), alter how fixed carbon is allocated, influence species composition and ecosystem structure, directly release carbon to the atmosphere or relocate it (i.e. wood products), and cause internal carbon transfers among ecosystem storage pools most importantly from live to dead. Disturbance events typically result in a near-term net reduction in ecosystem carbon stocks. Ensuing recovery is often gradual. Thus disturbances tend to have the aggregate effect of reducing land carbon stores even if disturbance processes are integral for the health and maintenance of forest ecosystems.

Disturbance events are globally ubiquitous and rising in both frequency and severity (Allen et al., 2010; van Mantgem et al., 2009). In the US, disturbance rates have generally been stable in the east since the 1980s, but the west has seen trends toward elevated tree mortality and stand scale disturbances in response to warming and drought, more frequent and larger fires as well as outbreaks of bark beetles and other pests (Masek et al., 2013; Raffa et al., 2008; Schleeweis et al., 2013; van Mantgem et al., 2009; Westerling et al., 2006). Nationwide rates of forest disturbance measured at a stand scale with remote sensing (order 1000 m<sup>2</sup>) average about 1.1% per year, but regions with intensive forestry such as the southeast experience 1.5% per year, rising even higher in the mountain West (>2%) where drought, fire and bark beetle disturbances have hastened (Masek et al., 2013; Schleeweis et al., 2013; Williams et al., 2014a). These rates place US forest cover change as high as anywhere in the world (Hansen et al., 2013).

Forests of the conterminous US currently hold about 40 Pg C in 270 million hectares of land (EPA, 2015). US forests are estimated to sequester about 0.20 Pg C y<sup>-1</sup> (excluding wood products) offsetting 13% of annual US carbon dioxide emissions from fossil fuel combustion (1.5 Pg C y<sup>-1</sup>) (EPA, 2015). Exactly what causes US forests to sequester so much carbon is not fully understood but one undeniable sink mechanism is the recovery of forests from past disturbances (Birdsey et al., 2006). Both historical and contemporary disturbances cause US forests to hold only about half of their theoretical maximum stocks (Williams et al., 2014a) and this imposes an age structure effect, or a so-called regrowth sink, that causes forestlands to naturally accrue carbon over time. Much of this regrowth sink is offset by disturbance emissions that take place offsite (i.e. wood products and processing emissions) or occurred previously (i.e. historical fire emissions). Thus, a sizeable portion of today's sequestration is compensating for the carbon losses from yesterday's disturbances. Indeed, US reporting to the UNFCCC indicates that contemporary harvesting removes 0.13 Pg C y<sup>-1</sup> and fires release another 0.03 Pg C y<sup>-1</sup> (EPA, 2011; EPA, 2015), which combine to offset some or all of the forest carbon sink from post-disturbance recovery (Williams et al., 2012b).

Meanwhile, US forests appear to be experiencing enhanced growth, contributing about 0.10 to 0.15 Pg C y<sup>-1</sup> to the total carbon sequestration in forests (Williams et al., 2012b; Zhang et al., 2012). Proposed enhancement mechanisms include climate trends, atmospheric inputs (CO<sub>2</sub>, N), management, and/or afforestation (e.g. Houghton, 2003; Thomas et al., 2009; Williams et al., 2012b), but the precise mix of drivers remains unclear. Evidence of enhanced growth is mounting,

consistent with a doubling of the global sink for atmospheric CO<sub>2</sub> since the 1960s from ~2.4 to 5 Pg C y<sup>-1</sup> in 2010 (Ballantyne et al., 2012) attributed largely to the land rather than ocean (Le Quéré et al., 2009), principally from increased carbon storage in global forests (Pan et al., 2011). Notably, this global-scale land sink trend offset about half the increase in fossil fuel and deforestation emissions since 1960 (Ballantyne et al., 2012), slowing the rate of increase in atmospheric greenhouse gases. Temperate and boreal forests, including those in the US, contribute substantially to this global forest sink for atmospheric carbon.

Enhanced land carbon storage is one of the most efficient and effective mechanisms at work mitigating anthropogenic carbon emissions, but this service could be in jeopardy as the changing climate threatens both forest carbon stocks and uptake (Allen et al., 2010; Anderegg et al., 2013a; Anderson-Teixeira et al., 2013; Bentz et al., 2010; Choat et al., 2012; Dale et al., 2001; Reichstein et al., 2013; Turner, 2010; U.S. Department of Agriculture, 2012; Williams et al., 2014a). Disturbance processes are one of the key vectors by which climate change initiates large-scale forest carbon releases (Peterson et al., 2014). Warming and drying is expected to drive further increases in the frequency and extent of high severity wildfire, drought, hurricane, and insect disturbances (Bender et al., 2010; Bentz et al., 2010; Dillon et al., 2011; Liu et al., 2010; Marlon et al., 2012) and recent trends in the US suggest that we may already be seeing this effect. Associated forest carbon releases have the potential to act as a significant feedback to climate change, and have even been identified as a possible tipping point in earth's climate system with the possible drying and collapse of major forest carbon stores such as in the Amazon (Lenton et al., 2008). Coupled with the expected decline in age-related regrowth from historical forest clearing, net sink strength in US forests appears poised to decline in coming decades, though the national scale impacts have yet to be fully quantified.

While these broad patterns are generally recognized, a comprehensive, quantitative synthesis is lacking. Estimates of each individual disturbance process are known to vary but have yet to be compared. Furthermore, the full suite of processes has yet to be integrated for a comprehensive, country-wide carbon balance assessment.

This paper seeks to fill that gap, presenting a review of the current state of knowledge regarding the impact of disturbances on the US forest carbon budget. It builds on a number of recent contributions that outline the theory, drivers, mechanisms, and extent of disturbance impacts on the carbon cycle of forests across North America (Amiro et al., 2011; Goetz et al., 2012; Hicke et al., 2012; Kasischke et al., 2013, 2011; Masek et al., 2011) by providing, here, a quantitative synthesis of carbon balance impacts from all of the major drivers. We first provide a general overview of how disturbance events alter the forest carbon cycle, and how impacts vary with disturbance attributes such as type and severity. We then present a synthesis of reported impacts of disturbances on the carbon balance of the conterminous US, spanning harvest, fire, insect outbreaks, drought, and windthrow events. We consider their combined role in the US-wide carbon budget now and into the future. Lastly we identify some key challenges and opportunities for future research needed to improve current understanding, advance predictive capabilities, and inform forest management in the face of these pressures.

## 2. General forest carbon dynamics following disturbance

Disturbance events have the potential to alter all aspects of the forest carbon cycle but a number of key perturbations are highlighted here, similar to those presented in Hicke et al. (2012) and elsewhere. Gross primary productivity ( $GPP$ ) and autotrophic respiration ( $R_a$ ) are both reduced primarily by the loss of leaf area and live biomass, though growth release of surviving individuals can compensate for these effects. Heterotrophic respiration ( $R_h$ ) responds to two opposing patterns including increase from disturbance-induced carbon inputs of dead wood and roots, but decrease from reduced productivity-derived carbon supply. Carbon stocks shift, with live biomass being transferred to dead pools as litter, dead roots, snags, and fine and coarse woody debris ( $CWD$ ), each with their own disposition and associated residence time, with some turning over in months, the bulk in a few years to decades, and the most recalcitrant or protected material remaining almost indefinitely (Harmon et al., 1986). Harvesting involves biomass carbon removal to offsite, with some being promptly emitted and some stored in long-lasting wood products. Fire directly combusts a portion of both live and dead carbon pools and emits it to the atmosphere, and can transform material into charcoal, ash, and other residual compounds. Burned remains can actually stimulate site fertility and can protect carbon from the decomposition processes as in the case of char (Knicker, 2007). Soil carbon responds to all of the above dynamics, and additionally the soil itself can be overturned or uncovered making it vulnerable to erosion. Nutrients can be released from the punctuated metabolic decomposition of labile, disturbance-killed material, from the residue of combusted material, or from insect waste, potentially altering a host of ecosystem properties that affect the regeneration environment such as site fertility and productive potential, carbon allocation patterns, and the chemical composition of plant tissues. Disturbance-induced changes in stand structure can have lasting impacts on the site's carbon balance, as can shifts in species composition including possible accelerated succession with advanced regeneration, or even wholesale changes in forest type. Such shifts can have direct effects on physiological rates of plant productivity and respiration, and may also alter carbon allocation and biomass chemistry, again with the potential to significantly alter the carbon balance for decades and even longer.

Despite the complexity of these varied and interacting processes, the temporal trajectory of net ecosystem productivity ( $NEP$ ) following disturbance undergoes a fairly consistent general pattern at the stand level, involving an initial reduction in carbon uptake from the atmosphere lasting years to decades, followed by a recovery of carbon sink strength as forest productivity outweighs respiration during regrowth. Where disturbance events are most severe, stand-level disturbance emissions dominate over productivity resulting in an initial annual source of carbon to the atmosphere until productivity overtakes respiration with transition to a net sink. Though this transition to a net carbon sink can occur fairly rapidly (i.e. <5 years) (Williams et al., 2014b), the carbon loss from disturbance is compensated more gradually as on-site carbon stocks often take many decades to recover to their pre-disturbance levels. When disturbance results in land conversion from forest to non-forest, a cumulative net carbon release remains as a lasting condition.

## 3. Defining characteristics of carbon impacts of disturbance

Disturbance events are highly diverse, both in terms of their driving processes and in terms of their material consequences. This motivates the identification of a set of defining characteristics that can be used to classify and organize event impacts based not only on the nature of the disturbance event itself but also by the leading factors determining ecosystem response. Here we identify five key characteristics that help to distinguish carbon cycle impacts of varied disturbance events. The first is disturbance *type*, meaning the immediate causal agent driving a disturbance event, such as harvest, fire, bark beetle outbreak,

windthrow, defoliation by insects, fungal attack, etc. Disturbance type partially determines which carbon transfers take place and their associated fate, with potential for combustion and release, removal off site and release or storage in the wood products processing chain, or within-ecosystem transfers from live to dead pools and internal processing. Type also identifies if a disturbance is of natural or human origin, where natural events includes fires that are not prescribed (i.e. wildfires, notably some of which are ignited by humans), windthrow, insect damage, drought, and other agents that occur in the absence of human action.

The second characteristic is disturbance *duration*, differentiating events that are abrupt or punctuated in time such as a clearcut or fire event from those that involve repeat exposure that gradually unfolds over multiple years or even decades such as a multi-year bark beetle outbreak or repeated, selective timber harvest. The third characteristic is disturbance *severity*, representing the intensity of disturbance impacts, principally the mortality of foliar, stem, and root biomass, and whole individuals, but also the rate of consumption and transformation of dead material (e.g. fire consuming or charring  $CWD$ , litter, or soil organic matter). The fourth characteristic is disturbance *sequence*, representing the temporal pattern of prior disturbances and their type, duration, and severity. Sequence captures legacy effects that can strongly influence ecosystem response to a current event, often influencing the pre-disturbance conditions of live biomass, litter,  $CWD$ , soil carbon, as well as stand structure and species composition.

The fifth characteristic we identify is post-disturbance *regeneration*, which includes a wide range of ecosystem structural and compositional attributes influencing the rate of carbon stock recovery post-disturbance. Regeneration dynamics include the nature of regrowth, be it from seed, resprouting, or the competitive release and rebounding of surviving individuals. It also includes aspects of vegetation demographics and structure, such as the frequency of seedling, sapling, and maturing individuals. Regeneration also encompasses changes in species composition and successional dynamics that ensue, which can depend on disturbance severity and sequence in important ways (e.g. Barrett et al., 2011; Johnstone et al., 2010). In some cases, regeneration involves post-disturbance management activities such as planting, fertilizing, or weeding. There is also the possibility of no forest regeneration because of land conversion such as with cutting for permanent settlement or agriculture, habitat degradation, or a shift in edaphic or climate conditions that do not favor forest reestablishment.

The five characteristics outlined above (*type*, *duration*, *severity*, *sequence*, and *regeneration*) are not meant to represent all determinants of the carbon cycle response to forest disturbance. Indeed, a number of additional factors need to be considered including edaphic factors such as site fertility and topographic setting, biotic factors such as the species composition of the forest exposed to disturbance and the potential biota available for regeneration, as well as the general climate setting and specific weather post-disturbance. While all of these need to be considered for a complete assessment of carbon balance impacts, we sought to highlight those that are most immediately related to the disturbance process itself.

We also note that the five characteristics overlap with other terms in common use. For example, disturbance *frequency* is commonly used to refer to the characteristic return time for an event type. This term was avoided here because it overlaps with our use of *sequence* and also because it is a statistical quantity, is ambiguous about disturbance type, and is too generic for representing the specific history of a particular stand. Nonetheless frequency can be valuable for characterizing disturbance rates, either generically (uninformed of type) or for a specific type (e.g. just harvest or just fire), especially useful at landscape or larger scales. We also avoided the term disturbance *synergy*, or coincident factors that mediate an ecosystem's response to a disturbance event of a particular type, duration, and severity, because this concept overlaps significantly with the way we characterized the other terms.



#### 4. Carbon impacts of US forest disturbances by type

##### 4.1. Harvest

Harvesting is arguably the most important disturbance process affecting forest C dynamics in the US, disturbing about 1.4% of US forestland each year (Masek et al., 2011), or 4.4 million hectares annually according to forest resources assessment (Smith et al., 2009). More than half of this (61%) involves partial cutting methods (Smith et al., 2009), with 1.72 million hectares of clearcutting and 2.66 million hectares of partial cutting each year, however we note that the intensity of partial treatments remains unclear and can include harvesting that leaves few residual trees.

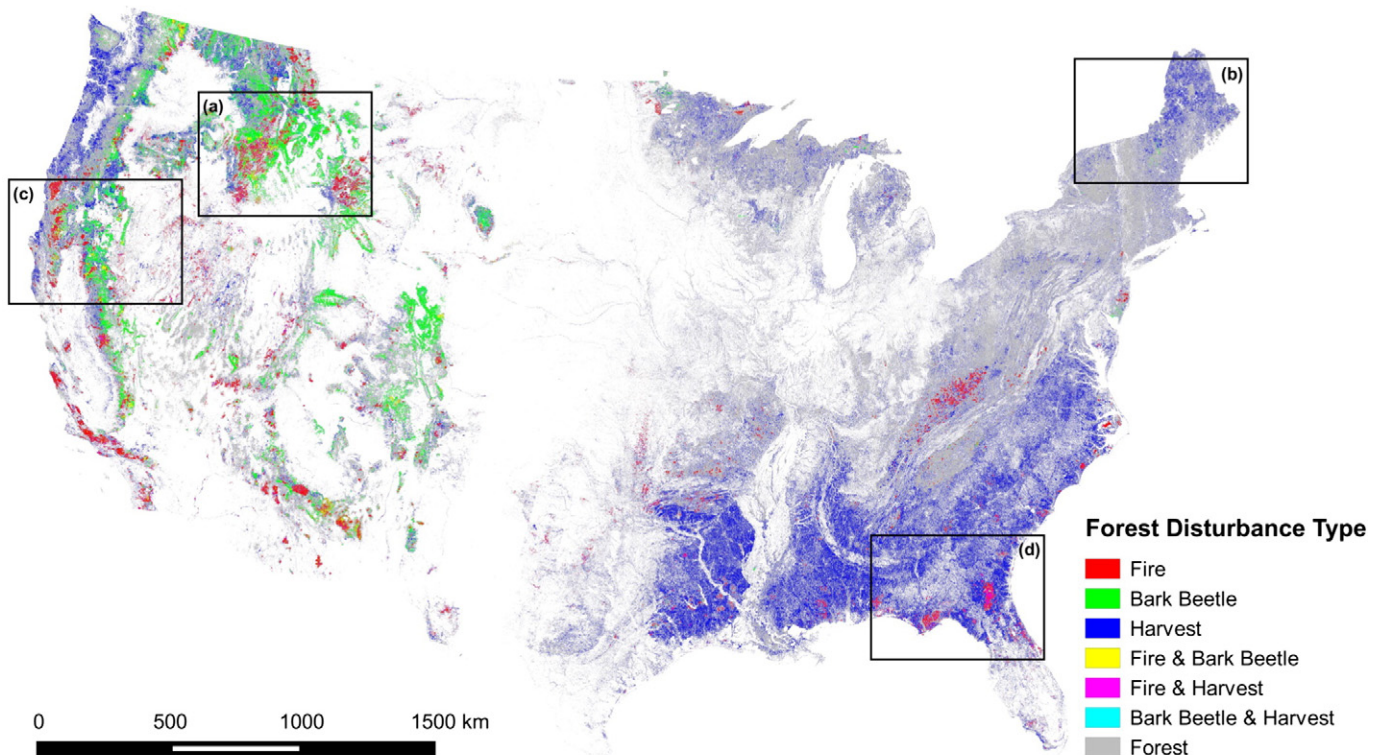
The percentage of forest area harvested varies widely from region to region, estimated at only 0.6% per year in the Northern and Rocky Mountain South regions, 0.7 to 0.9% per year in the Pacific Southwest and Rocky Mountain North regions, and reaching 1.6 to 1.8% per year in the Southern regions (Figs. 1, 2, Table 1). These figures are derived from our cursory attribution of the North American Forest Dynamics (NAFD) data product (Goward et al., 2015) which involves Landsat based mapping of moderate to high severity disturbances at a national-scale with the vegetation change tracker (VCT) algorithm of Huang et al. (2010b). We estimate harvest rates by excluding disturbed areas that are coincident with other major disturbances, principally fire and beetle outbreaks. This attribution is likely to over-attribute VCT disturbances to beetle impacts but under-attributes VCT events to windthrow with a likely aggregate effect of underestimating harvest rates based on our use of the NAFD product. Results are consistent with a similar but more detailed disturbance attribution effort by Schleeweis et al. (2013). Nonetheless, the wall-to-wall, nationwide data product offers a major leap forward so we include it here.

Using the most recent USFS forest resources assessment report (USFS FRA) (Smith et al., 2009) as a point of reference, we find that the harvest rates we derived from the NAFD VCT, namely those

remaining after attributing events to fire or beetles, generally lie between USFS rates for total harvest and clearcut-only disturbances. This is consistent with the expectation that the NAFD VCT algorithm detects clearcuts as well as some moderate to high intensity partial disturbances (Thomas et al., 2011). This pattern is true except for in the NE and PSW regions where the harvest rate we derive from NAFD VCT is lower than the clearcut rate reported by the USFS FRA (Table 1). Nationwide, harvesting is estimated to affect 1.04% of forestland per year according to our interpretation of the NAFD product, and 1.7% per year according to the USFS statistics, again noting that our simple attribution may under-estimate harvest events and that the NAFD product omits low and some moderate intensity events.

Forests regrow after cutting in nearly all cases taking place today in the US, with countrywide deforestation at about 0.12% per year (or 355,000 ha y<sup>-1</sup>) mostly related to housing and urban developments (Masek et al., 2011, based on the National Resources Inventory). Furthermore, deforestation is more than offset by forest gain from reforestation and afforestation, yielding a small net gain of forest area at about 0.21% per year, or 430,000 ha y<sup>-1</sup> (EPA, 2011; Smith et al., 2009). However, this nationwide assessment of net changes in forest area masks important region-specific patterns, with the North and Rocky Mountain regions seeing net gains in forested area over the past couple of decades and the Pacific Coast and South regions seeing net losses (Smith et al., 2009). It is also worth keeping in mind that US forestland today amounts to about 72% of the area that was forested in 1630, with net conversion of roughly 120 million hectares to other uses, mainly agricultural, concentrated during the period of 1850 to 1910 (Smith et al., 2009).

A number of direct and indirect effects need to be considered to fully account for the forest carbon impacts of harvesting. Direct effects primarily involve the direct removal of C from the system for storage or emission in the product's sector, as well as the transfer of live C to dead pools such as coarse and fine woody debris (slash) both above and below ground with gradual decomposition and emission. Indirect



**Fig. 1.** Major disturbance types mapped at a 30 m resolution across the conterminous United States based on NAFD, MTBS, and ADS datasets, the records for which span 1984–2010, 1984–2014, and 1997–2014, respectively.

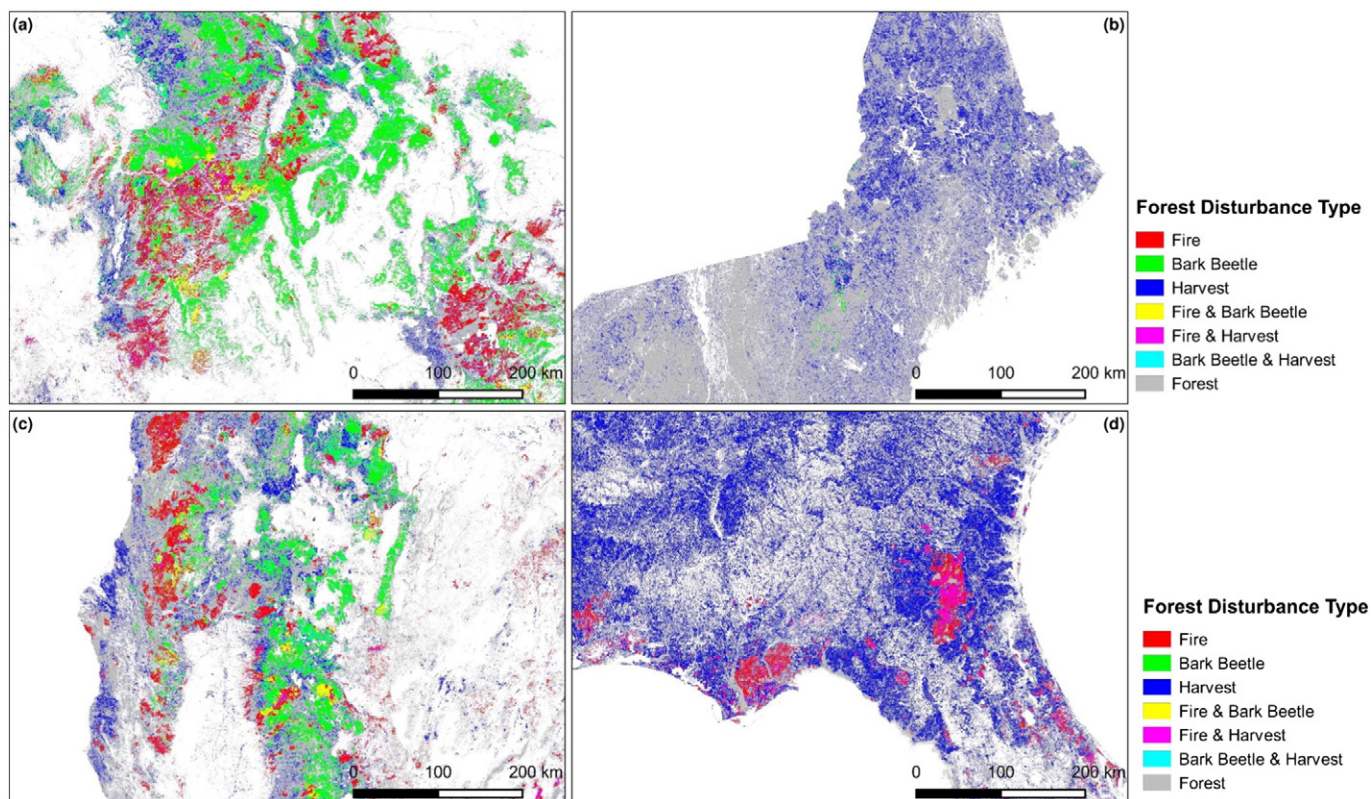


Fig. 2. Disturbances by type for select regions (see Fig. 1) across the conterminous United States based on NAFD, MTBS, and ADS datasets.

Table 1

Mean annual area disturbed and disturbance frequency for fire (F), beetle (B), and harvest (H) disturbance types and their combined sequences when separated by more than 3 years of each other (e.g. harvest then fire or fire then harvest, = H + F), along with total forestland for the conterminous US (excluding Alaska and Hawaii).

Data sources: MTBS is from Eidenshink et al. (2007), aerial detection survey (ADS) is from the USDA Forest Service, Forest Health Protection and its partners, NAFD is from Coward et al. (2012) and Huang et al. (2010b), and USFS is from Smith et al. (2009).

	Type	Fire	Beetles	Harvest	Harvest	Clearcut	Partial	H + F	H + B	F + B	Forestland <sup>a</sup>
	Source	MTBS	ADS	N-M-Ab	USFS	USFS	USFS	N&Mb	N&Ab	M&Ab	NAFD
	Years	84–14	97–14	86–10	01–05	01–05	01–05	86–10	97–10	97–14	86–10
NE	ha y <sup>−1</sup>	9,330	2,874	212,751	731,507	228,428	490,878	1,401	322	11	3,869,8159
	% y <sup>−1</sup>	0.02%	0.01%	0.55%	2.26%	0.70%	1.51%	0.00%	0.00%	0.00%	
NLS	ha y <sup>−1</sup>	5,524	6,180	138,973				722	605	26	24,265,936
	% y <sup>−1</sup>	0.02%	0.03%	0.57%				0.00%	0.00%	0.00%	
NPS	ha y <sup>−1</sup>	7,007	10,657	105,951				1,202	2,823	1,195	17,748,406
	% y <sup>−1</sup>	0.04%	0.06%	0.60%				0.01%	0.02%	0.01%	
NC	ha y <sup>−1</sup>	12,531	16,837	244,924	589,942	144,786	445,156	1,924	3,428	1,220	42,014,341
	% y <sup>−1</sup>	0.03%	0.04%	0.58%	1.74%	0.43%	1.31%	0.00%	0.01%	0.00%	
SE	ha y <sup>−1</sup>	38,425	1,313	653,365	932,232	385,801	546,431	14,682	212	216	36,232,919
	% y <sup>−1</sup>	0.11%	0.00%	1.80%	2.68%	1.11%	1.57%	0.04%	0.00%	0.00%	
SC	ha y <sup>−1</sup>	44,105	1,708	924,964	1,574,344	717,178	857,167	11,114	229	215	56,489,274
	% y <sup>−1</sup>	0.08%	0.00%	1.64%	3.30%	1.50%	1.80%	0.02%	0.00%	0.00%	
RMN	ha y <sup>−1</sup>	74,368	259,566	125,130				11,655	35,862	19,797	16,082,478
	% y <sup>−1</sup>	0.46%	1.61%	0.78%				0.07%	0.22%	0.12%	
RMS	ha y <sup>−1</sup>	106,510	282,128	166,930				16,106	25,307	25,372	30,810,910
	% y <sup>−1</sup>	0.35%	0.92%	0.54%				0.05%	0.08%	0.08%	
RM	ha y <sup>−1</sup>	180,878	541,694	292,060	219,551	84,585	134,965	27,761	61,169	45,169	46,893,389
	% y <sup>−1</sup>	0.39%	1.16%	0.62%	0.83%	0.32%	0.51%	0.06%	0.13%	0.10%	
PSW	ha y <sup>−1</sup>	72,664	119,109	94,249	108,782	55,718	53,065	10,420	17,547	16,692	13,202,447
	% y <sup>−1</sup>	0.55%	0.90%	0.71%	1.32%	0.68%	0.64%	0.08%	0.13%	0.13%	
PNW	ha y <sup>−1</sup>	43,187	157,508	217,235	222,371	97,488	124,883	6,511	28,544	14,561	20,582,695
	% y <sup>−1</sup>	0.21%	0.77%	1.06%	0.98%	0.43%	0.55%	0.03%	0.14%	0.07%	
Total	ha y <sup>−1</sup>	401,120	841,042	2,639,548	3,569,237	1,484,614	2,072,422	73,813	111,450	78,085	25,4113,224
	% y <sup>−1</sup>	0.16%	0.33%	1.04%	1.73%	0.72%	1.00%	0.03%	0.04%	0.03%	

NE: Northeast, NLS: Northern Lakes States, NPS: Northern Prairie States, NC: Northern Central (NLS + NPS), SE: Southeast, SC: South Central, RMN: Rocky Mountain North, RMS: Rocky Mountain South, RM: Rocky Mountain (RMN + RMS), PSW: Pacific Southwest, PNW: Pacific Northwest.

<sup>a</sup> Forestland is reported in hectares and was used to calculate disturbance rates for our NAFD-attributed harvest, MTBS fire, and ADS beetle disturbance types.

<sup>b</sup> N-M-A harvest is based on disturbed areas that remain after our simplistic attribution of NAFD disturbances to fire or beetles, N&M refers to sequences of NAFD harvest and MTBS fire, N&A refers to sequences of NAFD harvest and ADS beetles, and M&A refers to sequences of MTBS fire and ADS beetles, each for events in the same location separated by at least 3 years in either order.



effects include a legacy decomposition of disturbance-killed material as well as carbon stock accumulation with forest regeneration and recovery. Additional indirect effects can include soil degradation via nutrient removal, soil compaction, etc. as well as impacts of various management activities such as replanting, weeding, thinning and species selection all affecting post-disturbance regeneration. The fate of harvest removals must also be assessed as discussed below.

Annual harvest removals are a major component of the US forest carbon balance, similar in magnitude to annual forest regrowth (EPA, 2011; Williams et al., 2012b). Wood removals amounted to 440 million cubic meters in 2006 (Smith et al., 2009), translating to about 127 Tg C y<sup>-1</sup> (EPA, 2011) and contributing substantially to global removals estimated at about 1300 Tg C y<sup>-1</sup> (Hurtt et al., 2011). US harvest removals were even greater throughout the nineteenth and twentieth centuries, peaking in 1900 at about 800 Tg C y<sup>-1</sup> (Birdsey et al., 2006). Annual domestic harvest has reportedly declined in recent decades, at about 143, 134, and 95 Tg C y<sup>-1</sup> in 1990, 2000, and 2009, respectively (EPA, 2011), but rose to 103 Tg C y<sup>-1</sup> by 2013 according to the latest report (EPA, 2015). The latest forest resources assessment indicates that growing stock volumes are rising, with growth exceeding removals plus natural mortality across all forested regions and both softwoods and hardwoods (Table 2). Translating volume statistics to carbon in biomass (Table 3) shows a net growth in growing stock of about 145 Tg C y<sup>-1</sup> after growing stock removals of 84 Tg C y<sup>-1</sup> and natural mortality of 41 Tg C y<sup>-1</sup>.

While only a portion of the harvested stock is promptly emitted to the atmosphere, both contemporary and historical use of wood products leads to annual emissions from the products pool (~100 Tg C y<sup>-1</sup> in the 2000s) that are just less than annual inputs from new harvest (~130 Tg C y<sup>-1</sup> in the 2000s). The balance yields a transient storage of wood products that amounted to about 30 Tg C y<sup>-1</sup> in the 2000s, having fallen to 20 Tg C y<sup>-1</sup> by 2013 (EPA, 2015). Annual carbon release from wood products of domestic origin has decreased over the last decade, with 106, 102, and 81 Tg C y<sup>-1</sup> in 1990, 2000, and 2010 respectively, but rose to 88 Tg C y<sup>-1</sup> by 2013 (EPA, 2015). Meanwhile, the net annual change in carbon stocks in harvested wood products in use plus that in solid waste disposal sites has decreased from 36 Tg C y<sup>-1</sup> in 1990 to 19 Tg C y<sup>-1</sup> in 2013, indicating that both pools have shown a continued but declining rate of increase over the past two decades (EPA, 2015).

It is important to keep in mind that harvesting and wood products storage cannot itself create a direct sink for atmospheric carbon. However if harvested carbon resides in wood products stores for longer than the time it takes for forest regrowth to recover the carbon removed by harvesting, the net effect of the management activity on atmospheric carbon will appear as sequestration. This highlights the importance of

**Table 3**

Total dry live aboveground biomass (AGB, in Tg C), growing stock biomass (GSB, in Tg C), annual biomass removal (Tg C y<sup>-1</sup>), net growth of growing stock per year (Tg C y<sup>-1</sup>), natural mortality per year (Tg C y<sup>-1</sup>) in 2007 by region, based on Smith et al. (2009) and assuming average softwood and hardwood specific gravities of 0.41 and 0.45 tons of biomass per cubic meter and a carbon density of 0.5 g C g<sup>-1</sup> dry biomass.

	Total AGB	Growing stock B	Removals	Net growth	Mortality
NE	3703	778	7	18	5
NC	3063	627	9	19	6
SE	3397	703	23	33	7
SC	4471	903	29	39	9
RMN	1446	393	2	6	4
RMS	1145	310	0	3	3
PSW	1253	361	2	8	2
PNW	2832	843	10	18	5
Total	21,310	4920	84	145	41

full life cycle analysis to fully account for the balance of carbon emissions to the atmosphere and removals from the atmosphere by processes active in the aggregate forest sector (EPA, 2011; Law and Harmon, 2011).

#### 4.2. Fire

Fire is one of the dominant natural disturbance types affecting both forest and non-forest alike. It plays a major role in global biogeochemical cycles and atmospheric composition, and profoundly influences ecological and biophysical attributes of the land surface all with significant impacts on the climate system.

Fire burned between 1.4 and 2.7 Mha annually across the conterminous US during 1997 to 2008, with wildfire comprising about 70% and prescribed burns about 30% (Kasischke et al., 2011). Approximately half of the total burned area in the lower 48 states occurs in forestlands (EPA, 2015). The Monitoring Trends in Burn Severity (MTBS) dataset indicates mean annual burning of about 0.40 million ha y<sup>-1</sup> in forestlands from 1984 to 2014 (Table 1), with a notable increase in area burned since the 1990s. This is consistent with higher burning rates over the more recent 14 year period of 1999 to 2012 reported in the LANDFIRE database (LANDFIRE, 2008), more than double (0.87 million ha y<sup>-1</sup>) the MTBS '84 to '14 average, and affecting a total of 12 Mha of forest.

Wildfire frequency and burned area have increased dramatically in recent decades (Kasischke et al., 2011; Westerling et al., 2006). National burned area statistics reported by the National Interagency Fire Center indicate that mean annual burned area by wildland fires across the conterminous US trended upwards over the last five decades with 1.53, 1.29, 1.23, 1.93, and 2.77 million ha y<sup>-1</sup> for 1965–1974, 1975–1984,

**Table 2**

Growing stock net volume<sup>a</sup> (km<sup>3</sup>), annual volume removal<sup>b</sup> (km<sup>3</sup> y<sup>-1</sup>), net growth<sup>c</sup> per year (km<sup>3</sup> y<sup>-1</sup>), natural mortality per year (km<sup>3</sup> y<sup>-1</sup>), percent removed per year, and growth to removals ratio (G:R) for US timberlands in 2006 by region.

Based on Smith et al. (2009).

	Softwoods						Hardwoods					
	Net volume	Removals	Net growth	Mortality	% Removed	G:R	Net volume	Removals	Net growth	Mortality	% Removed	G:R
NE	0.970	0.010	0.024	0.008	1.0%	2.4	2.926	0.023	0.068	0.018	0.8%	3.0
NC	0.612	0.009	0.018	0.007	1.5%	2.0	2.515	0.038	0.076	0.024	1.5%	2.0
SE	1.606	0.084	0.110	0.017	5.2%	1.3	1.983	0.038	0.063	0.016	1.9%	1.7
SC	1.749	0.095	0.106	0.021	5.4%	1.1	2.832	0.058	0.096	0.026	2.0%	1.7
RMN	2.076	0.013	0.030	0.022	0.6%	2.4	0.036	0.000	0.001	0.000	0.0%	>100
RMS	1.412	0.001	0.014	0.013	0.1%	9.2	0.235	0.000	0.003	0.002	0.1%	20.0
PSW	1.555	0.013	0.039	0.008	0.8%	2.9	0.354	0.000	0.005	0.002	0.0%	59.2
PNW	4.134	0.051	0.086	0.024	1.2%	1.7	0.365	0.003	0.009	0.003	0.9%	2.5
Total	14.114	0.277	0.427	0.121			11.245	0.160	0.321	0.092		

<sup>a</sup> Growing stock refers to aboveground portions of live trees of commercial species meeting specified standards of quality or vigor excluding rough, rotten, or dead trees and tops and stumps of growing stock trees, and net volume is the gross aboveground volume less deductions for rot, roughness, and poor form, computed for the central stem from a 1-ft stump to a minimum 4.0-in. top diameter outside bark, or to the point where the central stem breaks into limbs.

<sup>b</sup> Removal refers to the net volume of growing stock trees removed as timber products harvested for processing by mills, logging residue including growing stock volume cut or killed but not utilized, and other removals such as pre-commercial thinning and land-use conversion, but excluding non-growing stock volume.

<sup>c</sup> Net growth is defined as the average annual growth in growing stock tree volume minus the volume lost through mortality, where mortality here includes only natural causes such as insects and disease, suppression by overstory trees, advanced tree age, wildfire, and severe weather events and does not include removals.

1985–1994, 1995–2004, and 2005–2014, respectively. Similarly, the MTBS database indicates that western US forests have experienced a 2.5 fold increase in burned area from 1984–1995 to 1996–2008, burning an average of 154,000 ha  $y^{-1}$  and 381,000 ha  $y^{-1}$ , respectively (Eidenshink et al., 2007; Ghimire et al., 2012). Kasischke et al. (2011) noted that this appears to be a continued trend since the 1960s. The recent increase in the extent of western US forest fires is partly attributed to warmer and drier conditions and earlier spring snowmelt (Westerling et al., 2006). But in some regions it is also thought to result from historical land use which produced a temporally focused pulse of forest regeneration following logging in the late 19th century and during a relatively fire-free period combined with decades of fire suppression efforts that have together led to denser forests with greater fire risk (Westerling et al., 2006). Contemporary insect infestations may alter fire regimes, though exactly to what degree remains unclear (Carswell, 2014; Jenkins et al., 2008; Simard et al., 2011), and spatial overlays of recent events do not suggest a strong interaction at landscape scales (Hart et al., 2015) (Figs. 1, 2, Table 1). Meanwhile, eastern US forests have seen a long-term decrease in burning since the 1960s. About one quarter of all western forest wildfire was classed as high severity and potentially stand replacing (Ghimire et al., 2012), compared to only 10% for the eastern US (Smith et al., 2009).

Fires cause carbon emissions through both the direct release to the atmosphere from combustion, but also from tree mortality and the transfer of C from live to dead pools where decomposition gradually releases disturbance killed material. Fires also initiate a process of regeneration whose character and rate can be highly variable with implications for the rate of carbon stock accumulation. All of these processes are sensitive to burn severity (e.g. Ghimire et al., 2012), with higher severity fires combusting more material and killing more trees. Higher severity burning can also delay NPP recovery, delay the recruitment of new woody vegetation if top soils are eroded or seed banks are scorched, or alter species composition. In only rare cases is this full suite of dynamics well described for an individual fire event or burn complex, and it is certainly lacking for landscape or continental scale analyses, necessitating broad generalizations and simplifications for large area assessments. Nonetheless, a number of studies have sought to estimate one or more of the relevant fluxes.

Most studies report the total direct plus indirect emissions associated with fires though some focus on combustion emissions alone. Estimates of total emissions for the CONUS states in the 2000s vary widely (Table 4, Fig. 3) averaging 37 Tg C  $y^{-1}$  and ranging from 9 to 80 Tg C  $y^{-1}$ . Part of the spread in estimates is due to interannual variability and trends in burned area, but methodological differences still likely dominate (Kasischke et al., 2011). In its greenhouse gas reporting, the EPA estimates direct combustion emissions from wildfire in the lower 48 states ranging from 8 to 68 Tg C  $y^{-1}$  for 1990 to 2013 and averaging 36 Tg C  $y^{-1}$  over the latest decade on record (2004 to 2013) (EPA, 2015). Prescribed fires add another 4 Tg C  $y^{-1}$  and wildfires in Alaska are reported to contribute a negligible amount ( $<0.01$  Tg C  $y^{-1}$ ) (EPA, 2015) though AK fire emissions may be biased low because of incomplete accounting. Canada and the lower 48 states of the US contributed roughly equal parts to North America's total emissions (50 to 80 Tg C  $y^{-1}$ ) in the late 1990s to early 2000s, with a much smaller contribution from Mexico (Kasischke et al., 2011) (Table 4).

One study that reported direct and indirect emissions separately for the western US found that direct combustion emissions amounted to about 40% of the indirect legacy emissions associated with the decomposition of fire-killed biomass (Ghimire et al., 2012). It also estimated the rate of post-fire carbon stock recovery with forest regrowth, reporting that the window of time required to balance contemporary mortality related and direct emissions were on average 50 years and 20 years, respectively. Another study, focusing on Yellowstone National Park, found that 90% of C lost from wildfires (both direct emissions and decomposition of killed biomass) was recovered within 100 years, a period shorter than the historically typical fire regime with a 150–300 year

frequency (Kashian et al., 2013). This indicates that if wildfires were a steady state disturbance process active across the Yellowstone landscape, the long term net effect of emissions would be zero even if any given decade or era exhibited a large net source or sink of carbon, a notion that applies to other such disturbance agents as well.

#### 4.3. Insects and diseases

Insects and pathogens affect a vast area of forests across North America every year affecting as many as 20 Mha of conterminous US forestland annually (Krist et al., 2007), or as much as 40 times the area of wildfire (Dale et al., 2001). They are estimated to place 6% of forest at risk of losing 25% or more of standing live basal area over the next 15 years (Krist et al., 2007), costing an average of \$1.5 billion annually in the US alone partly due to lost merchantable wood volume (Dale et al., 2001). Applying this rate ( $6\% \times 25\% / 15$  years) to the total live above-ground biomass of US forests (21 Pg C, Table 3) as a first approximation of the carbon implications, we estimate that as much as 21 Tg C  $y^{-1}$  of live aboveground biomass could be transferred to litter and woody debris pools annually by insect damage. Much of this damage occurs at a small, local scale that is diffusely distributed across forestlands. However damage can be far reaching, and is causing large-scale transformations of forest ecosystems and the services they provide.

The carbon cycle impacts of insect attacks depend strongly on insect type but can be broadly classified into direct tree killing, growth reducing, or defoliating effects (Hicke et al., 2012). The largest impacts result from insects that kill trees such as the widely reported outbreak of bark beetles in western North America. Bark beetles feed in the phloem of a tree causing direct damage as well as introducing fungi, both of which render transport tissues ineffective and can kill the tree. Bark beetle infestations in the western US are estimated to have affected 15 Mha of forestland from 1997 to 2014 (Tables 1, 4) and another 15 Mha in the south since 1980, collectively putting the greatest amount of basal area at risk among all insect damage (Hicke et al., 2012). Western bark beetles have killed 10 to 20 Tg C  $y^{-1}$  of live biomass (Ghimire et al., 2015; Hicke et al., 2013), and caused an associated reduction in NEP estimated to be about 3 Tg C  $y^{-1}$  from 2000 to 2009 rising to about 8 Tg C  $y^{-1}$  by the end of that interval (Ghimire et al., 2015), though some of this reduction could be compensated by a rapid growth release of surviving individuals. Canada has seen its own major infestations of bark beetles affecting 12 Mha in the 2000s, killing about 20 Tg C  $y^{-1}$  of live biomass in recent decades, estimated to result in a mean annual NEP reduction of 13.5 Tg C  $y^{-1}$  from 2000 to 2020 (Kurz et al., 2008).

Hemlock Woolly Adelgid (HWA) is another tree killer, feeding on the fluids in hemlock leaves, and killing branches and ultimately whole trees. HWA is causing wholesale mortality of hemlock across eastern US forests. Investigations into the C consequences of HWA infestation of *Tusga canadensis* in the eastern US have shown mortality emissions to be compensated by recovery (Orwig et al., 2013; Raymer et al., 2013). Raymer et al. (2013) found that in both experimental girdling simulation of HWA and a long term infested hemlock stand at Harvard Forest resulted in a shift in the ecosystem structure, but no significant loss in ecosystem C. There was, however, a large transfer of C from aboveground biomass (AGB) to CWD, especially standing dead wood. C loss from CWD decomposition was also compensated by released hardwood growth (transfer of C between age/size class), especially *Betula nigra*. A comparison of a mature *B. nigra* stand with a mature secondary *T. canadensis* stand found no significant difference in stand-level carbon content, indicating that long term C trajectories for HWA infested sites may show little effect from the species shift. These broad dynamics were reinforced at a landscape scale with a modeling study (Albani et al., 2010) reporting an 8% (11 Tg C  $y^{-1}$ ) decrease in net carbon uptake by US forests out to 2030 followed by 2040 to 2100 increase of around 15 Tg C  $y^{-1}$  as the area recovers from hemlock loss.

**Table 4**Carbon loss through forest disturbance events (Tg C yr<sup>-1</sup>).

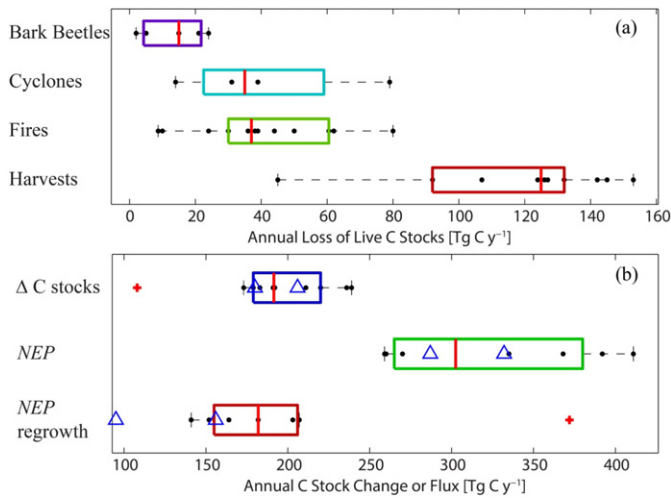
Source	Disturbance	Effect type	Method/model	Flux	Extent	Period
Wiedinmyer and Neff (2007)	Fire	Total emissions	MODIS fire & model	29.0	US48 <sup>a</sup>	2002–2006
French et al. (2011)	Fire	Total emissions	USFS inventories	133.0	US48	1900–1990
Kasischke et al. (2011)	Fire	Total emissions	GFED3 <sup>b</sup>	79.7	NA <sup>c</sup>	2001–2006
Kasischke et al. (2011)	Fire	Total emissions	MCD45A1 <sup>d</sup>	50.7	NA	2001–2006
Stinson et al. (2011)	Fire	Direct emissions	Inventory & CMB-CFS3 <sup>e</sup>	23.0	CAN <sup>f</sup>	2002–2007
Stinson et al. (2011)	Fire	Killed not combusted	Inventory & CMB-CFS3 <sup>e</sup>	27.0	CAN	2002–2007
Zheng et al. (2011)	Fire	Total emissions	MTBS <sup>p</sup> & Smith et al. (2006)	1.1	NOUS <sup>g</sup>	1992–2001
Zheng et al. (2011)	Fire	Total emissions	MTBS <sup>p</sup> & Smith et al. (2006)	0.8	SOUS <sup>h</sup>	1992–2001
Zheng et al. (2011)	Fire	Total emissions	MTBS <sup>p</sup> & Smith et al. (2006)	8.1	WUS <sup>i</sup>	1992–2001
Zheng et al. (2011)	Fire	Total emissions	MTBS <sup>p</sup> & Smith et al. (2006)	9.9	US48	1992–2001
Ghimire et al. (2012)	Fire	NEP reduction	CASA <sup>j</sup>	12.3	WUS	1984–2008
Ghimire et al. (2012)	Fire	Killed not combusted	CASA <sup>j</sup>	10.5	WUS	1984–2008
Ghimire et al. (2012)	Fire	Direct emissions	CASA <sup>j</sup>	4.0	WUS	1984–2008
Ghimire et al. (2012)	Fire	Total emissions	WFEIS <sup>k</sup>	7.0	WUS	2002–2006
Ghimire et al. (2012)	Fire	Total emissions	CASA <sup>j</sup>	6.9	WUS	2002–2006
Ghimire et al. (2012)	Fire	Total emissions	CASA <sup>j</sup> GFED <sup>b</sup>	3.5	WUS	2002–2006
Williams et al. (2012b)	Fire	Total emissions	CASA <sup>j</sup>	10.0	US48	2005
Williams et al. (2012b)	Fire	Total emissions	CASA <sup>j</sup>	30.0	US48	2005
van der Werf et al. (2010)	Fire	Total emissions	CASA <sup>j</sup> + MODIS	54.0	BONA <sup>l</sup>	1997–2009
van der Werf et al. (2010)	Fire	Total emissions	CASA <sup>j</sup> + MODIS	9.0	TENA <sup>m</sup>	1997–2009
van der Werf et al. (2010)	Fire	Total emissions	CASA <sup>j</sup> + MODIS	20.0	CEAM <sup>n</sup>	1997–2009
Zhang et al. (2012)	Fire	Total emissions	InTEC <sup>o</sup>	36.0	US48	1960–2010
Hicke et al. (2013)	Fire	Killed total	MTBS <sup>p</sup> & Blackard et al. (2008)	5.4–10.5	WUS	1984–2010
Hicke et al. (2013)	Fire	Killed total	MTBS <sup>p</sup> & Blackard et al. (2008)	7.2–14.1	WUS	1997–2010
Larkin et al. (2014)	Fire	Total emissions	GFED3 <sup>b</sup>	8.7	US48	2002–2011
Larkin et al. (2014)	Fire	Total emissions	FINN <sup>q</sup>	24.0	US48	2002–2011
Larkin et al. (2014)	Fire	Total emissions	NEI + <sup>r</sup>	60.5	US48	2007–2011
Larkin et al. (2014)	Fire	Total emissions	EPA GHG <sup>s</sup>	38.1	US48	
Vicente et al. (2014)	Fire	Total emissions	Biomass maps + CONAFOR <sup>t</sup>	2.5	MEX <sup>u</sup>	
Source	Disturbance	Effect type	Method/Model	Flux	Extent	Period
Ghimire et al. (2015)	Insect	NEP reduction	FIA <sup>v</sup> & USFS ADS <sup>w</sup>	2.5–3.7	WUS	2000–2009
Ghimire et al. (2015)	Insect	Killed	FIA <sup>v</sup> & USFS ADS <sup>w</sup>	5–15	WUS	2000–2009
Kurz et al. (2008)	Insect	Killed	CBM-CFS3 <sup>e</sup>	22.7	CAN	2000–2006
Dymond et al. (2010)	Insect	NEP reduction	CBM-CFS3 <sup>e</sup>	2	ECANBO <sup>x</sup>	2012–2024
Hicke et al. (2013)	Insect	Killed	ADS <sup>w</sup> & Blackard et al., 2008	2–24	WUS	1997–2010
Zeng et al. (2009)	Cyclone	Killed	Mortality models	79	US48	1851–1900
Zeng et al. (2009)	Cyclone	Killed	Mortality models	39	US48	1900–2000
Fisk et al. (2013)	Cyclone	Killed	ED <sup>y</sup>	31	US48	1851–1900
Fisk et al. (2013)	Cyclone	Killed	ED <sup>y</sup>	14	US48	1900–2000
Chambers et al. (2007)	Cyclone	Killed	MODIS & FIA <sup>v</sup>	105	USGULF <sup>z</sup>	2005

<sup>a</sup> Contiguous 48 US states.<sup>b</sup> Global Fire Emissions Database.<sup>c</sup> North America.<sup>d</sup> MODIS derived monthly burn product.<sup>e</sup> Carbon Budget Model – Canadian Forest Sector.<sup>f</sup> Canada.<sup>g</sup> Northern US.<sup>h</sup> Southern US.<sup>i</sup> Western US.<sup>j</sup> Carnegie Ames Stanford Approach.<sup>k</sup> Wildfire Emissions Information System.<sup>l</sup> Boreal North America, after Giglio et al., 2006.<sup>m</sup> Temperature North America, after Giglio et al., 2006.<sup>n</sup> Central America, after Giglio et al., 2006.<sup>o</sup> Integrated Terrestrial Ecosystem.<sup>p</sup> Monitoring Trends in Burn Survey.<sup>q</sup> Fire Inventory NCAR.<sup>r</sup> US EPA National Emissions Inventory extrapolated beyond published years.<sup>s</sup> US EPA Greenhouse Gas estimates.<sup>t</sup> Comisión Nacional Forestal burn extent maps.<sup>u</sup> Mexico.<sup>v</sup> US Forest Service Forest Inventory and Analysis database.<sup>w</sup> US Forest Service Areal Detection Survey.<sup>x</sup> Eastern Canadian boreal forest.<sup>y</sup> Ecosystem Demography model.<sup>z</sup> US states on the Gulf of Mexico.

Wood borers and root feeders can also cause tree mortality. Invasion of Emerald Ash Borer (EAB) in the Great Lakes region of the US has resulted in high mortality of *Fraxinus* species in affected stands, with some observations finding 100% *Fraxinus* mortality over a decade (Herms and McCullough, 2014). In the Great Lakes States where *Fraxinus* are concentrated, about 160 Tg C in aboveground biomass are

vulnerable to EAB attack, which could introduce another large disturbance emissions legacy. Correspondingly, Pugh et al. (2011) analyzed FIA data and found a large reduction in *Fraxinus* volume within 50 km of the introduction epicenter, reducing from 13 to 3 m<sup>3</sup> ha<sup>-1</sup> between the 2004 and 2009 inventories. However, compensatory growth by other species moderates the effect on *NPP* to some degree. For example,





**Fig. 3.** Boxplots of multiple estimates for (a) mean annual disturbance-induced fluxes over the last three decades in the conterminous US, and (b) the change in carbon stocks, total net ecosystem productivity (NEP) and NEP due only to disturbance and regrowth processes (NEP regrowth). Black dots show values from individual studies, red pluses indicate outliers, and blue triangles indicate process model estimates. Data for panel (a) are reported in Tables 4 and 5, except for Insects\* which is based on Krist et al. (2007) as noted in the text. Data for the ΔC stocks and NEP are based on studies using the stock-change method while NEP regrowth is based on studies using the age-accumulation method (Table 5). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Flowers et al. (2013) studied tree growth rates in stands of the Midwestern US and found that infestation caused a 32% reduction in NPP but that this was partially offset by compensatory growth by *Acer* and *Ulmus* species. Even if there is short term compensation for EAB C loss, this disturbance driven shift in species distribution could have large longer term consequences for NEP and forest C stocks.

Another class of insects directly feed on leaves causing defoliation, and include forest tent caterpillars, spruce budworms, and gypsy moths. Large-scale carbon impacts from defoliation by Gypsy Moth

(*Lymantria dispar* L.) can also be significant, threatening 40 million m<sup>2</sup> of basal area and affecting 5 Mha of forest in the northeastern US since the 1980s (Hicke et al., 2012). Clark et al. (2010) found a 41% reduction in NEP from Gypsy Moth defoliation of three upland mixed hardwood stands in New Jersey, 2005–2007. Their investigation utilized both ground based biometric estimates of NPP, as well as eddy covariance estimates of NEP. Medvigy et al. (2012) simulated gypsy moth defoliation at the Silas Little Experimental Forest in New Jersey for 200 years with a range of defoliation intensities and periodicities. Despite a continued net carbon uptake over the 200 year period, NPP exhibited a 7 g C m<sup>-2</sup> y<sup>-1</sup> decline on average. Spruce budworm, another defoliator, has affected 20 Mha of eastern US forests and 5 Mha in the west over recent decades, and places about 9 million m<sup>2</sup> of basal area at risk (Hicke et al., 2012). Spruce budworm damage extends into Canada as well where it is forecast to have the potential to transition eastern Canadian forests from a sink to a source for atmospheric carbon (Dymond et al., 2010).

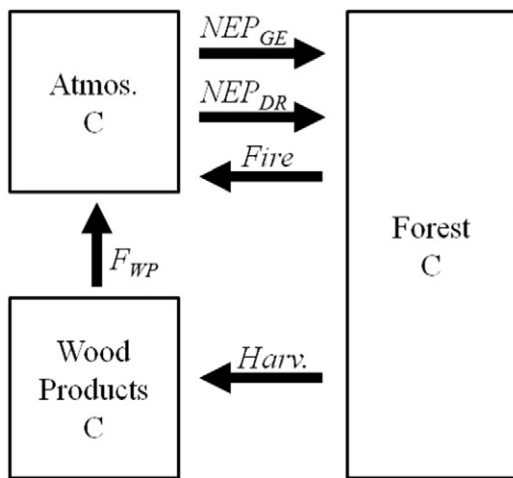
Climate change is broadly expected to increase the frequency and extent of insect infestations (Boyd et al., 2013). Rising temperatures are accelerating the maturation and development of insect populations and enabling greater insect survival over winter, enabling range expansion and stressing host trees (e.g. Bentz et al., 2010). Insects may outpace host tree responses to the changing climate because of their faster reproductive rates facilitating faster responses to natural selection pressures. Insect disturbances could also influence the rate of species distribution shifts in response to climate change by exacerbating physiological stresses experienced by host species at the margins of their distribution and accelerating ensuing forest compositional transitions (Bentz et al., 2010). Exactly how these factors will unfold in the future remains unclear but it is logical to expect a general decrease in live forest carbon stocks in response to continued infestations over at least the next several decades.

#### 4.4. Windthrow

Windthrow is a common tree mortality mechanism regularly opening tree-scale gaps in forests and in extreme cases causing blowdowns of whole stands from microbursts, tornadoes, cyclones or hurricanes (Boose et al., 2001; McNulty, 2002). Damage can be extensive, with wind events estimated to be one of the leading natural disturbances affecting forests of eastern North America (Boose et al., 1994; Boose et al., 2001). Dead trees and downed leaves and branches slowly decompose in the wake of such storms with the post-disturbance environment commonly being composed of surviving canopy trees, resprouts, understory saplings, and seedlings, all of which may experience a competitive release and accelerated growth in its aftermath.

There are relatively few studies providing large-scale estimates of wind damage and mortality, and those that are available tend to focus on individual events such as a single hurricane. While small-scale mortality of individual trees caused by windthrow events undoubtedly has a large aggregate effect when integrated to the country scale, such events are often viewed as being embedded in the typical pathway of forest development and succession, which may explain difficulty in finding estimates of their associated carbon impacts. Therefore, we were forced to focus on the carbon impacts of the larger-scale extreme disturbances documented to date.

Hurricanes are estimated to impact as much as 1.2 Mha of forestland in the US each year, or as much as 3 times as much as wildfires (Dale et al., 2001). Cyclone induced mortality involves a carbon transfer from living to dead pools, mostly in the form of CWD, much of which becomes a committed emission to the atmosphere as decomposition ensues. As such, the carbon impacts are already implicit in stock changes measured in extensive field inventories, though we note that even the most extensive field inventories still sample only a tiny fraction of all forestlands and are thus susceptible to biased omission of windthrow disturbance hotspots. These events also induce a corresponding forest regrowth



$$\begin{aligned}\Delta \text{Forest } C &= NEP_{GE} + NEP_{DR} - Harv. - Fire \\ &= NEP_{GE} + NDR\end{aligned}$$

**Fig. 4.** Schematic diagram displaying forest sector-atmosphere stocks and fluxes including carbon stocks in the atmosphere, forests, and wood products, and carbon fluxes from net ecosystem productivity stimulated by growth enhancements (NEP<sub>GE</sub>), NEP from disturbance and regrowth processes (NEP<sub>DR</sub>), direct fire emissions, harvest removals, and release of carbon from the wood products pool (F<sub>WP</sub>). NDR refers to the net flux from disturbance and regrowth processes.

legacy, with the annual net carbon flux responding to the balance of regrowth uptake and disturbance emissions both locally for any given event and also at larger scales in response to a long history of windthrow events.

Tree mortality from individual hurricane events in the US can amount to a sizeable fraction of the nation's average annual forest carbon uptake. For example, hurricanes Fran and Hugo are each estimated to have transferred 20 Tg C from live to dead pools based on aerial and ground surveys (McNulty, 2002). Using an advanced scaling from field plots to satellite remote sensing data of moderate resolution, Chambers et al. (2007) estimated that hurricane Katrina transferred about 105 Tg C from live to dead forest carbon pools. Such event-specific activity has been extended to longer-term, continuous estimation in several modeling studies (Fisk et al., 2013; Zeng et al., 2009) finding average annual biomass kill from these events to be of similar magnitude to total emissions from wildfire (Table 4, Fig. 3) but with very large interannual variability ranging from 0 to as much as 200 Tg C in any given year. However the net effect on carbon sequestration is close to neutral at large scales because disturbance emissions are largely offset by the regrowth legacy stimulated by past events. Both studies report wide variation in annual mortality from windthrow, with a relatively modest effect on annual net ecosystem carbon exchange which exhibits muted interannual variability because of lagged, gradual decomposition as well as landscape level compensation by large areas with regrowth sinks that were stimulated by prior events. This results in swings between modest C sources and modest sinks, for example, a net carbon sequestration of 1.5–6.5 Tg C y<sup>-1</sup> between 1970 and 1995, but a net carbon release of 1.3–2.6 Tg C y<sup>-1</sup> during 1995 to 2000 which had greater storm frequency (Fisk et al., 2013).

#### 4.5. Drought

Drought represents a deviation from the classical view of disturbance as a temporally discrete event (White and Pickett, 1985), with its impacts often unfolding as the drought event ensues. It is both a modulator of other disturbances and a direct cause of tree mortality with significance for global forest C stocks and feedbacks to climate change (Adams et al., 2009; Allen et al., 2010; Anderegg et al., 2013a; McDowell, 2011; Silva et al., 2010). As a modulator, drought can significantly alter the likelihood and severity of other disturbance types, for example by stressing trees and causing them to succumb to insect infestation, or by creating weather conditions that are more conducive to severe fires. Drought can also be an independent disturbance event of its own, causing pulses of tree mortality during severe and/or lasting dry periods (e.g. Anderegg et al., 2013b; Doughty et al., 2015; Nepstad et al., 2007).

In North America, forest mortality from drought has been reported for Canadian boreal forests (Ma et al., 2012; Peng et al., 2011), a range of aspen forests (Anderegg et al., 2013b; Hanna and Kulakowski, 2012; Hogg et al., 2008; Michaelian et al., 2011) and in the US West (van Mantgem et al., 2009). The exact mechanisms of drought-induced mortality remain somewhat elusive, involving a variable combination of carbon starvation and hydraulic failure depending on the nature of drought events and plant physiological adaptations (McDowell, 2011). Drought also reduces ecosystem carbon uptake by causing larger declines in productivity than respiration (Schwalm et al., 2010). A large-area assessment of drought impacts on the contemporary carbon balance of the US is lacking, though a number of studies illustrate the potential for significant reductions in carbon uptake and even large scale tree mortality events that leave a legacy of carbon release.

By investigating permanent sampling plots in the Canadian boreal forest, Ma et al. (2012) estimated that droughts reduced the Canadian forest C sink by  $7.28 \pm 3.3$  Tg C y<sup>-1</sup> from 1961 to 2003. With a combination of MODIS NPP/GPP and FLUXNET data, Schwalm et al. (2012) estimated 30–298 Tg C y<sup>-1</sup> C sink reduction (baseline of 177–623 Tg C y<sup>-1</sup>) in western North America during 2000–2004. The

European heat wave and drought of 2003 reportedly caused an anomalous carbon source of 5000 Tg C in that year, cancelling four years of net ecosystem carbon sequestration typical for the continent (Ciais et al., 2005). Huang and Anderegg (2012) reported that drought induced sudden aspen decline in the Rocky Mountains of southwestern Colorado, resulting in a loss of live aboveground biomass equaling about 3 Tg C destined for gradual release to the atmosphere. A similar analysis for Pinyon–Juniper woodlands suggested a roughly 5 Tg C loss of live aboveground biomass due to multi-year drought combined with insect and disease outbreaks (Huang et al., 2010a), and drying trends over the next century have been predicted to threaten widespread loss of evergreen needleleaf trees across the American West (McDowell et al., 2016).

Along with precipitation deficits during droughts, humidity tends to be lower than normal as well decreasing fuel moisture, increasing flammability, and increasing the risk of severe fires. Such warmer and drier air expected in the future with the changing climate is expected to exert growing pressure on forests in the future. For example, Williams et al. (2012a) developed a forest drought-stress index (FDSI) for the western US based on 1000 years of tree-ring increment data that was found to correlate well with warm season vapor pressure deficit and cold season precipitation. When coupled with CMIP3 climate model projections, the FDSI indicates megadrought conditions by 2050 exceeding the severity of any drought experienced in the last millennium. The full carbon implications of such a transition are unclear, representing not only a change in the frequency of extreme dry periods but also a secular shift toward a drier climate. This would have the likely effect of moving whole ecotones (e.g. Allen and Breshears, 1998) including the replacement of high carbon density forests with landscapes that have lower carbon stocks with the potential to release a large amount of carbon to the atmosphere.

#### 4.6. Integration for a US-wide forest carbon balance assessment

Multiple perspectives are needed to fully assess the carbon impacts of disturbance processes and here we focus on two: changes in live carbon stocks and the net flux between forests and the atmosphere, or net ecosystem productivity (NEP). Starting with carbon stocks, we find that harvesting causes the largest reduction in live tree biomass annually (median = 125 Tg C y<sup>-1</sup>), followed by fire and windthrow (37 and 35 Tg C y<sup>-1</sup>), with bark beetles (15 Tg C y<sup>-1</sup>) having had the most modest impact across the conterminous US (Tables 4 and 5, Fig. 3). Additional mortality caused by other insect types is less well documented but could easily be as large as that for bark beetles which would put total insect damage in the range of fire and windthrow disturbances as supported by a cursory calculation based on Krist et al. (2007) as noted above which suggested about 21 Tg C y<sup>-1</sup> in losses of live biomass from all insect damage. Loss of live carbon stocks from drought-induced mortality remains unclear but its direct effect is unlikely to amount to more than 10 Tg C y<sup>-1</sup> and its largest effect may be as a modulator of other disturbances by stressing trees and creating fire weather.

Together these disturbance processes resulted in an average annual gross reduction of live carbon stocks of about 210 Tg C per year over recent decades. This equates to 1% of the total live aboveground biomass in conterminous US forests (= 21 Pg C from Table 3). Harvest alone accounts for nearly 60% (= 125/210) of the loss of live C stocks, somewhat lower than the 66% estimated from forest service reporting of growing stock volume (= 84/128, Table 3), which notably suggests half as much mortality from non-harvest agents (41 compared to 87 Tg C y<sup>-1</sup>). It is important to keep in mind that disturbance-killed biomass can reside in ecosystems for years and even decades before ultimate decomposition and release to the atmosphere. Thus, disturbance emissions can be significantly lagged relative to the timing of mortality events, creating a transient increase in dead and downed wood

**Table 5**Literature estimates of annual forest carbon stock change and net ecosystem productivity (*NEP*) ( $\text{Tg C yr}^{-1}$ ), adapted from Williams et al. (2012b).

Source	Approach <sup>a</sup>	Mean <i>NEP</i> <sup>b</sup>	Low	High	Harvest	Fire	$\Delta C_{\text{stocks}}$	Period	Extent <sup>c</sup>
Williams et al. (2012a)	AA	141	116	166	153		–12	1986–2005	US48
Williams et al. (2014a) <sup>d</sup>	AA	152	128	176	126		26	1986–2005	US48
Williams et al. (2012b)	AA	164	136	192	107	10	47	2005	US48
Houghton (1999)	AA	182			92	80	10	1980s	US48
Turner et al. (1995)	AA	203			124		79	1990	US48
Houghton (2003)	AA	207			92	80	35	1990s	US48
Hurt et al. (2002)	AA	372	282	442	92	50	230	1980s	US48
Heath et al. (2011)	$\Delta C_{\text{stocks}}$	259				39	191	2005	US48 +
Heath et al. (2011)	$\Delta C_{\text{stocks}}$	260				44	192	2008	US48 +
Woodbury et al. (2007)	$\Delta C_{\text{stocks}}$	270	256	293	132	30	108	2005	US48
EPA (2012)	$\Delta C_{\text{stocks}}$	270				62	183	2012	US48
EPA (2008)	$\Delta C_{\text{stocks}}$	335			132	30	173	2005	US48
Birdsey and Heath (1995)	$\Delta C_{\text{stocks}}$	368			127	30	211	1992	US48
King et al. (2007)	$\Delta C_{\text{stocks}}$	411	383	439	145	30	236	1980s	US48
Pan et al. (2011)	$\Delta C_{\text{stocks}}$						179	1990–1999	US48 +
Pan et al. (2011)	$\Delta C_{\text{stocks}}$						239	2000–2007	US48 +
Pacala et al. (2001)	Synthesis	392	312	472	92	80	220	1980s	US48
Schimel et al. (2000)	P (clim, CO <sub>2</sub> )	80						1980–1993	US48
Zhang et al. (2012)	P (all procs)	287			45	36	206	1950–2000	US48
Zheng et al. (2011)	P (all procs)	332			142	10	180	1992–2001	US48
Pan et al. (2011)	$\Delta C_{\text{stocks}}$						26	1990–1999	CAN
Pan et al. (2011)	$\Delta C_{\text{stocks}}$						10	2000–2007	CAN
Stinson et al. (2011)	P	71	62	80	45	23	2	1990–2008	CAN
Pan et al. (2011)	$\Delta C_{\text{stocks}}$						1040	1990–1999	global
Pan et al. (2011)	$\Delta C_{\text{stocks}}$						1110	2000–2007	global
Lawrence et al. (2012)	P	2830			2030	410	390	1850–2005	global

<sup>a</sup> Estimates are classified according to approach: age structure-C accumulation (AA), stock change ( $\Delta C_{\text{stocks}}$ ), or process model (P) accounting for CO<sub>2</sub> and climate effects only (clim, CO<sub>2</sub>), or all processes (all procs). Low and High refer to 1 standard deviation about the mean estimate.

<sup>b</sup>  $NEP = \Delta C_{\text{stocks}} + \text{Harvest} + \text{Fire}$  where *NEP* is not reported.

<sup>c</sup> USA48 refers to the contiguous lower 48 US states; US48 + includes values from southern coastal Alaska (FIA); CAN refers to Canada.

<sup>d</sup> The first value represents estimates generated with age distributions partially informed by a NAFD Phase 2 Landsat product.

following above average disturbance years, or when disturbance rates trend upwards. Thus actual disturbance emissions over recent decades could be substantially lower than the reported 210 Tg C per year loss of live biomass.

Carbon stocks in US forests are increasing by about 190 Tg C per year (Table 5, Fig. 3) indicating that gross forest growth more than offsets disturbance and mortality losses. Stock increases in Canada are estimated to be much smaller at 10 to 30 Tg C per year (Table 5). The contemporary rise in US forest carbon stocks contributes substantially to the global stock change in forests, accounting for about 17% of the global total (1100 Tg C  $\text{yr}^{-1}$ ) (Pan et al., 2011).

Measured stock changes can be used to infer net ecosystem productivity of about 300 Tg C per year, according to synthesis estimates (Fig. 3), by adding back in the portions known to have been lost to harvest and fire ( $\Delta C = NEP - H - F$ ) (Fig. 4). If, simply to consider the magnitude of this carbon sink, we assumed that net carbon uptake was spread evenly over the roughly 260 Mha of forestland in the conterminous US it would imply *NEP* of about 115 g C  $\text{m}^{-2} \text{yr}^{-1}$ , or 1.15 Mg C  $\text{ha}^{-1} \text{yr}^{-1}$ . This is well within the range of carbon uptake rates (*NEP*) reported from eddy covariance sites in North American forests with a stand age greater than 20 years (Amiro et al., 2011), ranging 0 to 200 g C  $\text{m}^{-2} \text{yr}^{-1}$  for nearly all post-fire sites, and 0 to 800 g C  $\text{m}^{-2} \text{yr}^{-1}$  for all of the post-harvest sites.

There are a number of mechanisms that could contribute to the observed net carbon uptake. First, there is a well-known age-structure legacy in US forests, with stocks still recovering from historical clearing and ensuing afforestation, and also regrowing after more recent disturbance events of all types (Caspersen et al., 2000; Hurt et al., 2002). Climate may have trended toward conditions that are more favorable for carbon storage, with a tendency toward wetter conditions across the latter half of the 20th century (Schwalm et al., 2011). Enhanced growth from CO<sub>2</sub> and nitrogen fertilizations, as well as management impacts are also likely candidates for stimulating carbon sequestration in forests (Joos et al., 2002). Slowing mortality rates would have the potential to create a net

carbon sequestration, but research indicates the reverse at least for the Western US (van Mantgem et al., 2009).

Attempts to attribute the growth in forest carbon stocks to drivers with direct empirical analysis of the FIA plot data have been inconclusive because of data limitations and methodological challenges (Joos et al., 2002). However, results from two process models (Zhang et al., 2012; Zheng et al., 2011) that account for climate, CO<sub>2</sub>, age-structure, and management factors suggest that disturbance and regrowth processes account for about one-third to one-half of the *NEP* in US forests, somewhat lower than what is suggested by synthesis estimates (Fig. 3).

Additional insights about attribution can come from estimating the aggregate effect of disturbance and regrowth processes on forest *NEP* and comparing this to results from the stock-change method which includes effects of all processes (Fig. 4). The stock-change method relies on sequential measurement of tree diameters and/or wood volume from a large, distributed set of forest plots, converted into forest carbon stocks with biomass expansion factors that scale up to regions, and finally estimating yearly net change by dividing total change by the number of years in the measurement interval. In contrast, the disturbance and regrowth method, which we call “age-accumulation”, usually combines estimates of forest stand age with age-specific carbon accumulation rates derived either empirically from inventory measurements or estimated with a process oriented dynamic growth model. With its focus on stand age the method quantifies the leading effects of disturbance and regrowth processes. Because the method typically relies on a chronosequence developed from plots with different stand ages to characterize carbon stock accumulation with time since disturbance it omits some of the contemporary influences of climate variability and trends, trends in low to moderate severity disturbances that do not reset stand age, and effects of CO<sub>2</sub> and nitrogen fertilizations on forest growth and forest carbon stocks. As we have noted in our prior work (see Auxiliary Material, Part 4 in Williams et al., 2012a), responses to these trends are embedded in chronosequence data in complex ways, being largely implicit in the stocks reported for young aged stands but



progressively excluded toward older stands. Even so, comparing results of the stock-change and age-accumulation methods provides insights into the likely magnitude of effects for these missing processes.

The net effect of disturbance and regrowth processes on net ecosystem productivity in US forests is believed to be a sink for atmospheric carbon of about  $182 \text{ Tg C y}^{-1}$  (Fig. 3). From their process model study, Zhang et al. (2012) obtained a lower estimate of disturbance-induced NEP but their upper estimate is still within the range reported here (Fig. 3). The stock-change method reports a total NEP of  $300 \text{ Tg C y}^{-1}$ , which by comparison suggests an additional  $118 \text{ Tg C y}^{-1}$  from other factors ( $= 300 - 182 \text{ Tg C y}^{-1}$ ), also somewhat greater than the sink from non-disturbance drivers ( $50 \text{ Tg C y}^{-1}$ ) reported in the model study of Zhang et al. (2012). Put together, disturbance and regrowth processes are thought to account for about 60% of forest NEP ( $= 182 / 300 \text{ Tg C y}^{-1}$ ) with the other 40% being due to other mechanisms, again noting that these fractions are subject to the complications of using chronosequence data for the age-accumulation method. By comparison, attribution of the NEP for European forests ( $175 \text{ g C m}^{-2} \text{ y}^{-1}$ ) indicates 13% due to age structure, 26% to climate, and 61% to  $\text{CO}_2$  fertilization (Bellassen et al., 2011).

Attributing the change in forest carbon stocks requires a different computation than that used to attribute the drivers of NEP. To attribute the change in carbon stocks, we combine the NEP due to forest disturbance and regrowth estimated from the age-accumulation method ( $182 \text{ Tg C y}^{-1}$ ) with the removals from harvest ( $125 \text{ Tg C y}^{-1}$ ) and losses from direct fire emissions ( $37 \text{ Tg C y}^{-1}$ ) to obtain the net disturbance and regrowth flux (NDR) of  $20 \text{ Tg C y}^{-1}$  ( $= 182 - 125 - 37 \text{ Tg C y}^{-1}$ ). This NDR term reflects the aggregate effect of disturbance and regrowth processes as they contribute to the change in forest stocks (Fig. 4). It indicates that only about 11% ( $= 20 / 190$ ) of the forest stock accumulation is due to the net effect of disturbance and regrowth, with the remainder being due to other processes, presumably growth enhancements. This is true even though the NEP from net regrowth, or NDR ( $\sim 180 \text{ Tg C y}^{-1}$ ), is of similar magnitude to the total change in forest carbon stocks ( $\sim 190 \text{ Tg C y}^{-1}$ ) because the total change in carbon stocks also includes harvest and fire losses which are additional components of the sum total of disturbance and regrowth effects. There is no doubt that the net forest regrowth process plays a major role in offsetting disturbance losses and contributes significantly to annual net forest productivity. Furthermore, regrowth indeed contributes to a trend toward increased carbon stocks, however because regrowth is largely balanced by disturbance induced losses of carbon, much of the carbon stock increase is interpreted as being due to other factors.

We caution that these attribution exercises mix data from a number of different sources and derived with a range of methods that can have inconsistent assumptions. Even so, they provide insightful indications of the degree to which disturbance versus climate and growth enhancement factors may be driving the US forest carbon sink.

#### 4.7. Future carbon balance outlook and management

Protecting forest carbon storage and uptake is central to national and international policies aimed at mitigating climate change, offering one of the most cost effective means of curbing further rise of atmospheric  $\text{CO}_2$  (Canadell and Raupach, 2008). Correspondingly, national and international policy aimed at mitigating climate change by managing net carbon fluxes into the atmosphere will likely involve rewards for managing forest sinks and verification for treaty enforcement. Indeed, many countries are looking to the forest sector to meet their Intended Nationally-Determined Contributions (INDCs) to reduce greenhouse gas emissions. Forest carbon management, policy, and valuation need to be informed by full understanding of carbon sink/source mechanisms and the potential for not only continued sequestration in forests but also the permanence of forest carbon stores in the face of disturbances. Management must also consider risks of leakage whereby the protection of carbon stores and uptake in one area may be offset by management

activities elsewhere. Furthermore, the full climate benefit and costs of forestry must consider how other biophysical properties of the land surface influence the climate system, such as albedo and evaporation, which can significantly alter the net climate effect of forests such as in the snowy boreal zone where forest cutting can cause a net cooling due to albedo effects (Bonan, 2008; Hungate and Hampton, 2012; Jackson et al., 2008).

The future of the US forest carbon sink depends strongly on the mechanisms that are driving it. For instance, as forests age, their ability to accumulate carbon diminishes (Pregitzer and Euskirchen, 2004) and so the effects of past disturbance history should decrease as forests recover, presuming disturbance rates stabilize. This is true even in light of recent work showing that old growth forests can provide a larger carbon sink than was previously thought (Luyssaert et al., 2008). While ecosystem models consistently predict a strong  $\text{CO}_2$  fertilization sink in the world's forests over the coming century, the science is far from settled making this prediction highly uncertain. Some indications suggest it can be expected to slow as other limiting factors (e.g. nitrogen or water) preclude its utilization, and that sinks stimulated by rising  $\text{CO}_2$  may be limited by physiological constraints such as size-dependent mortality leading to shorter-tree lifetimes as tree growth accelerates. Even if the  $\text{CO}_2$  sink persists with rising  $\text{CO}_2$ , it will disappear rapidly when  $\text{CO}_2$  ceases to rise with respiration releases catching up to stimulated productivity. Considering other relevant sink mechanisms, efforts to improve air quality over large regional scales could lead to a decrease in nitrogen deposition and/or aerosol-enhancement of diffuse illumination, decreasing associated carbon sinks (Gruber and Galloway, 2008; Mercado et al., 2009). Predictions of how these drivers will change over the next several decades remain uncertain (Bellassen and Luyssaert, 2014), necessitating continued research with manipulative experiments to uncover mechanisms and sensitivities. Continued research is also needed to improve attribution of the contemporary forest sink in US forests, critical for forecasting its likely response to trends in drivers into the future.

Management activities are believed to have the potential to sustain and even increase carbon sequestration in US forests into the future, possibly even doubling its current magnitude over the next century (Birdsey et al., 2006; McKinley et al., 2011; Post et al., 2012). However, the prevailing management activity, harvesting, generally reduces land carbon stocks relative to what they would be in the absence of harvesting, even if carbon uptake tends to be higher in younger forests (Harmon et al., 1990; Harmon and Marks, 2002; Schulze et al., 2000). For example, carbon stores in forests plus the wood products pool combined are often maximized in the absence of harvesting, and stores decrease with more intense and/or more frequent harvesting as well as with lower structural retention of residual (unharvested) large trees (Nunery and Keeton, 2010). At the same time, trends in management toward activities that promote faster and more resilient forest regeneration have been shown to accelerate carbon stock recovery following harvest (e.g. Erb et al., 2013), enabling forest regrowth to offset the typical carbon losses of harvesting actions more rapidly. Birdsey et al. (2006) note a number of potential opportunities for enhancing forest sequestration in the US through management, including forest restoration, management of nutrients, residues and regeneration, lower impact harvesting, agroforestry, forest preservation, wood products management, urban forestry, and biomass energy, though the apparent greenhouse gas benefits of bioenergy are hotly contested (Schulze et al., 2012). Birdsey et al. (2006) also mention afforestation but others believe it to have limited practical potential in the US (Ray et al., 2009). Focusing harvest removals toward long-lived wood products that can substitute for more energy-intensive building materials, not only creates a transient but still lasting carbon sink if wood products last longer than the time required for forest regeneration, but also has the important effect of avoiding the release of fossil carbon which has a long atmospheric residence time (Bellassen and Luyssaert, 2014; Oliver et al., 2014). Still, while many of these activities could play a role, the greatest

potential for enhancing contemporary carbon sequestration would appear to come from reduced harvesting frequency and/or intensity.

The forest sink could be under threat if forest disturbance from fire, insects, drought, and windthrow continue to rise and as climate change and other factors induce additional stresses that could reduce forest carbon stock potentials (Peterson et al., 2014; U.S. Department of Agriculture, 2012). Such an increase in disturbance rates would have the near-term effect of reducing forest carbon stocks and would call into question the permanence of forest sinks as a mechanism for climate change mitigation (Canadell and Raupach, 2008; Le Page et al., 2013; McKinley et al., 2011). These trends have led some to promote preemptive treatments of forests with tree and/or fuel reductions that aim to lower the risk of high-severity disturbances (e.g. Hurteau et al., 2008; Hurteau and North, 2009; North et al., 2015). However, in at least some cases, such treatments are found to be ineffective in the case of western US wildfires (North and Hurteau, 2011), releasing as much or more carbon as they protect given that carbon losses from fuel removal exceed those avoided as combustion and also because the treatment area must be much larger than the area it ends up protecting from burning for the treatment to be effective (Boer et al., 2015; Campbell et al., 2011). Still others question the wisdom of preemptive and salvage logging based on the recognition of the ecological benefits of diverse and heterogeneous stands and landscapes resulting from natural disturbances, and because such treatments often adversely impact ecosystem structure and function, including carbon storage, more than the natural disturbances that they seek to avoid or mitigate (Foster and Orwig, 2006).

#### 4.8. Challenges and opportunities

There are a number of challenges hampering a full accounting of the carbon impacts of disturbances and forecasting the future of the carbon sink in US forests. Chief among them is the fact that disturbances can impose long lasting legacies, with gradual stock recovery and disposition of disturbance killed material. This requires a centuries-long time horizon for assessing impacts during which time global environmental changes continue to unfold. Another challenge is that the longevity of standing dead and downed wood is poorly quantified. Similarly, records of the origin and fate of harvested wood products could be improved. All of these are critical for assessing the full life-cycle impacts of various disturbances. It is also difficult to judge what makes an appropriate baseline scenario to be used as a reference characterization of the carbon dynamics that would have ensued in the absence of a particular disturbance. This becomes especially challenging given uncertain disturbance trends and disturbance interactions which affect both occurrence and impact.

Disturbance interactions can be highly complex and further research is required to understand the associate implications for carbon dynamics. For example, Kulakowski et al. (2012) and Kulakowski and Jarvis (2013) found that the effect of prior wildfire on tree and stand susceptibility to bark beetle attack was dependent on the severity of both the initial wildfire and the bark beetle outbreak. The converse, beetle outbreak contributing to wildfire, is also complex. While many expect increased fire risk post beetle outbreaks, forests experiencing high severity fire regimes tend to be insensitive to beetle outbreaks (Simard et al., 2011), forests in drier settings experience decreased fire susceptibility after beetle outbreaks (Donato et al., 2013), and a recent review indicates that bark beetle outbreaks generally have little to no effect on wildfire (Black et al., 2013). These and other interactions are just starting to be appreciated, with the need for additional research into carbon cycle implications.

Climate change and a long history of land management both affect contemporary disturbance rates, disturbance intensities, and post-disturbance regeneration pathways. This presents a major challenge to assessments of likely future forest carbon dynamics. For example, the large size and high severity of some recent fires in the western US

have the potential to lead to uncommonly slow forest regeneration, significantly altered species composition, and even shifts in whole ecotones. Where such events are taking place today, these case studies need to be closely monitored as a test of forestland resilience, as early warnings of what future landscapes may come to look like, and as a source of information for adaptive management responses.

Wall to wall, periodic monitoring of three-dimensional forest structure and biomass with remote sensing technologies, in combination with intensive field measurement supplemented with controlled experiments, is arguably the most promising way forward for assessing how all drivers are affecting forest carbon dynamics (Mascaro et al., 2014). It is now possible to conduct extensive, repeat measurements with aircraft and/or satellite platforms to measure and monitor changes in forest size structure and hence demographics, as well as aboveground biomass, both of which are key indicators of the impacts of disturbances and other global change factors.

Perhaps what is most valuable are platforms, such as the Forest Vegetation Simulator (FVS, <http://www.fs.fed.us/fmrc/fvs/>) and i-Tree (<https://www.itreetools.org/>), for studying the holistic impacts of disturbance trends and management scenarios in the context of uncertain global environmental changes to inform policy makers, land managers, industry, and the general public. Such platforms can be designed to consider a wide range of ecosystem values beyond simply carbon to assess full climate forcing (i.e. albedo impacts), as well as biodiversity, habitat, water quality and quantity, timber production, and other goods and services, and at the same time designed to be flexible enough to handle uncertainty in forest responses to the changing climate and interactive trends in management and natural disturbance regimes.

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#### References

- Adams, H.D., et al., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proc. Natl. Acad. Sci.* 106 (17), 7063–7066.
- Albani, M., Moorcroft, P.R., Ellison, A.M., Orwig, D.A., Foster, D.R., 2010. Predicting the impact of hemlock woolly adelgid on carbon dynamics of eastern United States forests. *Can. J. For. Res. Rev. (Canadienne De Recherche Forestiere)* 40, 119–133.
- Allen, C.D., Breshears, D.D., 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proc. Natl. Acad. Sci.* 95, 14839–14842.
- Allen, C.D., et al., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* 259, 660–684.
- Amiro, B.D., et al., 2011. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *J. Geophys. Res.* 115 G00K02.
- Anderegg, W.R.L., Kane, J.M., Anderegg, D.L., 2013a. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Chang.* 3, 30–36.
- Anderegg, W.R.L., et al., 2013b. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Glob. Chang. Biol.* 19, 1188–1196.
- Anderson-Teixeira, K.J., et al., 2013. Altered dynamics of forest recovery under a changing climate. *Glob. Chang. Biol.* 19 (7), 2001–2021.
- Ballantyne, A., Alden, C., Miller, J., Tans, P., White, J., 2012. Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* 488, 70–73.
- Barrett, K., McGuire, A.D., Hoy, E.E., Kasischke, E.S., 2011. Potential shifts in dominant forest cover in interior Alaska driven by variations in fire severity. *Ecol. Appl.* 21 (7), 2380–2396.
- Bellassen, V., Luyssaert, S., 2014. Managing forests in uncertain times. *Nature* 506, 153–155.
- Bellassen, V., et al., 2011. Reconstruction and attribution of the carbon sink of European forests between 1950 and 2000. *Glob. Chang. Biol.* 17, 3274–3292.
- Bender, M.A., et al., 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. *Science* 327 (5964), 454–458.
- Bentz, B.J., et al., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience* 60 (8), 602–613.
- Birdsey, R.A., Heath, L.S., 1995. Carbon changes in U.S. forests. In: Joyce, L.A. (Ed.), *Productivity of America's Forests and Climate Change*. Fort Collins.

- Birdsey, R., Pregitzer, K., Lucier, A., 2006. Forest carbon management in the United States: 1600–2100. *J. Environ. Qual.* 35 (4), 1461–1469.
- Black, S.H., Kulakowski, D., Noon, B.R., DellaSala, D.A., 2013. Do bark beetle outbreaks increase wildfire risks in the central US Rocky Mountains? Implications from recent research. *Nat. Areas J.* 33 (1), 59–65.
- Blackard, J.A., et al., 2008. Mapping U.S. forest biomass using nationwide forest inventory data and moderate resolution information. *Remote Sens. Environ.* 112, 1658–1677.
- Boer, M.M., Price, O.F., Bradstock, R.A., 2015. Wildfires: weigh policy effectiveness. *Science* 350 (6262), 920.
- Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444–1449.
- Boose, E., Foster, D.R., Fluet, M., 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecol. Monogr.* 64, 369–400.
- Boose, E.R., Chamberlin, K.E., Foster, D.R., 2001. Landscape and regional impacts of hurricanes in New England. *Ecol. Monogr.* 71 (1), 27–48.
- Boyd, I.L., Freer-Smith, P.H., Gilligan, C.A., Godfray, H.C.J., 2013. The consequence of tree pests and diseases for ecosystem services. *Science* 342 (6160), 1235773.
- Campbell, J.L., Harmon, M.E., Mitchell, S.R., 2011. Can fuel-reduction treatments really increase forest carbon storage in the western US by reducing future fire emissions? *Front. Ecol. Environ.* 10 (2), 83–90.
- Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. *Science* 320, 1456–1457.
- Carswell, C., 2014. Don't blame the beetles. *Science* 346 (6206), 154–156.
- Caspersen, J.P., et al., 2000. Contributions of land-use history to carbon accumulation in US forests. *Science* 290 (5494), 1148–1151.
- Chambers, J.Q., et al., 2007. Hurricane Katrina's carbon footprint on U.S. Gulf Coast forests. *Science* 318, 1107.
- Chapin III, F.S., Matson, P.A., Vitousek, P., 2012. *Principles of Terrestrial Ecosystem Ecology*. New York.
- Choat, B., et al., 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491 (7426), 752–755.
- Ciais, P., et al., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437 (7058), 529–533.
- Clark, K.L., Skowronski, N., Hom, J., 2010. Invasive insects impact forest carbon dynamics. *Glob. Chang. Biol.* 16 (1), 88–101.
- Dale, V.H., et al., 2001. Climate change and forest disturbances. *Bioscience* 51 (9), 723–734.
- Dillon, G.K., et al., 2011. Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. *Ecosphere* 2 (12, art), 130.
- Donato, D.C., Harvey, B.J., Romme, W.H., Simard, M., Turner, M.G., 2013. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. *Ecol. Appl.* 23 (1), 3–20.
- Doughty, C.E., et al., 2015. Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature* 519, 78–82.
- Dymond, C.C., et al., 2010. Future spruce budworm outbreak may create a carbon source in eastern Canadian forests. *Ecosystems* 13 (6), 917–931.
- Eidenshink, J., et al., 2007. A project for monitoring trends in burn severity. *Fire Ecol.* 3, 3–21.
- EPA, 2008. Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990–2006. United States Environmental Protection Agency, Washington, DC.
- EPA, 2011. Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990–2009. United States Environmental Protection Agency, Washington, DC.
- EPA, 2012. Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990–2010. United States Environmental Protection Agency, Washington, DC.
- EPA, 2015. Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990–2013. United States Environmental Protection Agency, Washington, DC.
- Erb, K.-H., et al., 2013. Bias in the attribution of forest carbon sinks. *Nat. Clim. Chang.* 3, 854–856.
- Fisk, J.P., et al., 2013. The impacts of tropical cyclones on the net carbon balance of eastern US forests (1851–2000). *Environ. Res. Lett.* 8 (4), 045017.
- Flowers, C.E., Knight, K.S., Gonzalez-Meier, M.A., 2013. Impacts of the emerald ash borer (*Agilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. *Biol. Invasions* 15, 931–944.
- Foster, D.R., Orwig, D.A., 2006. Preemptive and salvage harvesting of New England forests: when doing nothing is a viable alternative. *Conserv. Biol.* 20 (4), 959–970.
- French, N.H.F., et al., 2011. Model comparisons for estimating carbon emissions from North American wildland fire. *J. Geophys. Res. Biogeosci.* 116 G00K05.
- Ghimire, B., Williams, C.A., Collatz, G.J., Vanderhoof, M.E., 2012. Fire-induced carbon emissions and regrowth uptake in western U.S. forests: documenting variation across forest types, fire severity, and climate regions. *J. Geophys. Res.* 117, G03036.
- Ghimire, B., et al., 2015. Large carbon release legacy from bark beetle outbreaks across western United States. *Glob. Chang. Biol.* 21 (8), 3087–3101.
- Giglio, L., van der Werf, G.R., Randerson, J.T., Collatz, G.J., Kasibhatla, P., 2006. Global emissions of burned area using MODIS active fire observations. *Atmos. Chem. Phys.* 6, 957–974.
- Goetz, S.J., et al., 2012. Observations and assessment of forest carbon dynamics following disturbance in North America. *J. Geophys. Res.* 117, G02022.
- Goward, S.N., et al., 2012. NACP North American Forest Dynamics Project: Forest Disturbance and Regrowth Data Available on-line from [http://daac.ornl.gov] ORNL DAAC, Oak Ridge, Tennessee, U.S.A. <http://dx.doi.org/10.3334/ORNLDAAC/1077>.
- Goward, S.N., et al., 2015. NACP NAFD Project: Forest Disturbance History from Landsat, 1986–2010. ORNL DAAC, Oak Ridge, Tennessee, USA <http://dx.doi.org/10.3334/ORNLDAAC/1290>.
- Gruber, N., Galloway, J.N., 2008. An earth-system perspective of the global nitrogen cycle. *Nature* 451, 293–296.
- Hanna, P., Kulakowski, D., 2012. The influences of climate on aspen dieback. *For. Ecol. Manag.* 274, 91–98.
- Hansen, M.C., et al., 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342, 850–853.
- Harmon, M.E., Marks, B., 2002. Effects of silvicultural practices on carbon stores in Douglas-fir–western hemlock forests in the Pacific Northwest, USA: results from a simulation model. *Can. J. For. Res.* 32, 863–877.
- Harmon, M.E., et al., 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15, 133–288.
- Harmon, M.E., Ferrell, W.K., Franklin, J.F., 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247, 699–702.
- Hart, S.J., Schoennagel, T., Veblen, T.T., Chapman, T.B., 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proc. Natl. Acad. Sci.* 112 (14), 4375–4380.
- Heath, L.S., Smith, J.E., Skog, K.E., Nowak, D.J., Woodall, C.W., 2011. Managed forest carbon estimates for the US greenhouse gas inventory, 1990–2008. *J. For.* 109 (3), 167–173.
- Hermes, D.A., McCullough, D.G., 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annu. Rev. Entomol.* 59, 13–30.
- Hicke, J.A., et al., 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Glob. Chang. Biol.* 18 (1), 7–34.
- Hicke, J.A., Meddens, A.J.H., Allen, C.D., Kolden, C.A., 2013. Carbon stocks of trees killed by bark beetles and wildfire in the western United States. *Environ. Res. Lett.* 8, 035032.
- Hogg, E.H., Brandt, J.P., Michaelian, M., 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Can. J. For. Res. Rev. (Canadienne De Recherche Forestiere)* 38 (6), 1373–1384.
- Houghton, R.A., 1999. The annual net flux of carbon to the atmosphere from changes in land use 1850–1990. *Tellus Ser. B Chem. Phys. Meteorol.* 51 (2), 298–313.
- Houghton, R.A., 2003. Why are estimates of the terrestrial carbon balance so different? *Glob. Chang. Biol.* 9 (4), 500–509.
- Huang, C.-Y., Anderegg, W.R.L., 2012. Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. *Glob. Chang. Biol.* 18, 1016–1027.
- Huang, C.-Y., Asner, G.P., Barger, N.N., Neff, J.C., Floyd, M.L., 2010a. Regional aboveground live carbon losses due to drought-induced tree dieback in pinon–juniper ecosystems. *Remote Sens. Environ.* 114, 1471–1479.
- Huang, C., et al., 2010b. An automated approach for reconstructing recent forest disturbance history using dense Landsat time series stacks. *Remote Sens. Environ.* 114, 183–198.
- Hungate, B.A., Hampton, H.M., 2012. Valuing ecosystems for climate. *Nat. Clim. Chang.* 2, 151–152.
- Hurteau, M.D., North, M., 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. *Front. Ecol. Environ.* 7, 409–414.
- Hurteau, M.D., Koch, G.W., Hungate, B.A., 2008. Carbon protection and fire risk reduction: toward a full accounting of forest carbon offsets. *Front. Ecol. Environ.* 6, 493–498.
- Hurt, G.C., et al., 2002. Projecting the future of the US carbon sink. *Proc. Natl. Acad. Sci. U. S. A.* 99 (3), 1389–1394.
- Hurt, G.C., et al., 2011. Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Clim. Chang.* 109 (1–2), 117–161.
- Jackson, R.B., et al., 2008. Protecting climate with forests. *Environ. Res. Lett.* 3 (4), 044006.
- Jenkins, M.J., Hebertson, E., Page, W., Jorgensen, C.A., 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *For. Ecol. Manag.* 254, 16–34.
- Johnstone, J.F., Hollingsworth, T.N., Chapin III, F.S., Mack, M.C., 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Glob. Biogeochem. Cycles* 16, 1281–1295.
- Joos, F., Prentice, I.C., House, J.I., 2002. Growth enhancement due to global atmospheric change as predicted by terrestrial ecosystem models: consistent with US forest inventory data. *Glob. Chang. Biol.* 8, 299–303.
- Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., Ryan, M.G., 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of *Pinus contorta*-dominated forests. *Ecol. Monogr.* 83 (1), 49–66.
- Kasischke, E.S., et al., 2011. Quantifying burned area for North American forests: implications for direct reduction of carbon stocks. *J. Geophys. Res. Biogeosci.* 116 (G4).
- Kasischke, E.S., et al., 2013. Impacts of disturbance on the terrestrial carbon budget of North America. *J. Geophys. Res. Biogeosci.* 118, 303–316.
- King, A.W., et al., 2007. The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle. NOAA, National Climatic Data Center, Asheville, NC.
- Knicker, H., 2007. How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. *Biogeochemistry* 85 (1), 91–118.
- Krist Jr., F.J., Sapio, F.J., Tkacz, B.M., 2007. Mapping Risk from Forest Insects and Diseases. USDA, Washington, DC.
- Kulakowski, D., Jarvis, D., 2013. Low-severity fires increase susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado. *For. Ecol. Manag.* 289, 544–550.
- Kulakowski, D., Jarvis, D., Veblen, T.T., Smith, J., 2012. Stand-replacing fires reduce susceptibility to mountain pine beetle outbreaks in Colorado. *J. Biogeogr.* 39, 2052–2060.
- Kurz, W.A., et al., 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452 (7190), 987–990.
- LANDFIRE, 2008. Vegetation Disturbance, LANDFIRE 1.1.0, U.S. Department of the Interior, Geological Survey (Accessed June 2015 at <http://www.landfire.gov/disturbance.php>).
- Larkin, N.K., Raffuse, S.M., Strand, T.M., 2014. Wildland fire emissions, carbon, and climate: US emissions inventories. *For. Ecol. Manag.* 317, 61–69.
- Law, B.E., Harmon, M.E., 2011. Forest sector carbon management, measurement and verification, and discussion of policy related to climate change. *Carbon Manag.* 2 (1), 73–84.
- Lawrence, P.J., et al., 2012. Simulating the biogeochemical and biogeophysical impacts of transient land cover change and wood harvest in the Community Climate System Model (CCSM4) from 1850 to 2100. *J. Clim.* 25 (9), 3071–3095.



- Le Page, Y., et al., 2013. Sensitivity of climate mitigation strategies to natural disturbances. *Environ. Res. Lett.* 8 (015018), 6.
- Le Quéré, C., Raupach, M.R., Canadell, J.G., Marland, G., et al., 2009. Trends in the sources and sinks of carbon dioxide. *Nat. Geosci.* 2, 831–836.
- Lenton, T.M., et al., 2008. Tipping elements in the Earth's climate system. *Proc. Natl. Acad. Sci.* 105 (6), 1786–1793.
- Liu, Y., Stanturf, J., Goodrick, S., 2010. Trends in global wildfire potential in a changing climate. *For. Ecol. Manag.* 259, 685–697.
- Luyssaert, S., et al., 2008. Old-growth forests as global carbon sinks. *Nature* 455 (213–215).
- Ma, Z., et al., 2012. Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proc. Natl. Acad. Sci.* 109 (7), 2423–2427.
- Marlon, J.R., et al., 2012. Long-term perspective on wildfires in the western USA. *Proc. Natl. Acad. Sci.* 109 (9), E535–E543.
- Mascaro, J., Asner, G.P., Davies, S., Dehgan, A., Saatchi, S., 2014. These are the days of lasers in the jungle. *Carbon Bal. Manag.* 9, 7.
- Masek, J.G., et al., 2011. Recent rates of forest harvest and conversion in North America. *J. Geophys. Res.* 116 G00K03.
- Masek, J.G., et al., 2013. U.S. forest disturbance trends observed with Landsat time series. *Ecosystems* 1–18.
- McDowell, N., 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiol.* 155, 1051–1059.
- McDowell, N.G., et al., 2016. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nat. Clim. Chang.* (advance online publication).
- McKinley, D.C., et al., 2011. A synthesis of current knowledge on forests and carbon storage in the United States. *Ecol. Appl.* 21 (6), 1902–1924.
- McNulty, S.G., 2002. Hurricane impacts on US forest carbon sequestration. *Environ. Pollut.* 116, S17–S24.
- Medvigy, D., Clark, K.L., Skowronski, N.S., Schäfer, K.V.R., 2012. Simulated impacts of insect defoliation on forest carbon dynamics. *Environ. Res. Lett.* 7 (4), 045703.
- Mercado, L.M., et al., 2009. Impact of changes in diffuse radiation on the global land carbon sink. *Nature* 458.
- Michaelian, M., Hogg, E.H., Hall, R.J., Arseneault, E., 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Glob. Chang. Biol.* 17 (6), 2084–2094.
- Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P., Cardinot, G., 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* 88 (9), 2259–2269.
- North, M.P., Hurteau, M.D., 2011. High-severity wildfire effects on carbon stocks and emissions in fuels treated and untreated forest. *For. Ecol. Manag.* 261 (6), 1115–1120.
- North, M.P., et al., 2015. Reform forest fire management. *Science* 349 (6254), 1280–1281.
- Nunery, J.S., Keeton, W.S., 2010. Forest carbon storage in the northeastern United States: net effects of harvesting frequency, post-harvest retention, and wood products. *For. Ecol. Manag.* 259 (8), 1363–1375.
- Oliver, C.D., Nassar, N.T., Lippke, B.R., McCarter, J.B., 2014. Carbon, fossil fuel, and biodiversity mitigation with wood and forests. *J. Sustain. For.* 33 (3), 248–275.
- Orwig, D.A., et al., 2013. Foundation species loss affects vegetation structure more than ecosystem function in a northeastern USA forest. *PeerJ* 1 (e41).
- Pacala, S.W., et al., 2001. Consistent land- and atmosphere-based US carbon sink estimates. *Science* 292 (5525), 2316–2320.
- Pan, Y., et al., 2011. A large and persistent carbon sink in the world's forests. *Science* 333 (6045), 988–993.
- Peng, C., et al., 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nat. Clim. Chang.* 1 (9), 467–471.
- Peterson, D.L., Vose, J.M., Patel-Weyand, T., 2014. Climate change and United States forests. *Advances in Global Change Research* 57. Springer, Dordrecht.
- Post, W.M., Izaurralde, R.C., West, T.O., Liebig, M.A., King, A.W., 2012. Management opportunities for enhancing terrestrial carbon dioxide sinks. *Front. Ecol. Environ.* 10 (10), 554–561.
- Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Glob. Chang. Biol.* 10, 2052–2077.
- Pugh, S.A., Liebhold, A.M., Morin, R.S., 2011. Changes in ash tree demography associated with emerald ash borer invasion, indicated by regional forest inventory data from the Great Lakes States. *Can. J. For. Res. Rev. (Canadienne De Recherche Forestiere)* 41 (11), 2165–2175.
- Raffa, K.F., et al., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58, 501–517.
- Ray, D.G., Seymour, R.S., Scott, N.A., Keeton, W.S., 2009. Mitigating climate change with managed forests: balancing expectations, opportunity, and risk. *J. For.* 107 (1), 50–51.
- Raymer, P.C., Orwig, D.A., Finzi, A.C., 2013. Hemlock loss due to the hemlock woolly adelgid does not affect ecosystem C storage but alters its distribution. *Ecosphere* 4 (5, art), 63.
- Reichstein, M., et al., 2013. Climate extremes and the carbon cycle. *Nature* 500, 287–295.
- Schimel, D., et al., 2000. Contribution of increasing CO<sub>2</sub> and climate to carbon storage by ecosystems in the United States. *Science* 287 (5460), 2004–2006.
- Schleeweis, K., et al., 2013. Regional dynamics of forest canopy change and underlying causal processes in the contiguous U.S. *J. Geophys. Res. Biogeosci.* 118, 1035–1053.
- Schulze, E.D., Wirth, C., Heimann, M., 2000. Climate change: managing forests after Kyoto. *Science* 289 (5487), 2058–2059.
- Schulze, E.D., Koerner, C., Law, B.E., Haberl, H., Luyssaert, S., 2012. Large-scale bioenergy from additional harvest of forest biomass is neither sustainable nor greenhouse gas neutral. *Global Change Biol. Bioenergy* 4, 611–616.
- Schwalm, C.R., et al., 2010. Assimilation exceeds respiration sensitivity to drought: a FLUXNET synthesis. *Glob. Chang. Biol.* 16 (2), 657–670.
- Schwalm, C.R., Williams, C.A., Schaefer, K., 2011. Carbon consequences of global hydrologic change, 1948–2009. *J. Geophys. Res.* 116, G03042.
- Schwalm, C.R., et al., 2012. Reduction in carbon uptake during turn of the century drought in western North America. *Nat. Geosci.* 5, 551–556.
- Silva, L.C., Anand, M., Leithead, M.D., 2010. Recent widespread tree growth decline despite increasing atmospheric CO<sub>2</sub>. *PLoS One* 5 (7), e11543.
- Simard, M., Romme, W.H., Griffin, J.M., Turner, M.G., 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecol. Monogr.* 81 (1), 3–24.
- Smith, J.E., Heath, L.S., Skog, K.E., Birdsey, R.A., 2006. Methods for Calculating Forest Ecosystem and Harvested Carbon with Standard Estimates for Forest Types of the United States, Philadelphia, USA.
- Smith, W.B., Miles, P.D., Perry, C.H., Pugh, S.A., 2009. Forest Resources of the United States, 2007. Gen. Tech. Rep. WO-78. USDA, Forest Service, Washington Office, Washington, DC, p. 336.
- Stinson, G., et al., 2011. An inventory-based analysis of Canada's managed forest carbon dynamics, 1990 to 2008. *Glob. Chang. Biol.* 17 (6), 2227–2244.
- Thomas, R.Q., Canham, C.D., Weathers, K.C., Goodale, C.L., 2009. Increased tree carbon storage in response to nitrogen deposition in the US. *Nat. Geosci.* 3, 13–17.
- Thomas, N.E., et al., 2011. Validation of North American forest disturbance dynamics derived from Landsat time series stacks. *Remote Sens. Environ.* 115, 119–132.
- Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91 (10), 2833–2849.
- Turner, D.P., Koerper, G.J., Harmon, M.E., Lee, J.J., 1995. A carbon budget for forests of the conterminous United States. *Ecol. Appl.* 5 (2), 421–436.
- U.S. Department of Agriculture, F.S., 2012. Forest Service, Future of America's Forest and Rangelands: Forest Service 2010 Resources Planning Act Assessment. Gen. Tech. Rep. WO-87, Washington, D.C.
- van der Werf, G.R., et al., 2010. Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009). *Atmos. Chem. Phys.* 10, 11707–11735.
- van Mantgem, P.J., et al., 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323 (5913), 521–524.
- Vicente, F.B., Carbajal, N., Pineda Martínez, L.F., 2014. Estimation of total yearly CO<sub>2</sub> emissions by wildfires in Mexico during the period 1999–2010. *Adv. Meteorol.*
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313, 940–943.
- White, P.S., Pickett, S.T.A., 1985. Ch 1 – Natural disturbance and patch dynamics: an introduction. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Inc., pp. 3–13.
- Wiedinmyer, C., Neff, J.C., 2007. Estimates of CO<sub>2</sub> from fires in the United States: implications for carbon management. *Carbon Bal. Manag.* 2 (10), 1–12.
- Williams, C.A., Collatz, G.J., Masek, J.G., Goward, S., 2012a. Carbon consequences of forest disturbance and recovery across the conterminous United States. *Glob. Biogeochem. Cycles* 26, GB1005.
- Williams, A.P., et al., 2012b. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Chang.* 3, 292–297.
- Williams, C.A., Collatz, G.J., Masek, J.G., Huang, C., Goward, S., 2014a. Impacts of disturbance history on forest carbon stocks and fluxes: merging satellite disturbance mapping with forest inventory data in a carbon cycle model framework. *Remote Sens. Environ.* 151, 57–71.
- Williams, C.A., Vanderhoof, M.E., Khomik, M., Ghimire, B., 2014b. Post-clearcut dynamics of carbon, water and energy exchanges in a midlatitude temperate, deciduous broad-leaf forest environment. *Glob. Chang. Biol.* 20, 992–1007.
- Woodbury, P.B., Smith, J.E., Heath, L.S., 2007. Carbon sequestration in the U.S. forest sector from 1990 to 2010. *For. Ecol. Manag.* 241, 14–27.
- Zeng, H., et al., 2009. Impacts of tropical cyclones on US forest tree mortality and carbon flux from 1851 to 2000. *Proc. Natl. Acad. Sci.* 106 (19), 7888–7892.
- Zhang, F., et al., 2012. Attributing carbon changes in conterminous U.S. forests to disturbance and non-disturbance factors from 1901 to 2010. *J. Geophys. Res.* 117, G02021.
- Zheng, D., Heath, L.S., Ducey, M.J., Smith, J.E., 2011. Carbon changes in conterminous US forests associated with growth and major disturbances: 1992–2001. *Environ. Res. Lett.* 6, 014012.