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Observations and assessment of forest carbon dynamics following disturbance in North America

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[1] Disturbance processes of various types substantially modify ecosystem carbon dynamics both temporally and spatially, and constitute a fundamental part of larger landscape-level dynamics. Forests typically lose carbon for several years to several decades following severe disturbance, but our understanding of the duration and dynamics of post-disturbance forest carbon fluxes remains limited. Here we capitalize on a recent North American Carbon Program disturbance synthesis to discuss techniques and future work needed to better understand carbon dynamics after forest disturbance. Specifically, this paper addresses three topics: (1) the history, spatial distribution, and characteristics of different types of disturbance (in particular fire, insects, and harvest) in North America; (2) the integrated measurements and experimental designs required to quantify forest carbon dynamics in the years and decades after disturbance, as presented in a series of case studies; and (3) a synthesis of the greatest uncertainties spanning these studies, as well as the utility of multiple types of observations (independent but mutually constraining data) in understanding their dynamics. The case studies—in the southeast U.S., central boreal Canada, U.S. Rocky Mountains, and Pacific Northwest—explore how different measurements can be used to constrain and understand carbon dynamics in regrowing forests, with the most important measurements summarized for each disturbance type. We identify disturbance severity and history as key but highly uncertain factors driving post-disturbance carbon source-sink dynamics across all disturbance types. We suggest that imaginative, integrative analyses using multiple lines of evidence, increased measurement capabilities, shared models and online data sets, and innovative numerical algorithms hold promise for improved understanding and prediction of carbon dynamics in disturbance-prone forests.

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1. Introduction

[2] Forest disturbances modify ecosystem properties and processes, and in some cases initiate a range of feedbacks between terrestrial ecosystems and climate, while constituting a fundamental part of landscape-level carbon dynamics. The *type* of disturbance (whether caused by fire, insects, storms, harvest, or some other agent) influences the magnitude of change as well as the timeframe over which the impacts of the change are expressed [*Amiro et al.*, 2010]. The *severity* of disturbance [*Turner*, 2010], determined by climate, management, stand structure and biomass and other factors, also determines the magnitude, and in some cases even the direction, of subsequent carbon cycle changes. We refer generally to disturbance severity as the product of intensity (e.g., energy of a fire, extent of defoliation, number

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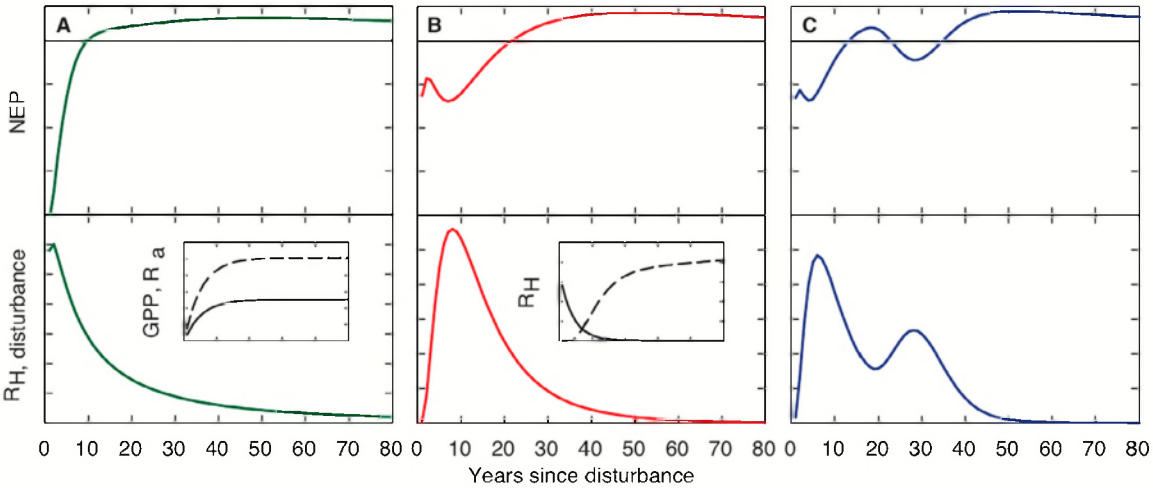

Figure 1. Conceptual model of the impact of climate and disturbance type on net ecosystem productivity (NEP, upper panels) and the timing of peak heterotrophic respiration associated with disturbance ($R_{H,disturbance}$; lower panels). Cases include (a) whole-stand harvest in a warm climate, (b), whole-stand harvest in a cool climate, and (c) stand-killing fire (leaving many standing dead trees). Integrated R_H, GPP and R_a (inset) are assumed equal in all cases. R_H associated with the legacy pool (inset, solid line) and the regrowing forest (inset, dashed line) are also included, and assumed equivalent across the three cases. See *Harmon et al.* [2011] for a related discussion.

of trees infected) and duration (e.g., the period over which insect infestation or wind disturbance occurs; at the same intensity level, longer-duration disturbances consume more organic matter than do shorter ones). As part of the North American Carbon Program (NACP) disturbance synthesis, we address some of these processes in the context of observations that have been used to quantify types of disturbance and the various factors affecting post-disturbance C dynamics.

[3] The dynamics of carbon and disturbance—a temporary change in environmental conditions that produces long-lived changes in ecosystem structure and function—are tightly linked in many ecosystems. These links, and our understanding of them, have significant consequences: forestry and land-use emissions of greenhouse gases constitute one of the most important components of national inventories of carbon emissions, but have high uncertainties primarily associated with disturbance [*McKinley et al.*, 2011]. More broadly, *Pan et al.* [2011a] estimates that global established forests outside the areas of tropical land-use changes currently account for the entire terrestrial C sink (~2.4 Pg C yr^{-1}), with young to middle-aged forests typically strong sinks. This sequestration constitutes and offsets a substantial fraction of anthropogenic fossil fuel emissions [*Le Quéré et al.*, 2009]. However, the benefit of the large amount of atmospheric CO_2 sequestered by natural forest ecosystems (~4.0 Pg C yr^{-1}) is substantially offset by the C losses from tropical deforestation (~2.9 Pg C yr^{-1}) [*Pan et al.*, 2011a]. This illustrates the tightly linked dynamics between vegetation succession and C uptake, and vegetation disturbance and C release.

[4] Forests follow many possible trajectories depending on the severity and frequency of disturbance, the dynamics of legacy carbon pools, variations in climate and local environmental conditions, differences in vegetation characteristics, and other factors [*Kira and Shidei*, 1967]. Classical theory, however, generally suggests post-disturbance forests spend a short period as net carbon sources to the atmosphere, several years to decades of increasing net ecosystem production (NEP), and then a slow NEP decline to near carbon-neutral in old forests [*Odum*, 1969]. Such behavior is frequently assumed and hard-wired into some models [*Turner*, 2007]. A recent synthesis of temperate and boreal forests between 15 and 800 years of age showed that NEP (computed from eddy covariance, biometry, and chamber methods) is usually positive, however, and that old forests continue to sequester carbon [*Luyssaert et al.*, 2007], in contrast to the view that they are carbon neutral [*Keeton et al.*, 2011].

[5] There are a number of additional uncertainties. The time at which young forests become net carbon sinks again after stand-replacing disturbance remains poorly constrained. The average time was 15 years in *Luyssaert et al.* [2007], and 5–20 years in *Amiro et al.* [2010], although the data sets used by these studies overlap somewhat. The sequestration rates of intermediate-age and mature forests also vary substantially [*Gower et al.*, 1996; *Hudiburg et al.*, 2009; *Mack et al.*, 2008; *Ryan et al.*, 2004]. Finally, the resiliency of forests to subtle (non-stand-replacing) disturbances is only beginning to be explored, e.g., in experiments aiming to accelerate succession [*Nave et al.*, 2011] and studies exploring links between post-disturbance stocks and subsequent carbon trajectories [*Pfeifer et al.*, 2011].

[6] Figure 1 illustrates conceptual responses in net ecosystem productivity associated with a range of scenarios following disturbance. These conceptual models are based on increasing evidence that no single model applies universally, but rather models must account for disturbance type, severity, frequency, and climate [*Johnstone et al.*, 2010; *Law et al.*, 2004]. The cases in Figure 1, each of which is discussed in greater depth below, illustrate how the timing and magnitude of the period of net carbon release can vary

Table 1. Abbreviations Used in the Text

Abbreviation	Explanation
NEP	Net Ecosystem Production
NECB	Net Ecosystem Carbon Balance
NPP	Net Primary Production
GPP	Gross Primary Production
LAI	Leaf Area Index
ORCA	Oregon and Northern California
MODIS	Moderate-Resolution Imaging Spectroradiometer
R_H	Heterotrophic respiration
R_S	Soil respiration

across disturbance types and biomes. Generally, rapid, immediate decay leads to a short period where the ecosystem is a carbon source, followed by a long period of uptake. A delayed peak in microbial respiration (R_H), typically due to snag fall dynamics [*Angers et al.*, 2011; *Harmon et al.*, 2011], may delay the onset of sustained carbon uptake. To capture the major features of these processes, measurement systems and sampling protocol must be designed to operate at a relatively fine temporal scale, especially in the early years following disturbance. We revisit these conceptual models later, in evaluating evidence for their behavior across different systems and disturbance types.

[7] A series of questions about the carbon dynamics of forest disturbance and regrowth inspired this paper and are of great interest for contemporary carbon cycle scientists. The questions listed below define the types of measurements used, and thus relate to a range of research on the carbon implications of disturbance across North America: (1) What is the post-disturbance magnitude of the carbon source versus the sink, at both local and large (all of North America) scales? (2) How do changes in the rates (frequency, intensity) of disturbance interact with forest age structure to affect successional pathways and carbon flows? (3) What drives different trajectories of post-disturbance carbon uptake? (4) How do the spatial extent and severity of disturbance events interact, and how do surviving trees affect subsequent successional trajectories? (5) What are the roles of management and/or climate in modulating forest response to disturbance?

[8] Here we explore these questions by examining the distribution of disturbances across North America, presenting a series of case studies focusing on ecosystem dynamics and the integrated measurements used to understand them (following the structure of Figure 1), and synthesizing crosscutting themes related to the carbon implications of post-disturbance forest recovery. We conclude with a discussion of the largest gaps in our understanding of post-disturbance carbon dynamics, tying these gaps back to the questions above, and recommendations for future work. We focus primarily on carbon cycling, particularly NEP and its main determinants, net primary production (NPP) and R_H. Abbreviations used in the text are listed in Table 1.

2. History and Distribution of Disturbance Types Across North America

[9] Disturbances have had significant impacts on the historical carbon cycle. Millennial (paleo) data document recurring North American fires and storms throughout the Holocene [*Camill et al.*, 2009; *Payette et al.*, 2008]. Large areas were regularly burned by humans [*Pyne*, 1984; *Whitney*, 1994], but North American forests were probably in rough equilibrium with the atmosphere by 1770–1800 [*Birdsey et al.*, 2006; *Houghton et al.*, 2000]. After this date, emissions from harvest and forest conversion to agriculture climbed rapidly, peaking in the U.S. at 350–800 Tg yr^{-1} around the turn of the 20th century [*Hurtt et al.*, 2002; *Birdsey et al.*, 2006; *Houghton*, 1999]. In the past hundred years land conversion has slowed but fires remain significant [*Houghton et al.*, 2000]. Most recently, between 2000 and 2005, some 18.7 Tg yr^{-1} of forest carbon were lost to forest fires in the lower 48 U.S. states, and 14.5–27.8 Tg C yr^{-1} in Alaska (Table 2). Such disturbance records and estimates are valuable, but have significant uncertainty: historically, wildfires often occurred in remote areas, limiting the ability of assessment teams to quantify their area and impact [*Kasischke et al.*, 2011; *Stocks et al.*, 2002]. Stand-level estimates of tree loss were typically recorded as a loss in volume of the commercially important tree components, ignoring leaves and belowground components, and the USDA ceased recording wildfire-caused volume loss in 1990. Most recently, *Turetsky et al.* [2011] and *Kasischke and Hoy* [2012] showed substantial additional losses of carbon in Alaskan boreal forests from burning of organic soils in boreal forests, representing 54–70% of carbon lost during fires (Table 2). For these reasons historical reconstructions often supplement older data with modern-day measurements and remote sensing data.

[10] The distribution of the dominant types of disturbance in North America vary as a result of the interacting influences of topography, vegetation, weather patterns, climate gradients, proximity to human settlement and other factors. New satellite-based disturbance detection methodologies [see *Frolking et al.*, 2009a] have significantly improved our ability to observe the location, extent, and severity of large-scale ecosystem disturbances across continental scales (Figure 2). These observations show how fire dominates much of the western boreal ecosystems of Canada, storms impact the Gulf Coast of the United States, insect damage is widespread but currently concentrated in western regions, and harvest prevails in the southeastern U.S. Similar results have been noted using samples of higher resolution but less

Table 2. Estimates of Historic Gross Carbon (C) Loss From Wildfire Disturbance[a]

Year	Lower 48	Alaska	Alaska (2)	Canada
1920–29	128.5	3.2	-	-
1930–39	132.5	2.7	-	-
1940–49	79.8	2.5	-	-
1950–59	29.4	6.0	11.2	6.7
1960–69	17.2	1.8	7.7	13.6
1970–79	17.4	4.0	5.9	21.0
1980–89	25.6	2.6	3.4	37.0
1990–99	13.4	5.8	9.4	42.2
2000–05	18.7	14.5	27.8	-

[a]Values in Tg C yr^{-1}. Emission values for Canada are from *Amiro* [2001] and were not estimated in the same manner as the USDA Forest Service values for the U.S. [*Kasischke et al.*, 2011], which depend on converting commercial volume loss to carbon fluxes. The second "Alaska" column gives new estimates based on new estimates based on improved understanding of forest floor losses [*Turetsky et al.*, 2011] and a new approach for estimating fuel consumption from all vegetation classes [*Kasischke and Hoy*, 2012].

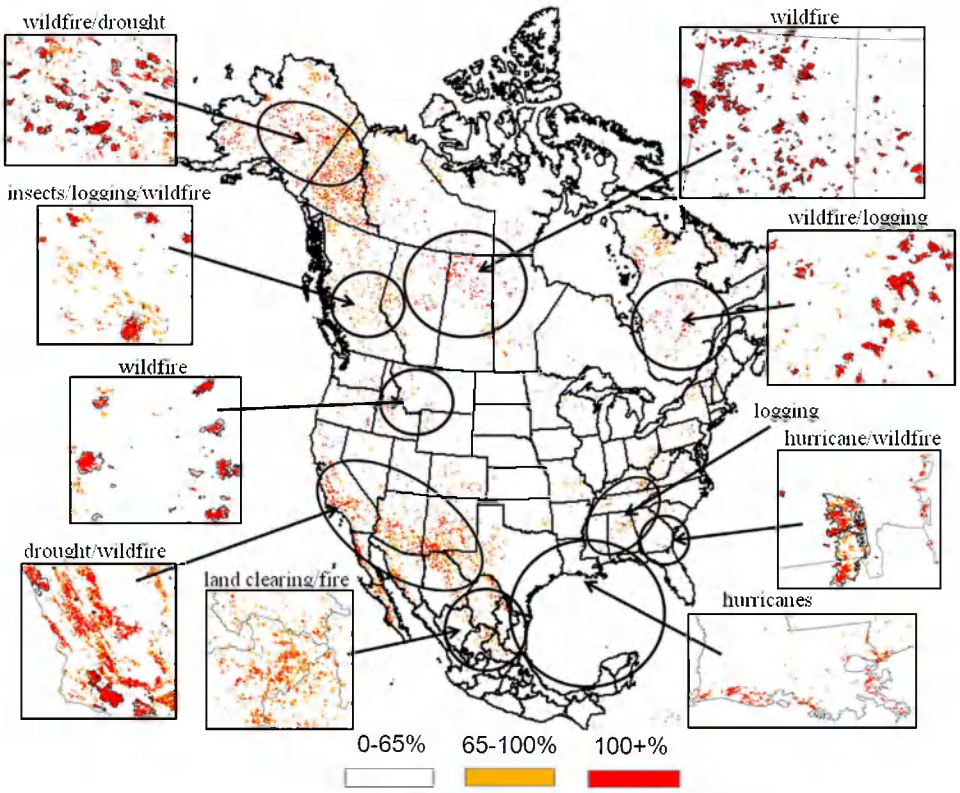

Figure 2. MODIS Global Disturbance Index (MGDI) results from 2005 to 2009 illustrate the geographic distribution of major ecosystem disturbance types across North America (based on *Mildrexler et al.* [2007]). Moderate severity disturbance is mapped in orange and represents a 65–100% divergence of the current year MGDI [*Mildrexler et al.*, 2009] value from the range of natural variability, defined as the mean of all MGDI values prior to the current year. High severity disturbance (in red) signals a divergence of over 100%.

temporally frequent satellite imagery [*Huang et al.*, 2010; *Masek et al.*, 2008].

[11] These natural and anthropogenic disturbances interact across the landscape, but natural disturbances dominate at high latitudes (Figure 2). An important characteristic of natural disturbances is that they may occur as a temporal cluster of different individual events, such as prolonged drought followed by insect attack and then fire [*Fleming et al.*, 2002; *Kulakowski and Veblen*, 2006], lasting for multiple years or even decades. As a result, they can affect a significant portion (2–20%) of the entire landscape in a very short time period, driving forest carbon budgets at decadal and longer time scales [*Bond-Lamberty et al.*, 2007; *Kurz et al.*, 2008a].

3. Disturbance Case Studies

[12] The case studies and synthesis that follow draw upon a range of analyses of post-disturbance carbon dynamics. We use them to present the integrated measurements and experimental designs required to quantify forest carbon dynamics in the years and decades after disturbance in different geographic regions of North America, and illustrate how investigators have used such multiple lines of evidence to address the questions listed in section 1 above.

3.1. Whole-Stand Harvest in a Warm Climate: The Southeast U.S.

[13] The southeastern region of the United States has a vast forestland base, with over 50% of the land area allocated for forestry use [*Wear and Greis*, 2002b], and is thought to be the largest carbon sink across the conterminous United States [*Pacala et al.*, 2001]. It is also a region that has been, and continues to be, subject to intensive human management and land-use change—e.g., cropland establishment and cultivation, cropland abandonment, and subsequent forest regrowth—with significant effects on landscape carbon storage and fluxes [*Chen et al.*, 2006]. These characteristics have specific implications for the measurement and modeling of the structure and function of Southeastern forests.

3.1.1. Southeast U.S. Forests, Land Use, and Disturbance

[14] Southeast U.S. forests are typically highly disturbed. While total forest area has remained relatively stable over the last few decades, gross forest cover losses due to harvest and other disturbance events rival those in the Amazon and other tropical regions [*Hansen et al.*, 2010]. Annual forest disturbance rate was estimated at 2.6% for the southeastern U.S. [*Masek et al.*, 2008], and in Mississippi and Alabama about 40% of the forests were disturbed at least once

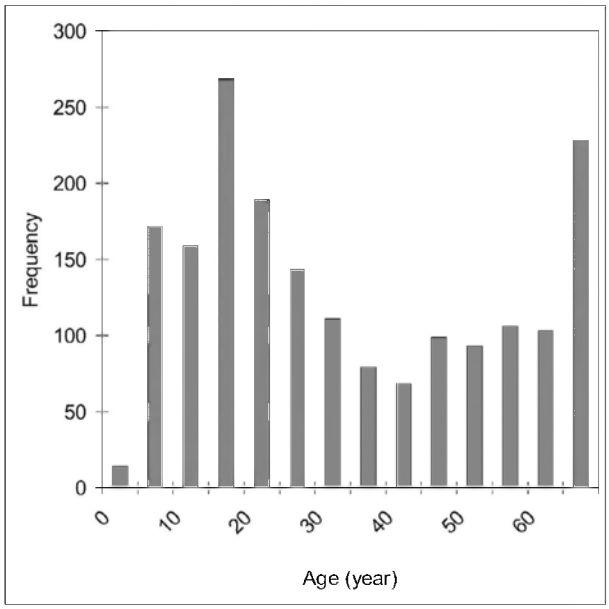

Figure 3. Frequency of different stand ages for Mississippi forests (C. Huang, unpublished data, 2012). Frequent disturbance results in an age structure dominated by young forests (30 years or younger).

between 1985 and 2005 [*Li et al.*, 2009a; 2009b]. The majority of forest disturbances in this region are human-managed events, including harvest and selective logging [*Masek et al.*, 2011]. However, significant portions of the forests are also affected by natural disturbances, including hurricanes [*Chambers et al.*, 2007; *Dolan et al.*, 2011; *Zeng et al.*, 2009], disease and insect outbreaks, and prescribed and natural fire [*Kasischke et al.*, 2011]. The disturbance from hurricanes alone resulted in 1825–2000 losses of 25 Tg C yr^{-1} losses from regional forests [*Zeng et al.*, 2009].

[15] Some forest disturbances convert land to other uses—for example, 0.37% of the forestland in the Southeast U.S. is converted to urban uses on an annual basis [*Birdsey and Lewis*, 2003; *Loveland et al.*, 2002]. Most, however, are harvests followed by forest regeneration. Owing to favorable temperature and moisture conditions, the Southeast U.S. has some of the fastest-growing forests in North America; trees can grow ~1 m yr^{-1} during their first 20 years, although such high rates often depend on significant fertilizer applications to counteract the effect of nutrient-poor soils and debris burning [*Thornton et al.*, 2002]. Significant improvements in growth and yield can be achieved through use of intensive management practices, and the region has seen significant increases in the use of intensive management practices over the last few decades [*Siry*, 2002]. By 1997, its share of timber production reached 58% in the U.S. and 16% globally [*Wear and Greis*, 2002a].

[16] High forest disturbance results in an age structure dominated by young forests (Figure 3) and a strong carbon sink, although the carbon costs of fertilizer and debris burning costs are rarely considered (as opposed to decomposition of debris on-site). A significant portion of the harvested biomass is converted to paper or wood products, which provides medium to long-term carbon storage [*Skog*, 2008; *Skog and Nicholson*, 1998]. *Liu et al.* [2004] suggested that ~10% of the carbon sequestered by forests in the Southern Plains was in wood products, while *Mickler et al.* [2004] noted that the percentage could be higher when the products both in use and in landfills were considered. The lifetime and dynamics of such commercial carbon streams remains poorly constrained.

3.1.2. Historical Disturbance and Carbon Balance in the Southeast U.S.

[17] The Southeast U.S. was a net carbon source for much of the last two centuries, mainly due to massive forest clearing and agriculture expansion that occurred in the 18th and 19th centuries, and extensive commercial logging during the 20th century [*Birdsey et al.*, 2006], but has probably been a net carbon sink since the mid-20th century [*Chen et al.*, 2006]. Forest inventory data revealed that the southeastern states have seen steady accumulation of forest carbon since the 1950s, with average accumulation rates ranging from just over 1 Tg C yr^{-1} in Oklahoma to almost 6 Tg C yr^{-1} in Georgia and Alabama [*Mickler et al.*, 2004]. *Birdsey and Lewis* [2003] estimated that the total carbon accumulation from 1987 to 1997 in forests was over 30 Tg yr^{-1} in the Southeast. Based on model assessment at sample locations, *Liu et al.* [2004] concluded that the southeastern plains has been a carbon sink over the last three decades, absorbing on average 0.89 Mg C ha^{-1} yr^{-1}. An analysis of satellite-derived NPP during 1982–1998 identified the Southeast U.S. as one of the areas in North America experiencing the greatest increase in NPP, and suggested that management played a major role driving this change [*Hicke et al.*, 2002]. These estimates differ in time frame, geographic region, and carbon pools considered, but all point to a recent, multi-decadal carbon sink in the region.

3.1.3. Combining Field and Remote Sensing Data in Southeast U.S. Forests

[18] Recent progress in mapping forest structure using remote sensing may lead to future improvements in quantifying carbon fluxes due to forest disturbance and regrowth. Specifically, algorithms have been developed to reconstruct forest disturbance history with unprecedented temporal detail [*Huang et al.*, 2010, 2009; *Kennedy et al.*, 2010]. These algorithms allow wall-to-wall mapping of forest disturbances at sub-hectare spatial resolution [*Li et al.*, 2009a, 2009b]. In addition, lidar remote sensing allows improved assessment of forest structure and biomass [*Goetz and Dubayah*, 2011; *Lefsky*, 2010; *Lefsky et al.*, 2005]. Together, these techniques will complement field inventory data by providing better spatial and temporal coverage, reducing uncertainty and improving consistency in carbon modeling. Better data sets on wood products and soil carbon are also needed, however, for improved quantification of these carbon pools.

3.2. Whole-Stand Harvest and Fire in a Cool Climate: The Pacific Northwest

[19] Wildfire and harvest constitute the major disturbances in Pacific Northwest forests, in which biomass levels are comparable to those of tropical forests [*Hudiburg et al.*, 2009]. Production is also high, with total NPP of forests in Oregon, Washington and California estimated at 109 Tg C yr^{-1} [*Hudiburg et al.*, 2009]. Harvest peaked in the late 1980s, before declining on public lands following implementation of the Northwest Forest Plan, yet levels are still relatively high [*Masek et al.*, 2011]. Significant fires also

occur, interacting with the harvest regime in complex ways [*Thompson et al.*, 2007].

3.2.1. Modeling Ecosystem Productivity Following Fire and Harvest

[20] In a West Coast regional study focused on the effect of disturbance and climate on carbon balances in Oregon and Northern California (ORCA), Landsat data were used to map type and year of stand-replacing disturbance (fire versus harvest). The Biome-BGC model [*Thornton et al.*, 2002] was calibrated to mean biomass within age classes (young, mature, old) of a major forest type within ecoregions using inventory data and Omernik Level III ecoregion delineation [*Law et al.*, 2006]. Combustion factors for different pools and burn severities, determined from field studies in the region [*Campbell et al.*, 2007], were applied following fire, and post-disturbance carbon pools determined [*Sun et al.*, 2004]. Generalized Likelihood Uncertainty Estimation was used to compare Biome-BGC simulated NEP with plot data at different developmental stages since disturbance.

[21] At young, mature and old semi-arid pine flux sites, the model overestimated the portion of GPP lost through autotrophic respiration, and thus underestimated NEP, particularly in mature and old stands [*Mitchell et al.*, 2011]. The model also predicted a more rapid shift from source to sink during the early stages of stand development following disturbance, with the modeled peak sink strength occurring ~25 years, compared to the observed peak of 70–100 years [*Law et al.*, 2003]. The integral of NEP over years also showed a tendency for simulated accumulation of live mass to be too rapid during the first 50–100 years [*Meigs et al.*, 2011]. Thus, the model predicts a pattern similar to the classic Odum curve, but this does not match observations in semi-arid temperate forests in the region. In these forests, it can take years to decades for a successful cohort to establish after disturbance due to seedling mortality during summer droughts. Higher rates of water use by young trees can lead to hydraulic system failure during drought, whereas old trees are more buffered (stem and canopy water storage, hydraulic redistribution of soil water by deep roots) [*Anderegg et al.*, 2012; *Brooks et al.*, 2002; *Irvine et al.*, 2004].

3.2.2. Influence of Multiple Burning Events and Carbon Storage in Char

[22] Landscape history is likely to include multiple disturbances that can affect carbon pools, soil processes, and canopy structure, and recent modeling efforts incorporate prescription of multiple disturbances [*Turner*, 2007]. This requires disturbance history from remote sensing data as far back in time as possible, with some back-casting or other extrapolation method [e.g., *Balshi et al.*, 2007] available to extend the record throughout the model's spinup period. The ORCA project found that reseeding conifers in twice-burned areas in SW Oregon appeared to have been facilitated by the mosaic of different fire severities, with live-tree seed sources retained across much of a reburned area that had burned ~17 years earlier [*Donato et al.*, 2009a]. The two sequential fires did not lead to a depleted forest community, but rather to an increase in plant species richness, with little evidence of species loss. Managers had expected reduced tree species density, reduced dead pools, and large shrub fields in the twice-burned areas, assumptions that would have altered NEP estimates in sequential fires. Natural post-fire conifer regeneration in this region is often spatially and temporally irregular due to varying post-fire environmental conditions. Hence, there are multiple pathways of structural succession, and although conceptual models have been applied broadly, they have not adequately characterized structural succession following a range of natural disturbances [*Donato et al.*, 2012].

[23] A frequently ignored aspect in post-fire carbon balances is the transition of some of the carbon to char, which contributes to long-term carbon storage and soil productivity [*DeLuca and Aplet*, 2008; *Kane et al.*, 2007]. Conversion of wood biomass to char by wildland fire can be substantial, in some cases equivalent to the amount that is completely consumed [*Tinker and Knight*, 2000]. Much of it is eventually incorporated into soil, but failure to account for mass loss due to charring can result in overestimation of down wood biomass and decomposition. Black carbon generation on down wood was estimated to be ~300 kg ha^{-1} in areas experiencing only one high-severity fire, compared to ~655 kg ha^{-1} in stands that experienced two successive fires [*Donato et al.*, 2009b]. Char data from a range of fires and forest types could thus help reduce uncertainty in dead pools, long-term carbon storage, and post-fire decomposition and NEP.

3.2.3. Drivers of Post-Disturbance Carbon Balance in the Pacific Northwest

[24] Studies in the Pacific Northwest region indicate that forests in this region can become a sink about ten years after stand-replacing disturbance in favorable climates (e.g., mesic coastal coniferous forests [*Campbell et al.*, 2004]) to 20 years in drought-prone forests [*Law et al.*, 2004]. A carbon balance study in the semi-arid Metolius ponderosa pine area of Oregon two years after fire showed that NEP was significantly lower in severely burned compared with unburned stands, with NPP more important than R_H in determining NEP [*Irvine et al.*, 2007]. Large trees suffered only 34% mortality under moderate severity fire and contributed up to 91% of postfire bole wood production, and growth rates of trees that survived the fire were comparable with their prefire rates. The average stand ratio of NPP to R_H suggested that more severely burned stands have higher soil respiration relative to their productivity rates, and are thus more likely to be sources than sinks of carbon.

[25] Harvest removals had the largest impact on net ecosystem carbon balance, even though there were record wildfires during the time period in question. Assuming that West Coast forests generate merchantable bole wood at rates of 50–60% of the total wood harvested, and 54% of this wood remains in use or is in landfills after 20 years (wood product storage) [*Lippke et al.*, 2010; *Smith et al.*, 2006], harvest still has a larger impact on the carbon budget in a life-cycle assessment [*Hudiburg et al.*, 2011]. Prior to implementation of the Northwest Forest Plan (NWFP, intended to preserve late successional species on public lands) in 1993, models showed the net ecosystem carbon balance (NECB) to be a net source due to high harvest rates [*Turner et al.*, 2011]. From the mid-1990s through the next decade, reduction in harvest on public lands due to the NWFP resulted in a large carbon sink (Figure 4). In contrast, on private lands, which were subject to a much smaller harvest reduction, the NECB fluctuated around zero. Direct emissions of carbon from fire were small relative to NECB. The net effect on carbon sequestered as NECB, plus

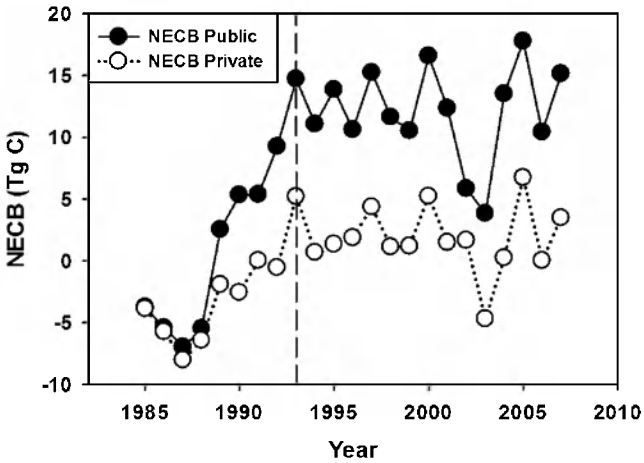

Figure 4. Net ecosystem carbon balance (NECB) on public versus private lands, adapted from *Turner et al.* [2011]. Vertical line shows establishment of the Northwest Forest Plan in 1993.

accumulation of forest products in slow turnover pools, is equivalent to ~50% of the annual emissions of fossil fuel CO_2 for Oregon [*Law et al.*, 2004]. Complementary observations can and should be used to reduce uncertainties in landscape-level modeling, e.g., satellite estimates of burn severity should be used for model input [*Meigs et al.*, 2011; *Miller and Thode*, 2007]. There is also a need to improve model-data integration during the extreme changes in carbon pools and fluxes in the first few years after disturbance from fire.

3.3. Stand-Killing Disturbance in a Cold Climate: Fire in the Boreal Forest

[26] Fire is the primary disturbance agent in most of the North American boreal forest, and has been increasing over the last four decades in many regions (Figure 5), driven by regional temperature and precipitation changes [*Flannigan et al.*, 2005; *Skinner et al.*, 2006]. Lightning-ignited fires dominate the area burned in boreal ecosystems, and fire return intervals vary by an order of magnitude or more, from only a few decades in dry jack pine forests to perhaps millennia in moist coastal areas [*Balshi et al.*, 2009; *Pan et al.*, 2011b]. Boreal forests in eastern North America are less

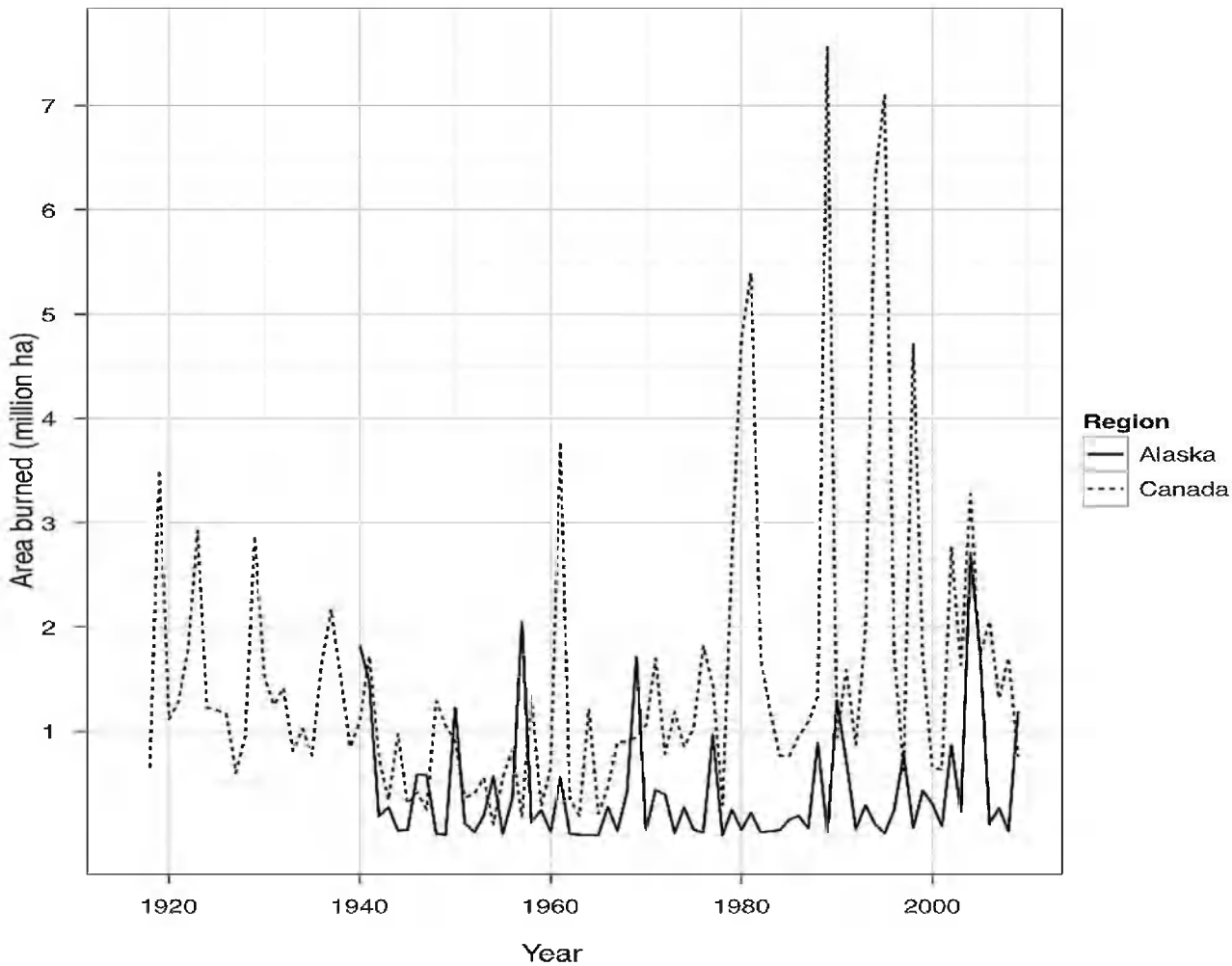

Figure 5. Area burned across boreal North America over the last 90 years, drawn from the data of *Kasischke et al.* [2011].

prone to drought [*Ma et al.*, 2012] and thus fire [*Girardin et al.*, 2009], and are intensively managed in ways that deviate considerably from the natural fire regime [*Cyr et al.*, 2009].

[27] The poorly drained nature of much of the boreal landscape results in significant complexity in the fire regime. In such areas, non-vascular bryophytes form a significant and productive component of the landscape carbon cycle [*Turetsky*, 2003], with relatively poorly understood biogeochemical and successional pathways. Moreover, fewer studies have been conducted in peatlands and forested wetlands, and ecosystem- to global-scale models usually are not designed to handle the unique characteristics of these ecosystems [*Frolking et al.*, 2009b].

3.3.1. Post-Fire Carbon Dynamics in Central Canada

[28] One of the most comprehensive studies of post-fire carbon dynamics was performed in central Manitoba, Canada, in the area of the 1990s BOREAS project. The region is mid-continental boreal forest, with cold winters, short but hot summers, and floristically simple forests dominated by black spruce (*Picea mariana*) and mosses. The study design was a seven-stand chronosequence ranging in age from 1 to 154 years since fire. The stands were matched by forest type and remote sensing data [*Goulden et al.*, 2006], and 14 additional stands served as landscape-level replicates [*Bond-Lamberty et al.*, 2004]. *Goulden et al.* [2011] summarized the techniques used, which included eddy covariance [*Litvak et al.*, 2003], biometry [*Wang et al.*, 2003], chamber fluxes [*Bond-Lamberty et al.*, 2002], sap flux [*Ewers et al.*, 2005], radiocarbon analyses [*Czimczik et al.*, 2006], and stand- to landscape-level modeling [*Bond-Lamberty et al.*, 2007]. A great deal of emphasis was put on quantifying R_H, both from woody debris and the soil, and on the differential responses of well- and poorly drained forests in the region.

[29] In this region, NEP recovered within 11–12 years, from large losses a year or two after fire to large sequestration in 25–75 year-old stands. The oldest stand in the chronosequence was a small C sink [*Goulden et al.*, 2011; *Litvak et al.*, 2003], with NEP uncorrelated to tree ring width [*Rocha et al.*, 2006]. The three different methods used to calculate NEP—eddy covariance, biometry and chamber data, and difference in C stocks—provided reasonable agreement and matched decadal and millennial model results well [*Goulden et al.*, 2011]. NPP peaked with NEP before declining sharply in the oldest stand [*Bond-Lamberty et al.*, 2004], driven by increased autotrophic respiration [*Goulden et al.*, 2011] and tree mortality [*Bond-Lamberty and Gower*, 2008]. R_H exhibited a double peak [*Harmon et al.*, 2011], one immediately after fire and one when standing snags fell, but was relatively constant after ~20 years [*Wang et al.*, 2002]. A large-scale modeling analysis [*Bond-Lamberty et al.*, 2007] found that fire was the primary driver of landscape-level carbon balance. The use of multiple methods to measure and constrain the major C fluxes thus worked well, yielding a wealth of data and significant insights in these post-fire stands [*Goulden et al.*, 2011].

3.3.2. Fire Severity, Soil Carbon, and Ecosystem Succession

[30] Future fire may be more locally severe as well as burn greater areas [*Girardin et al.*, 2009; *Xiao and Zhuang*, 2007], and how it may interact with various forms of soil C in high-latitude forests is poorly understood. Fire severity, the combination of fire intensity and duration, drives direct emissions from biomass burning [*French et al.*, 2011; *Turetsky et al.*, 2011] and affects the depth of the organic layers protecting permafrost [*Camill et al.*, 2009; *Turetsky et al.*, 2002]. Field-based inventories to quantify carbon consumed across different forest types and severity levels are needed, ideally matched with new remote sensing techniques [*Barrett et al.*, 2010; *Kasischke et al.*, 2008]. Changes in fire severity may also affect recalcitrant char, whose dynamics are not well understood [*Wardle et al.*, 2008] and rarely modeled [*Kane et al.*, 2010]. Reviews of char in boreal forests have suggested that given what we know about this soil organic matter pool, there should be more of it in boreal soils than is currently observed [*Czimczik and Masiello*, 2007; *Preston and Schmidt*, 2006], given estimated char production rates, forest ages, and fire return intervals [*Harden et al.*, 2000]. Thus char is a significant source of uncertainty, as in some temperate forests (see section 3.2.2 above).

[31] An emerging area of study focuses on how fire severity affects the successional trajectories of boreal forests [*Goetz et al.*, 2007; *Johnstone et al.*, 2010; *Shenoy et al.*, 2011]. In many cases, fire converts mature evergreen conifers to young deciduous stands, which have fundamentally different energy, water, carbon and nitrogen flux patterns [*Beck et al.*, 2011; *Chapman et al.*, 2006; *Hart et al.*, 2005; *O'Halloran et al.*, 2012]. This in turn drives forest productivity, carbon balance and ecosystem dynamics, particularly carbon balance at local to regional scales [*Chambers and Chapin*, 2002; *Goetz et al.*, 2007]. Changes in fire severity may interact with other disturbance agents such as insects [*Metz et al.*, 2011], leading to unexpected changes in ecosystem- to landscape-level processes.

[32] In summary, boreal ecosystems are floristically simple but subjected to fire regimes of varying lengths and intensities. Understanding how changing disturbance regimes might affect the carbon cycling and climate feedback of these carbon-rich ecosystems is complicated by a number of factors – in particular the expense of working in remote sites, poorly understood wetland and permafrost thaw dynamics, and uncertain modeling of post-fire ecosystem respiration. The interaction between these effects will ultimately determine landscape carbon balance as climate and disturbance regimes change. Integrated research on these topics is thus required to advance our knowledge of disturbance-mediated changes in the boreal biome [*Goetz et al.*, 2011].

3.4. Insect Outbreaks in a Temperate Montane Climate: The Western Mountains

[33] Insect outbreaks are major forest disturbances in North America. Bark beetles have affected millions of hectares of forest in recent decades [*Raffa et al.*, 2008], and the mountain pine beetle is one of the most damaging insect species in the region [*Samman and Logan*, 2000]. These beetles attack and kill several species of pines, with lodgepole pine (*Pinus contorta*) and ponderosa pine (*Pinus ponderosa*) among the most common [*Amman et al.*, 1990]; in epidemics, over 75% of the overstory trees can be killed [*Jorgensen and Mocettini*, 2005; *Pfeifer et al.*, 2011]. Major outbreaks affected 2 Mha in the early 1980s as well as in

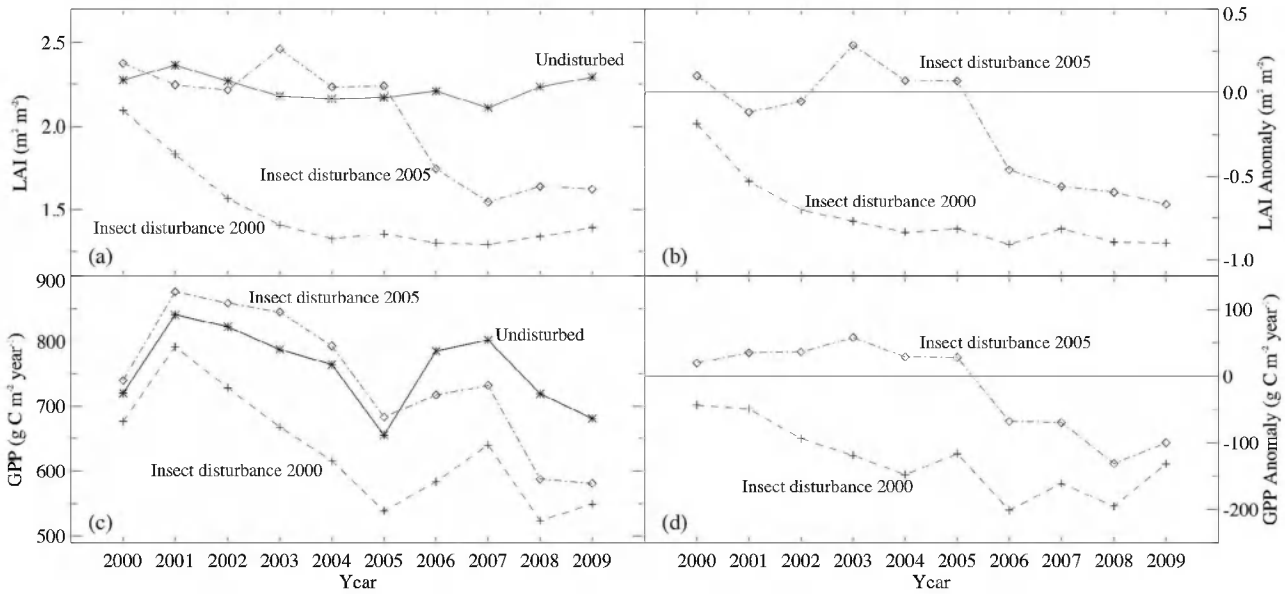

Figure 6. Trajectories of (a) leaf area index (LAI, $m^2\ m^{-2}$) and (c) gross primary production (GPP, g C $m^{-2}\ yr^{-1}$) from MODIS satellite products of pixels with mountain pine beetle disturbances (beginning in 2000 and 2005) as well as an undisturbed pixel. (b and d) Anomalies of the disturbed pixels relative to the undisturbed case.

recent years [*USDA Forest Service*, 2009], with a reduced period in between, and have affected 13 Mha in an ongoing outbreak in British Columbia [*Kurz et al.*, 2008b].

[34] Tree mortality results in reduced photosynthesis and increased heterotrophic respiration from the decay of relatively decomposable foliage once it falls (3–5 years post-attack), and prolonged decay of tree boles and branches over decades after snagfall [*Hicke et al.*, 2012]. In all cases R_H increases as a result of the enhanced dead carbon pools [*Harmon et al.*, 2011]. Surviving trees that are not attacked, typically non-host tree species or younger and smaller trees, respond by increasing productivity [*Cole and Amman*, 1980; *Pfeifer et al.*, 2011]. As a result, net ecosystem productivity may be negative (a carbon source) in the first years after insect attack, followed by an increase to positive (C sink) values, depending on the disturbance severity [*Hicke et al.*, 2012]. Here we discuss past studies and ongoing work that quantifies the rate at which carbon stocks and fluxes increase following insect outbreaks, focusing on mountain pine beetle outbreaks in the Rocky Mountains and Pacific Northwest of the U.S. and Canada.

3.4.1. Field Measurements of Post-Disturbance Dynamics

[35] Biometric measurements have been widely used to track forest changes following insect disturbance. Bole volume increment measured in stands attacked by mountain pine beetle in Yellowstone National Park, an indicator of primary productivity, showed stand-level productivity decreased 25–50% immediately following attack, but productivity reached pre-outbreak values within 10–15 years as a result of growth release in surviving trees [*Romme et al.*, 1986]. *Hawkes et al.* [2005] measured basal area immediately following a major mountain pine beetle outbreak in central British Columbia, and then 15 years later, and reported no significant change for one plot and a decrease of nearly 50% for a second plot. In both cases, the lack of expected increase was due to additional tree mortality following the initial outbreak that was caused by mountain pine and *Ips* beetles.

[36] Eddy covariance measurements have also been used to assess recovery following insect disturbance. *Brown et al.* [2010] estimated the post-outbreak carbon balance of two forest stands in British Columbia that differed in tree mortality, timing of mortality, and understory structure. The stand with more recent (but less complete) mortality was a net source of carbon to the atmosphere in two measurement seasons following beetle infestation, whereas the second was a carbon source in the first season and a small sink in the second. In both stands, surviving trees and understory contributed substantially to photosynthesis and were likely responsible for the reduction in carbon source or switch to a net carbon sink in the second year.

3.4.2. Remote Sensing of Bark Beetle Disturbance

[37] A significant number of studies have investigated detection of insect disturbances using remote sensing techniques, but most quantify ecosystem regrowth spectrally rather than using measures of vegetation productivity. Declines in the Normalized Difference Moisture Index derived from Landsat imagery following the year of attack have been documented, with values increasing only slightly in the subsequent 10 years [*Goodwin et al.*, 2008]. More recent space-borne sensors, in particular the Moderate-Resolution Imaging Spectroradiometer (MODIS), have enabled new applications in tracking post-insect disturbance forest dynamics. As an example, biogeochemical and biophysical data were used to assess regrowth following a mountain pine beetle outbreak in central Colorado [*Pfeifer et al.*, 2011]. LAI declined following insect disturbance in both disturbed locations (Figures 6a and 6b) before reaching a minimum 3–4 years after disturbance onset. Thereafter

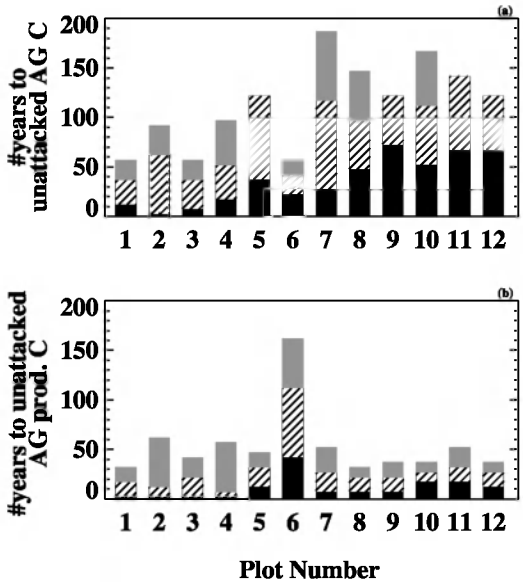

Figure 7. Variability in simulated responses of carbon stocks and fluxes within a forest experiencing a bark beetle outbreak. Number of years for (a) modeled aboveground carbon stocks and (b) production of woody carbon initialized with observed beetle-caused mortality ("attacked") to reach simulations without beetle-caused tree mortality ("unattacked"). Solid fill indicates attacked values reaching 70% of unattacked values; hatching, reaching 90%; gray, reaching 100% (i.e., full recovery relative to an unattacked stand).

LAI increased slightly, likely corresponding to the release of understory vegetation and subdominant trees (mountain pine beetle prefers larger diameter trees). Both disturbed locations showed reductions in GPP, with GPP more variable than LAI because vegetation productivity was influenced by the yearly climatic variation as well as leaf area (Figures 6c and 6d).

3.4.3. Integration of Field, Remotely Sensed, and Modeling Data

[38] An example of the use of multiple lines of evidence to elucidate carbon dynamics is provided by *Pfeifer et al.* [2011], who studied lodgepole pine stands in central Idaho attacked by mountain pine beetle. They used a combination of field measurements and modeling to quantify aboveground woody carbon stocks and productivity across a range of severity and tree mortality. Modeled carbon stocks and aboveground woody production declined, but recovered to pre-outbreak values in 1–25 years, although aboveground woody production never recovered to pre-outbreak levels because of the decline in NPP with stand age (present in the control simulations as well). Regrowth rates of carbon stocks and fluxes were also assessed with respect to simulations performed without beetle-caused mortality, and were highly variable among plots (Figure 7). Carbon stocks reached those of unattacked simulations in 50–150 years and aboveground woody production of carbon recovered in ~30–60 years. Although the range of responses in C stocks and fluxes within this outbreak likely represents the range of responses across bark beetle outbreaks in North America, additional research is needed to quantify these findings. Both the level of mortality and post-outbreak size distribution of surviving trees were key drivers of variability among plots.

[39] Other integrated modeling-field studies have studied similar variables in insect-infested forests. Using a growth model initialized by field measurements, *Coates and Hall* [2005] studied forest basal area growth following mountain pine beetle attack of lodgepole pines in British Columbia. Bark beetles killed 18–81% of plot basal area, which subsequently recovered to pre-outbreak levels within 20–80 years. In one plot with 96% of basal area killed, basal area did not recover to pre-outbreak values during the 100-year simulation.

[40] Outbreak impacts have also been quantified at regional scales, for example by *Kurz et al.* [2008b], who used historical observations and modeling to estimate C dynamics over two decades in British Columbia. Mountain pine beetle outbreaks were predicted to result in a net carbon source for most of the study period as a result of continued beetle attacks, reduced productivity, and enhanced decomposition. In the year of greatest impact, the carbon source was equivalent to 75% of Canada's average forest fire emissions (cf. Table 1) and the integrated carbon emissions for the study period were 270 Tg C (990 Tg CO_2e), equivalent to five years' emissions from Canada's transportation sector.

[41] In summary, relatively few studies have quantified the responses of carbon stocks and fluxes following mountain pine beetle outbreaks, but stand-level recovery generally occurs within several decades, depending on the C metric of interest (NPP, NEP, or carbon stocks), metric of comparison (pre-outbreak versus undisturbed), number and size of surviving trees, and the amount of shrub and herbaceous understory. At the regional scale, the recovery of carbon fluxes can be delayed for decades depending on the extent, severity, and duration of the outbreak as well as subsequent disturbances [*Kulakowski and Veblen*, 2006; *Kurz et al.*, 2008b].

4. Synthesis of Post-Disturbance Carbon Dynamics

4.1. Uncertainty and Variability of the 'Odum Curve'

[42] The case studies presented herein underscore several points that cut across the range of disturbance types and their implications with respect to addressing the questions listed in section 1.1. First, it is apparent that the metrics of the classic 'Odum curve', including the size of the pulse, the time of zero crossing, the peak uptake and its timing, and the time a new equilibrium is reached, are not universal. Rather, they vary considerably for boreal, temperate conifer, temperate broadleaf and other forest types across North America based on ecosystem and disturbance characteristics – and our models are not always able to capture the full range of this variability. The range of case studies discussed above demonstrates the large number of potential factors affecting post-disturbance carbon dynamics, but we can identify a few key areas of high uncertainty and large effect.

[43] **Disturbance severity, and its potentially nonlinear effects, constitutes one key uncertainty.** Severity plays a key role in driving the post-disturbance magnitude of carbon sources versus sinks, i.e., net exchange, was one of the key questions that inspired this paper (section 1 above), and

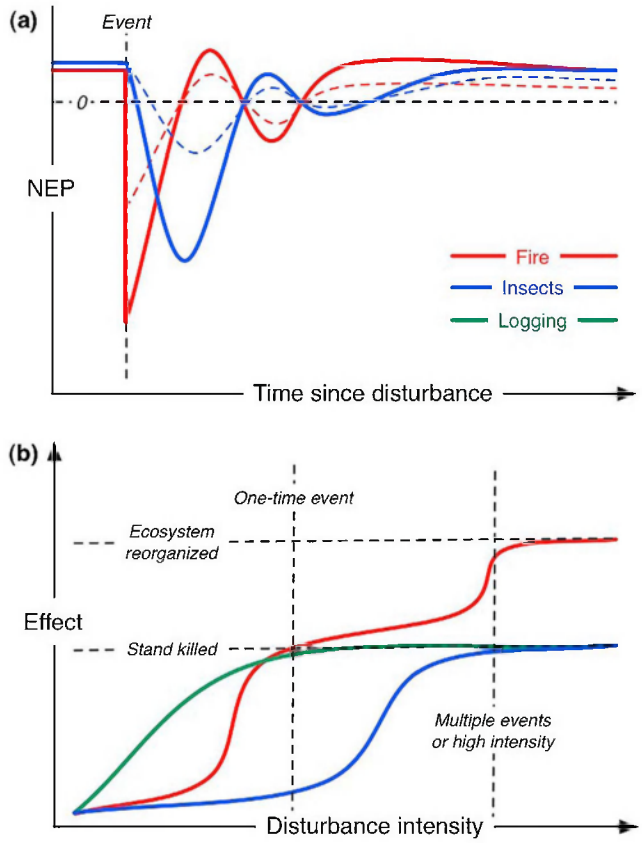

Figure 8. Conceptual figures, by disturbance type. (a) How net ecosystem production (NEP) can change over time due to the initial disturbance and secondary decadal effects such as dead wood decay and disturbance interaction. Solid and dashed lines indicate high- and low-intensity disturbance, respectively. (b) How increasing disturbance intensity can exert nonlinear effects (with "effect" broadly integrating changes to carbon, energy, and species dynamics). Lines shown are not intended to represent relative impact exactly, but rather to illustrate that the effect of "disturbance" depends strongly on the disturbing agent and intensity (or frequency) at which it is applied. Jumps in lines occur when the entire stand is killed and when system reorganization occurs into a new successional trajectory. The "insects" line here refers to defoliators; an insect borer (e.g., bark beetle) disturbance might follow a line similar to that shown for logging.

recurs in all the case studies above. Different trajectories of post-disturbance carbon uptake, through multiple mechanisms, are conceptualized in Figure 8a. For example, as severity increases across all disturbance types, there is a commensurate increase in vegetation mortality that results in larger emissions of carbon to the atmosphere (although the timing of this carbon pulse may differ for different disturbance types) [e.g., *Edburg et al.*, 2011]. Severe disturbance increases heterotrophic respiration relative to productivity rates by enhancing dead carbon pools and leaving little live vegetation behind to compensate through increases in productivity. Conversely, as disturbance severity decreases and more trees survive the disturbance event, productivity often increases in these surviving trees resulting in a quicker post-disturbance carbon recovery. Fire and logging tend to affect stands at shorter time scales (within a growing season) than insects and disease [*Fleming et al.*, 2002], causing more rapid tree mortality and accelerating the response of the carbon cycle. Moreover, high-severity fires and clear-cutting remove a greater proportion of biomass than insects and disease, which are often host-specific and disproportionate with respect to tree size or age class. Post-disturbance biomass associated with these different types of disturbance not only influence the trajectories of component carbon fluxes, but also the interaction of multiple disturbances on net exchange. For example, longer-term insect and disease disturbance may delay and even mute responses related to fire and harvest [*Fleming et al.*, 2002].

[44] Other nonlinear effects are possible and particularly poorly understood (Figure 8b). For example, in many ecosystems low-severity wildfires produce relatively small carbon losses and transient effects [*Mack et al.*, 2008], whereas when fires burn deeply in organic soils or become stand-killing canopy events, carbon loss increases and succession is reset. As fire intensity increases further, the entire post-disturbance plant community type can be altered, shifting landscapes to different successional trajectories [*Barrett et al.*, 2011; *Johnstone et al.*, 2010] with significant carbon consequences [*Turetsky et al.*, 2011]. While clearly an important factor in the boreal forest, where fire severity changes have occurred under the amplified warming of recent decades [*Beck et al.*, 2011; *Kasischke and Turetsky*, 2006], large-scale intense disturbances are increasing in other ecosystems as well [*Westerling et al.*, 2006], and in the process altering plant community types [e.g., *Waring et al.*, 2011]. Insect attacks also exhibit nonlinear and poorly understood dynamics, as intensity scales from routine herbivory to single defoliations (rarely fatal) to multiple defoliations, tree death and increased fire risk [*Fleming et al.*, 2002], with a range of subsequent carbon cycle responses [*Hicke et al.*, 2012]. Whether these changes result in a positive or negative change to the carbon balance requires an understanding of local disturbance history, but areas affected by severe disturbance tend to shift from net sinks or near neutral exchange to net carbon sources in the early years following disturbance [*Kurz and Apps*, 1999; *Randerson et al.*, 2006].

[45] **Understanding large-scale and long-term disturbance dynamics is a second area with large uncertainty.** It is difficult to ascertain how much disturbance regimes have changed in the past [*Houghton*, 2007], and thus how to partition the carbon sink of today's forests between land use, climate, external forcing factors (CO_2, N deposition, etc.), and ongoing carbon uptake from (e.g.) reduced disturbance rates — changes that may have happened years to centuries ago [*Gough et al.*, 2007; *Pan et al.*, 2011b]. This uncertainty has consequences at all scales, from cases in which stand-level carbon balance cannot be reproduced without assuming residual carbon 'drift' [*Carvalhais et al.*, 2010; *Pietsch and Hasenauer*, 2006], to the difficulty of reproducing landscape-level carbon balance at high latitudes if a steady state is assumed [*Bond-Lamberty et al.*, 2007], to centuries-long effects of plagues, continental land-use change [*Pongratz et al.*, 2009], and climate change [*Marlon et al.*, 2008]. We are also uncertain how much changes in current disturbance regimes represent long-term trends (for example, cycles in the age structure and flammability of forests across large

Table 3. Summary of Gaps in Understanding, and Appropriate Measurements, by Disturbance Type

Disturbance	Critical Gaps in Understanding	Approach or Measurements
Wildfire	Immediate post-fire respiration	Tower and chamber studies
	Burn severity	Remote sensing; biometry
	Successional dynamics	Long-term studies
Harvest	Fate of wood products	Life-cycle analyses
Insects	Resilience of forest stands	Study different levels of mortality
	Outbreak extent and severity	Remote sensing
Storms	Immediate post-disturbance respiration	Tower and chamber studies
All	Forecasting and spatial upscaling	Mutually constraining data sets; model-data integration; remote sensing
	Changes in disturbance regimes and long-term patterns	Historical reconstructions Modeling; ongoing data collection
	Disturbance intensity and interactions	Historical record; integrative studies

scale); natural variability; or responses to external forcings, and how these factors will interact. For example, climatic changes are known to increase the intensity and severity (i.e., including duration) of natural disturbances such as hurricanes in the Southeast U.S. and wildfire/insect outbreaks elsewhere, which often interact through positive feedbacks with more-susceptible species assemblages, many of which may be outside the range of historical variability in climate and associated disturbance regimes (timing, intensity, frequency) [*Kurz et al.*, 2008a; *Westerling et al.*, 2006]. Moreover, changes in natural disturbance regimes and human management of ecosystems can interact synergistically and reinforce one another resulting in ecosystem modification that cannot be reversed [*Lindenmayer et al.*, 2011]. Finally, as exemplified in the Pacific Northwest case study, increased drought may in the future inhibit post-disturbance NEP by affecting seedling germination, vegetation (tree and shrub) density, plant productivity, and disturbance regime dynamics.

[46] These areas of high uncertainty give broader context to the case studies above, and further illustrate the importance of integrating field, remotely sensed, and modeling data in order to more fully address the questions listed in section 1.1 and shown in Figure 1. For example, satellite-based disturbance detection approaches have greatly expanded our ability to quantify the timing, location, magnitude and extent of large-scale ecological disturbances over broad areas (see Figure 2), allowing quantification of disturbance rates across a range of North American ecosystems. These observations graphically illustrate how the spatial extent of moderate and high severity disturbances interact across the landscape, shedding light on longer-term dynamics as data are systematically acquired through time. This latter point underscores the need for continued systematic earth observation satellites and associated disturbance data products, but also a need for synergistic use of field measurements (of various sorts, including eddy covariance, forest inventory, stand-level biometry, etc.) with satellite observations and ecosystem biogeochemistry models.

4.2. Measurements and Specific Disturbances

[47] Do the necessary—or at least most useful—measurements change with the type of disturbance, after considering the broader uncertainties outlined above? Yes, both because of the difference in processes involved and knowledge gaps uniquely associated with each disturbance type. This is discussed in the case studies above, and summarized below and in Table 3.

[48] For fire-prone ecosystems, there is clearly a need to improve measurements and model-data integration during the extreme changes in carbon pools and fluxes in the first few years after disturbance. Some of the greatest uncertainties in these stages include the fraction of biomass burned, the magnitude of carbon released due to heterotrophic soil respiration [*O'Neill et al.*, 2006], the production and subsequent degradation of char, and the decomposition of legacy carbon, in particular woody debris [*Harmon et al.*, 2011; *Zeng et al.*, 2009]. More chamber- and tower-based observations will help reduce modeling uncertainties [*Mitchell et al.*, 2011]. We suggest that improving estimates of heterotrophic soil respiration is particularly important, especially in topographically complex regions [*Riveros-Iregui et al.*, 2012] and where high soil moisture variability is linked to micro-topographic relief (e.g., boreal landscapes). Finally, large-scale field measurements [*Turetsky et al.*, 2011] and increasingly accurate satellite estimates of burn severity [*Barrett et al.*, 2011; *Miller and Thode*, 2007] should be incorporated into modeling experiments.

[49] The areas of uncertainty are different for harvest-related disturbances. Biomass removed during harvest is relatively easily to measure, although carbon release due to post-harvest management treatments (e.g., chop and burn, an often-ignored carbon loss) must be quantified. Determining whether forests were planted (and if so, the density of trees per hectare) and fertilized or are a result of natural regeneration also significantly affects post-disturbance regrowth assumptions [*Bergeron et al.*, 2008]. Finally, tracking the fate of the wood that was removed from the site is critical for integrated life-cycle analyses [*Hudiburg et al.*, 2011] to be constructed. This is a critical issue, as the relatively simple decay dynamics of a natural forest cannot be assumed for harvested wood.

[50] Tracking insect-related disturbance (whether caused by defoliators, which do not necessarily kill trees, or more aggressive bark beetles, which do; cf. Figure 8 caption) requires measurements of other components — in particular, reductions in tree ring widths and canopy biomass [*Hogg et al.*, 2005], estimates of herbivory as carbon is transformed from foliage to litter via frass [*Townsend et al.*, 2004], and insect mortality and respiration. At the landscape scale, insect outbreaks exhibit complex nonlinear dynamics, making their prediction exceedingly difficult. Thus for insect outbreaks, key questions whose answers are unclear include: (a) the amount of mortality required to cause a stand to become a C source following disturbance

[*Nave et al.*, 2011], and if so for how long; (b) the spatial extent and amount of mortality within large outbreaks; (c) patterns of post-outbreak ecosystem processes such as tree establishment, surviving tree growth, and snagfall that influence net carbon fluxes.

[51] Documenting carbon dynamics of forests associated with storm or hurricane damage requires specific measurements to best characterize the types of changes that have taken place, including the level of damage done to individual trees [*Luley and Bond*, 2006], the mortality of trees of different age classes, and variability in the intensity of the disturbance [*Chambers et al.*, 2007; *Dolan et al.*, 2011]. The sheer quantity of hurricane-generated dead biomass can also pose significant challenges for accurate and safe field measurements [*Vargas and Allen*, 2008].

[52] Finally, the problem of temporal and spatial scaling is critical for all disturbance types. Chronosequences provide an assumed temporal scaling, but an increased use of repeated measurements, or 'vectors' [*Harmon et al.*, 2000], allows for a rigorous test of time-for-space assumptions. Attempts to extend observations spatially benefit from the use of remote sensing tied to models, particularly those using coupled models [e.g., *Nemani et al.*, 2009], as opposed to using models or remote sensing alone to extend plot-level observations. Such coupled approaches are particularly valuable given the dynamic nature of disturbance and associated changes in vegetation state. Land cover classification derived from remote sensing may be limited in these highly dynamic disturbance cases, e.g., changes to different cover type classes are typically quite rapid relative to updates of land cover maps. Moreover, a forest may be classified as deciduous, for example, but that label does little to quantify the variability of forest properties modified by disturbance or the processes these properties reflect (such as gross and net productivity).

5. Conclusion

[53] We have provided an overview and synthesis of some of the major types of disturbance that occur across North America, investigating associated vegetation recovery and carbon dynamics through case studies focused on harvest and storms in the southeastern U.S., harvest and fire in the Pacific Northwest, fire in boreal forests, and insects in western North America. These case studies provide insight into the types of measurements that are needed to capture regrowth dynamics and their carbon implications. They also emphasize the utility of multiple types of observations (typically field biometry, eddy covariance, chamber measurements, long-term forest inventories, and satellite remote sensing), incorporated into biogeochemical models using data assimilation and numerical algorithms, to constrain and understand C dynamics.

[54] It has been clear for decades that post-disturbance carbon balance can be highly variable across space, time and disturbance type, and that ecophysiological models fail to reproduce the full range of this variability. We suggest that our understanding of the many pathways of post-disturbance carbon fluxes is particularly limited by our understanding of (i) disturbance severity, which has many linear and nonlinear effects, and (ii) longer- and larger-scale disturbance dynamics, and how they may interact. Both of these uncertainties involve legacies extending across a wide range of time scales. Incorporating in situ and satellite-derived observations into models will help refine the magnitude and duration of those legacies. We also have attempted to identify the specific measurements most useful to improving our understanding in particular ecosystems, noting that heterotrophic respiration, insect outbreak dynamics, and life-cycle analyses would particularly benefit from further research.

[55] Finally, we argue that imaginative, integrative analyses using long-term repeat observations, multiple lines of data, multiple scales of analysis, increased measurement capabilities, improved representation of disturbance effects in models, shared models and online data sets, and innovative numerical algorithms hold huge benefits for understanding the carbon dynamics of disturbance-prone forests. Such analyses will improve our understanding of the rates (frequency, timing, intensity) of disturbance, and potential changes in those rates. This is particularly relevant to capturing potential state changes that may be underway as a result of climate change. A range of measurements is needed to address these changes, document them with reduced uncertainty, and thereby to assess whether they are likely to cross critical thresholds [*Scheffer et al.*, 2009]. To say simply that "more measurements are needed"— a standard closing of many research publications — is not adequate. Only by use of multiple techniques and integrative science can we quantify, constrain uncertainties, and accurately predict the dynamics of forest carbon regrowth following equally dynamic disturbance regimes.

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