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Redistribution of forest carbon caused by patch blowdowns in subalpine forests of the Southern Rocky Mountains, USA

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[1] Patch blowdowns varying in size from 0.1 to 33 ha affected several areas in Rocky Mountain National Park, Colorado, USA, during the winter of 2011–2012. These blowdowns resulted in substantial redistribution of forest carbon by snapping and uprooting trees, thereby increasing instream wood recruitment, recruitment of dead wood to the forest floor, and exposure of organic soil on uprooted tree plates. Estimates of carbon redistribution at five sites in Rocky Mountain National Park range as high as 308 Mg C/ha in high-severity patches to 106 Mg C/ha in low-severity patches, of which typically 10–30% is soil C and the remainder is downed wood. Masses of carbon redistributed from living to dead biomass at high-severity sites represent a substantial portion of average total biomass in old-growth subalpine forests in the region. Consequently, the potential for increasing frequency and/or severity of blowdowns under a warming climate represents a significant potential source of terrestrial carbon to the atmosphere. The majority of this carbon is in the form of downed wood that becomes a carbon source to the atmosphere, although interactions between downed wood and river processes can locally increase carbon storage in floodplain soil. Predictions of changes in precipitation and wind patterns, and associated changes in wildfire and insect infestation, suggest that blowdowns may become more common in future in the Southern Rockies, but the consequences for carbon dynamics depend on site-specific interactions between blowdowns and other processes such as floodplain storage of organic matter.

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1. Introduction

[2] Disturbances with a range of frequency and spatial extent structure forests and the distribution of organic carbon within living and dead biomass in a forest ecosystem [*Turner*, 2010; *McKinley et al*., 2011]. Although previous studies have quantified altered carbon fluxes within a forest ecosystem following disturbance [*Law et al*., 2004; *Chambers et al*., 2007; *Zeng et al*., 2009; *Amiro et al*., 2010; *Harmon et al*., 2011; *Pfeifer et al*., 2011; *Edburg et al*., 2012; *Kasischke et al*., 2013], few examine how disturbances interact with site-specific conditions to shape carbon storage in complex ways. Here, I examine how trees toppled by blowdowns in old-growth (stand age > 200 years, *sensu Binkley et al*. [2003]) subalpine forest of the U.S. Southern Rocky Mountains interact with the local geomorphic setting — stream and valley geometry — to influence carbon redistribution following disturbance. Redistribution in this context refers to changes in the nature of carbon pools (e.g., living biomass transferred to dead biomass when trees are killed, or subaerial exposure and erosion of formerly in situ forest soils when trees are uprooted).

[3] Blowdown refers to toppling of trees as a result of strong winds. Severe wind damage can occur to trees when wind speeds exceed ~ 100 km/h, although gusts — which can be up to two times the hourly mean wind speed — are particularly important in damaging trees [*Ancelin et al*., 2004; *Nicoll et al*., 2005; *Martin and Ogden*, 2006]. High-intensity winds typically result in a greater proportion of toppled trees being uprooted rather than snapped [*Veblen et al*., 2001; *Hilimire et al*., 2013]. Whether a tree breaks off along the trunk or uproots also reflects factors such as: the depth and lateral extent of the root system; wind speed and direction; soil depth and water content; topographic position; canopy position; crown size and shape; trunk strength as influenced by tree species, age and health; tree height; and whether the tree is struck by other falling trees [*Schaetzl et al*., 1989b; *Martin and Ogden*, 2006; *Peterson*, 2007; *Rich et al*., 2007; *Urata et al*., 2012]. Shallow-rooted species of *Abies*, *Picea*, and *Pinus* are particularly prone to uprooting while alive [*Schaetzl et al*., 1989b; *Veblen et al*., 2001],

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Table 1. Characteristics of the Study Sites and Results of Analyses of Wood, Soil, and Total Organic Carbon Redistributed During Blowdowns

Site[a]	Elevation (m)	Size[b] (ha)	S_{valley}[c] (m/m)	$S_{hillslope}$[d] (m/m)	m[c] wood/ m[b] area	Mg C/ha (wood)	m[c] soil/ m[b] area	Mg C/ha (soil)	Mg C/ha[e] (Total)
Glacier Creek (*n* = 6)	3160–3030	33 (1–9)	0.034	0.334	0.11	220	0.04	26.4–87.6	246–308
Icy Brook (*n* = 6)	3220–3040	0.1 (0.1–1)	0.244	0.046	0.09	180	0.03	19.8–65.7	200–246
North Fork Big Thompson River (*n* = 5)	2740–2350	2.5 (0.1–4)	0.155	0.038	0.04	80	0.04	26.4–87.6	106–168
North St. Vrain Creek (*n* = 7)	3050–2970	1.0 (0.1–6)	0.058	---	0.10	200	0.04	26.4–87.6	226–288
Hunters Creek (*n* = 5)	2860–2590	0.1 (0.1–0.6)	---	0.393	0.08	160	0.03	19.8–65.7	180–226

[a]Sample size (number of patch blowdowns surveyed) listed for each site.
[b]Size for Glacier Creek is total extent of blowdown; size for other sites is average of widely scattered patches; parenthetical values are range for patch blowdown size, to nearest 0.1 ha.
[c]S_{valley} is downstream gradient in along channel where blowdowns occur in a valley bottom.
[d]$S_{hillslope}$ is downslope gradient along valley sides where blowdowns occur on valley sides.
[e]Combined estimates from soil and downed wood; lower value assumes soil TOC of 4.4%, upper value assumes soil TOC of 14.6%.

and these species dominate subalpine forests in the Southern Rocky Mountains.

[4] Blowdowns span a damage gradient from extreme (> 50% forest mortality) to light [*Frolking et al*., 2009], and a spatial continuum from isolated, uprooted trees to widespread, catastrophic events covering thousands of hectares of forest [*Schaetzl et al*., 1989a]. The largest documented blowdown in the Southern Rockies occurred on the Routt National Forest in Colorado in October 1997, when > 10,000 ha of trees were blown down by winds estimated at 200–250 km/h [*Baker et al*., 2002]. The entire affected area was composed of hundreds of blowdown patches with a mean size of 25 ha and a patch density of 6.5 patches per km^2 [*Lindemann and Baker*, 2001]. In discussing abrupt forest disturbances that generate gaps > 0.001 km^2, *Frolking et al.* [2009] characterize blowdowns as large disturbances that typically cover ~0.01 to 10^3 km^2. The blowdowns described in this paper, like those of the 1997 Routt blowdown, are not spatially continuous, but instead consist of discrete patches that are typically 0.1–2.5 ha in area, and separated by equal-sized patches of undisturbed trees. I refer to these as patch blowdowns.

[5] The return interval of blowdowns is difficult to estimate. Tree ring chronologies suggest that blowdowns in the Southern Rocky Mountains are frequent but low severity events that recur every one to two decades within an area of ~10^2 km^2 [*Veblen et al*., 1991]. Susceptibility to blowdowns increases with stand age [*Baker et al*., 2002; *Kulakowski and Veblen*, 2002], however, and substantial tree mortality caused by blowdowns within an individual stand of subalpine forest likely occurs less frequently — perhaps on the order of time intervals > 100 years in old-growth forest.

[6] Old-growth stands such as those examined for this study are more susceptible to blowdowns than are younger forest stands [*Veblen et al*., 1991]. As a type of disturbance common in old-growth forests of the western United States, blowdowns can significantly influence the carbon balance of a forest through at least two mechanisms. First, blowdowns topple trees and rapidly transfer large amounts of living biomass to dead material that becomes a carbon source during decomposition. This results in net release of carbon to the atmosphere at a rate reflecting tree regeneration and decomposition of downed wood [*Harmon et al*., 1990; *Janisch and Harmon*, 2002; *Turner*, 2010; *McKinley et al*., 2011].

[7] Second, blowdowns uproot trees, disturb soils (supporting information Table 1) and alter the storage of carbon in forest soils. As a result of uprooting, at least a portion of the root plate and associated soil and organic matter is upheaved, subaerially exposed, and eroded by rainfall or snowmelt [*Schaetzl et al*., 1989a; *Gallaway et al*., 2009]. Reported values of disturbed soil surface associated with tree uprooting range from 1.5 to 16 m^2 per tree [*Schaetzl et al*., 1989b], with maximum root plate volumes of 4 m^3 [*Burns*, 1981; *Schaetzl et al*., 1990]. The resulting sediment yield from downslope transport of this disturbed soil ranges from 0.02 t/ha/y [*Swanson et al*., 1982] to 1.3 t/ha/y [*Burns and Tonkin*, 1987], which can equate to more than 10% of the total sediment yield from a drainage basin [*Reid*, 1981]. Shallow roots, topographic exposure, a tree weakened by drought or insects, and soil with low cohesion or shear strength can all increase uprooting [*Schaetzl et al*., 1989b]. Standing dead trees are more likely to be snapped, but living trees are more likely to be uprooted [*Veblen et al*., 2001].

[8] A potential third influence of blowdowns on carbon balance involves recruitment of toppled trees into adjacent streams. Instream wood increases the hydraulic roughness of streams, which facilitates storage of sediment and particulate organic matter in areas of flow separation. Rapid recruitment of large numbers of trees into a stream during or shortly after a blowdown can create logjams that span a stream channel. These channel-spanning jams are particularly effective at creating backwater areas with substantial storage volume. Accumulation of sediment in these backwaters can result in reduced stream cross-sectional area, leading to overbank flow during higher discharges [*Brummer et al*., 2006]. Relatively shallow, slower velocity overbank flow facilitates further deposition and storage of organic matter on the floodplain, and can result in the formation of secondary channels [*Jeffries et al*., 2003] that also store organic matter as a result of shallower, lower velocity flows [*Wohl et al*., 2012]. The resulting multithread channel planform is more common in old-growth forest streams where greater volumes of instream wood are present [*Wohl*, 2011; *Collins et al*., 2012]. Carbon discharged to the oceans is only a fraction of that entering rivers from terrestrial ecosystems [*Cole et al*., 2007; *Aufdenkampe et al*., 2011]. The riverine physical complexity and storage of organic matter created by instream wood facilitate both burial of organic carbon in

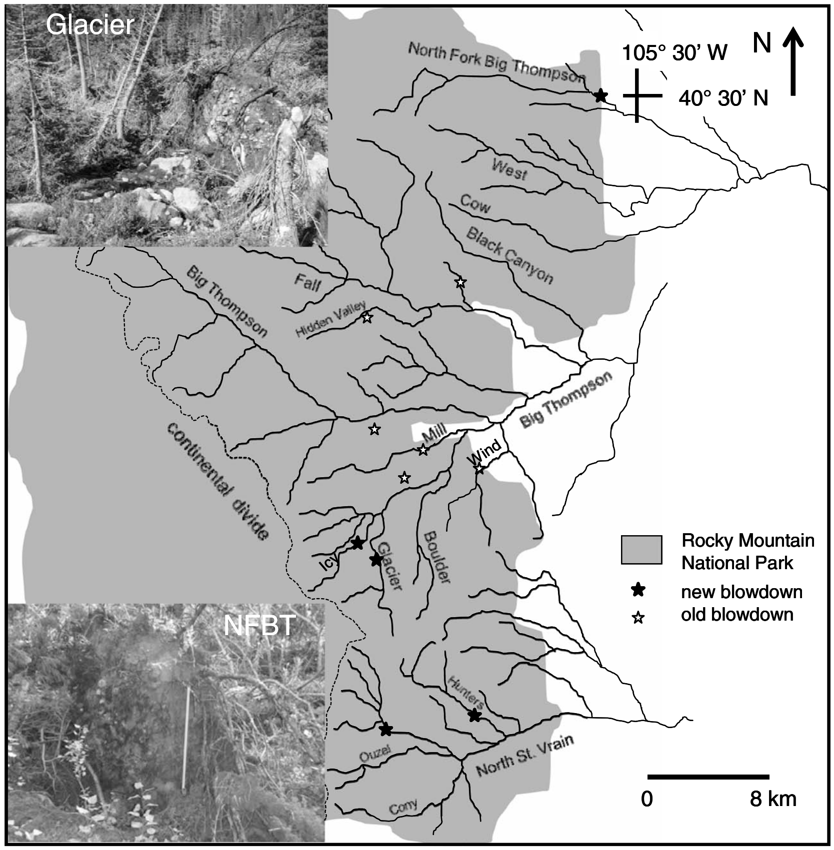

Figure 1. Location map of drainage network and recent (2012) and older documented blowdowns within Rocky Mountain National Park in Colorado, USA. Inset photo at upper left shows uprooted and snapped trees in a high-severity blowdown patch along Glacier Creek. Inset photo at lower left shows an uprooted tree along the North Fork Big Thompson River; white line at center of photo is 1 m long.

sediment reservoirs and biological uptake of carbon by aquatic and riparian organisms [*Battin et al.*, 2008].

[9] Although large blowdowns generate a great deal of attention, smaller, patch blowdowns occur each year in the Southern Rocky Mountains. I use measurements from five blowdown patches that occurred in subalpine forests within Rocky Mountain National Park (RMNP), Colorado during the winter of 2011–2012 to illustrate the magnitude of carbon redistribution associated with this type of forest disturbance. My objective is to document redistribution of forest carbon via changes in instream wood recruitment, and downed wood and soil organic carbon on the forest floor, caused by the blowdowns. I then consider the site-specific interactions that govern how carbon is redistributed in riverine and floodplain environments, and the potential implications of changes in disturbance regime for such redistribution.

2. Study Area

[10] All of the patch blowdowns examined here are either within RMNP or the adjoining Roosevelt National Forest (Figure 1). The sites are at elevations between 2350 and 3220 m (Table 1) and thus lie mostly within subalpine forest dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*), and aspen (*Populus tremuloides*), although the lower sites along the North Fork Big Thompson River are within the montane zone, which is dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) [*Veblen and Donnegan*, 2005]. All of the sites are within old-growth forest.

[11] Although the winters of 2009–2010 and 2010–2011 had substantial snowpacks, the several preceding years had been quite dry, as was the winter of 2011–2012 when the blowdowns occurred. Trees in the region were thus stressed by continuing drought [*Hanson and Weltzin*, 2000], as well as by a rapidly expanding outbreak of the mountain pine beetle (*Dendroctonus ponderosae*), and a spruce beetle (*Dendroctonus rufipennis*) that affects some of the Engelmann spruce. Mean annual precipitation within the elevation range of the study sites is ~80 cm, the majority of which falls as snow.

[12] The region is characterized by extremely strong winds throughout the year, with the most frequent gusts occurring during October to March. Subalpine sites can have gusts reaching 150 km/h and an average daily maximum wind speed of nearly 80 km/h [*Glidden*, 1982]. During the period of 1 October 2011 to 30 September 2012, for example, the main weather station in the subalpine zone at Loch Vale in RMNP recorded 132 days with gusts exceeding 80 km/h, including

gusts of 130 km/h at both 2 m and 6 m above the ground (http://co.water.usgs.gov/lochvale/data.html, accessed Feb. 2013).

[13] The largest blowdown of the five study sites discussed here occurred in November 2011, a month in which 16 days had wind gusts exceeding 80 km/h: descriptions posted online by hikers in the study area suggest that the blowdown occurred on 21 November, during a 7 day period of very high winds. This and the other blowdowns were likely caused by a microburst, a type of downburst in which a cold air mass accelerates downward, forming a very powerful downdraft that spreads out when it hits the surface [*Peterson*, 2000].

[14] The North St. Vrain and Hunters Creek sites have Pinedale-age glacial till overlying the Precambrian-age crystalline bedrock. Soils are gravelly to very cobbly sandy loam [*NRCS*, 2006]. The organic layer is typically only a few cm thick, with mineral soil to a depth of 0.7 m or less. All of the sites were covered by Pleistocene valley glaciers, and have moderately broad (50–200 m wide) valley bottoms with relatively moist soils.

[15] Forest ecologists have documented numerous blowdowns in subalpine forests of the southern Rocky Mountains. Small blowdowns covering less than a hectare to several hectares are common in this region [*Alexander*, 1964; *Veblen et al*., 1991], although *Veblen et al*. [1991] noted that these small blowdowns can be roughly synchronous with those in other subalpine stands located 12–15 km away. Moderate (10^1–10^2 ha) and large (>10^3 ha) blowdowns have also occurred [*Flaherty*, 2000; *Baker et al*., 2002; *Kulakowski and Veblen*, 2003]. Blowdowns are more common in the subalpine zone than in the montane zone because of more frequent extreme winds at higher elevations, more shallow-rooted trees, and shallow or poorly drained soils [*Alexander*, 1987; *Veblen and Donnegan*, 2005]. High-relief terrain can create highly turbulent winds, and blowdown is enhanced where topography constricts and accelerates winds [*Alexander*, 1964]. Published records of blowdowns at various sites in RMNP, and my own observations of older blowdowns in the park (supporting information Table 2), suggest average recurrence intervals of one to two decades at a site.

[16] Blowdowns contribute to instream wood in channels flowing through subalpine forest. I surveyed instream wood loads (volume of wood per unit surface area of channel) and the location of channel-spanning logjams in the 16 primary drainages on the eastern side of RMNP during the summers of 2010 and 2011. These surveys extended from near timberline to the eastern boundary of the national park on each drainage (4–29 km lengths) [*Wohl and Beckman*, 2013b] and provided a baseline against which to compare wood loads following the 2012 blowdowns.

3. Methods

[17] Field work was conducted during July and August of 2012. I located all sites using a handheld GPS unit with $\pm$3 m horizontal resolution. I calculated valley and hillslope gradients from topographic maps. The Glacier Creek blowdown was the largest and most severe of the five sites described here. For this blowdown, I mapped the perimeter of the entire blowdown using the handheld GPS, as well as the perimeter of the moderate and high severity portions. I then randomly selected six 100-m^2 plots (10 × 10 m) within the blowdown for detailed measurements. For the four remaining sites, each of which had widely scattered patches of blowdown in which each patch was typically < 1 ha, I randomly selected at least 5 10 × 10 m plots, each of which coincided with a blowdown patch. Within each plot, I tallied all freshly downed trees (i.e., those toppled during the recent blowdown), distinguished uprooted and snapped trees, and measured the length and diameter at breast height (DBH) of each tree, as well as the volume of the root plate for uprooted trees. I measured total basal area and basal area of dominant tree species in a patch of undisturbed forest adjacent to each plot, and total basal area of standing trees within each plot.

[18] I estimated the volume of soil displaced by uprooted trees using the partitioning method of *Richards et al*. [2011] based on a grid of depths in which the pit is partitioned into numerous narrow rectangular prisms and the volume of the prisms is then summed. I collected soil samples from the upturned root plate and from the adjacent undisturbed soil for analyses of bulk density and total organic carbon. I collected six root plate samples and six soil samples at the Glacier Creek blowdown, and six root plate and six soil samples at the North St. Vrain Creek blowdown. Soil samples were analyzed at the Colorado State University Soil Testing Lab for total carbon with a LECO TruSpec CN furnace [*Nelson and Sommers*, 1982]. Each sample was analyzed for CO_3-C by treating the sample with 0.4 N HCl and measuring the CO_2 loss gravimetrically [*NRCS*, 1996]. Total organic carbon was calculated as total carbon-CO_3-C.

[19] Following the methods of the preblowdown instream wood surveys, I measured the length and average diameter of each piece of wood within the active channel for which diameter was > 10 cm and length was > 1 m. Calculations of wood volume assumed each tree was a cylinder. Channel-spanning logjams are those with at least three pieces of wood in contact, forming an obstruction that spans the entire channel width and creates at least minimal backwater effects. Instream wood surveys focused on the Glacier Creek site because this blowdown had the greatest length along the channel and thus the greatest effect on instream wood recruitment. The other study sites had only single, small patch blowdowns (typically < 100 m long) immediately adjacent to a creek.

4. Results and Discussion

4.1. Instream Wood Recruitment

[20] Blowdowns at three of the five sites (Glacier, North St. Vrain, North Fork Big Thompson) influenced instream wood recruitment. Most of the patch blowdowns at Icy Brook and Hunters Creek were along the valley side slopes or portions of the valley bottom away from the active channel. I focused on the Glacier Creek site, where blowdown occurred adjacent to an 1840 m length of channel.

[21] I had surveyed instream wood and channel-spanning logjams along this portion of Glacier Creek in 2010, when I found 12 m^3 wood/ha channel surface and ~ 1 jam/100 m channel. The 2011 blowdown recruited ~30.6 m^3 of wood to the channel within the blowdown zone. This equates to ~ 10.4 m^3 wood/ha channel surface (or 4.16 Mg wood/ha) added to the channel. The portion of Glacier Creek affected by the blowdown was at the lower end of the range of wood loads for headwater streams on the eastern side of RMNP [*Wohl and Cadol*, 2011] prior to the blowdown, and the blowdown nearly doubled the wood load in this portion of

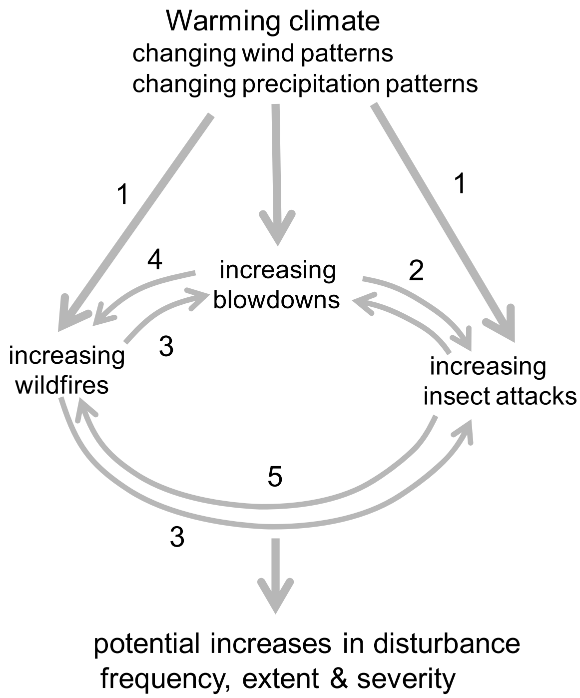

Figure 2. Conceptualization of potential interactions among changing climate and various types of forest disturbance in the Southern Rocky Mountains. This conceptualization represents a simplistic scenario that does not account for effects such as differing stand age or species composition. Supporting citations are: 1 (increases in thermal regimes conducive to population success for mountain pine beetles [*Bentz et al*., 2010]; longer fire season in the western U.S. under warming climate [*Flannigan et al*., 2000]), 2 (blowdowns can trigger beetle outbreaks [*Veblen et al*., 1989]), 3 (fire-injured trees can be more susceptible to beetles and to blowdown [*Veblen*, 2000]), 4 (blowdown-affected stands can burn more severely [*Kulakowski and Veblen*, 2007]), 5 (some characteristics of fuels and fire are enhanced following beetle outbreaks, although time since outbreak exerts a strong influence [*Hicke et al*., 2012]).

the creek. Assuming that the wood is 50% organic carbon, this represents ~ 12.2 Mg C in total or 2.1 Mg C/ha added to the channel within the blowdown zone.

[22] The 2012 blowdown also created new jams, resulting in ~ 1 jam/92 m channel during the summer 2012 stream survey. Although the blowdown did not immediately substantially increase the number of channel-spanning logjams within Glacier Creek, the volume of wood recruited to and trapped within this portion of Glacier Creek is likely to increase with time. Numerous trees leaning over the channel remain from the blowdown. Also, more than half of the trees knocked into and across the channel remain partly attached to the bank via rootwads. These ramped wood pieces tend to be less mobile and to effectively trap wood in transit, creating jams [*Wohl and Goode*, 2008]. The snowmelt peak flow in 2012 was exceptionally low, so that there was relatively little instream wood transport and limited formation of new jams at the newly recruited wood pieces. The 2013 peak flow was closer to an average year, with much greater stream transport of smaller wood pieces that facilitate jam formation at the anchored ramps. A channel survey in July 2013 indicated 1 jam/54 m of channel. Continuing effects of the 2012 blowdown thus resulted in decreasing the downstream spacing between channel-spanning logjams by nearly half relative to preblowdown conditions. Ongoing surveys of logjams in headwater streams of RMNP suggest that individual jams typically persist for several years, so the blowdown will likely cause increased storage of instream wood at a decadal scale.

[23] The formation of channel-spanning logjams as a result of toppled trees can also exert secondary effects on carbon distribution. A large jam associated with the newly recruited wood along Glacier Creek created a sufficient backwater to enhance in-channel sediment accumulation and overbank flow that triggered a multithread pattern along about a hundred-meter length of channel. Some of the toppled trees in the patch blowdowns along North St. Vrain Creek also triggered the formation of secondary channels. Multithread channel segments are relatively rare in the narrowly confined headwater valleys common in RMNP, and are almost always associated with channel-spanning logjams [*Wohl*, 2011]. Where the combined effects of a slightly wider valley bottom and closely spaced in-channel obstructions create multithread channels and overbank flow, a substantial floodplain carbon sink [living and dead vegetation and floodplain soils total 600–800 Mg C/ha in old-growth forest] can result from deposition of wood and finer organic matter that remains in storage for up to thousands of years [*Wohl et al*., 2012] (supporting information Figure 1).

4.2. Soil and Organic Carbon Redistribution in the Forest

[24] Across all sites, the volume of soil associated with individually uprooted trees varied widely, from 0.004 to 4.2 m^3, and averaged 0.6 m^3 per tree. Rootwad volume correlated well with tree diameter at breast height both at a site and across all sites (supporting information Figure 2), as demonstrated in studies from other regions [*Cremeans and Kalisz*, 1988; *Gallaway et al*., 2009; *Lenart et al*., 2010]. Using patch size to assess uprooted soil volume on a per area basis, the blowdown moved 0.03 to 0.04 m^3 soil per m^2 of surface area, or 450–600 t/ha (assuming an average soil bulk density of 1.5 g/cm^3; *Wohl et al*., 2012). Much of this soil, however, will not be moved off-site. Observations of older uprooted trees indicate that some soil can adhere to upturned root plates for nearly a decade. The very limited rainfall and slope wash or overland flow at these high-elevation, snow-dominated sites suggests that cohesive mineral soil eroded from the upturned root plate will not necessarily be transported far across the surface over a period of several years to a few decades.

[25] Soil on upturned root plates at the Glacier and North St. Vrain Creek sites had total organic carbon contents ranging from 3 to 6%, with an average value of 4.4%. The adjacent, undisturbed soil organic layer and uppermost mineral soil varied from 10 to 19% total organic carbon (TOC), and averaged 14.6% (supporting information Figure 3). The significant difference between the populations likely reflects drying, oxidation and loss of organic carbon from the soil exposed on the root plates [*Davidson and Janssens*, 2006], as well as erosion of fine-grained organic material from the upturned root plates during snowmelt and rainfall (the individual blowdowns occurred between November 2011

and February 2012, and sampling occurred during July 2012). The litter and duff in the exposed soil are likely to be more readily eroded during rainfall and snowmelt than the mineral soil adhering to the upturned roots. Masses of 450–600 t/ha of soil equate to ~20–26 Mg C/ha assuming 4.4% TOC, and ~66–88 Mg C/ha assuming 14.6% TOC.

[26] In addition to soil carbon, the blowdown altered the distribution of carbon within living and downed trees. Volume of wood toppled per unit area varied from 0.04 m^3 wood/m^2 surface area in low-severity blowdown patches to 0.09–0.11 m^3/m^2 in high-severity patches along Glacier and North St. Vrain Creeks (Table 1). Assuming average wood density of 400 kg/m^3 [*Forest Products Laboratory*, 2010] and organic carbon content of 50%, this equates to ~80 Mg C/ha in low-severity blowdown areas and ~200 Mg C/ha in high-severity blowdown areas. Of the 33 ha affected by blowdown along Glacier Creek, about half (14 ha) experienced high severity blowdown with > 50% tree mortality. Using the values for low- and high-severity blowdowns estimated above, this suggests that as much as ~ 5930 Mg of wood and soil C could have been redistributed during the 2011 blowdown along Glacier Creek.

4.3. Blowdown Carbon Redistribution in Relation to Total Biomass and Other Types of Disturbance

[27] Values of aboveground (AG) tree carbon for subalpine forests in the southern Rocky Mountains provide perspective regarding the estimated masses of carbon redistribution during the 2011–2012 patch blowdowns. *Binkley et al*. [2003] estimated AG tree carbon stocks averaging 127 Mg C/ha (range 65–244) for old-growth, subalpine spruce-fir forests in north-central Colorado. Other studies in the region indicate that AG tree carbon averages ~ 30% of total ecosystem carbon [*Arthur and Fahey*, 1992; *Bradford et al*., 2008].

[28] Based on these numbers, blowdowns such as the 2011–2012 events within RMNP can redistribute a substantial mass of carbon locally, by subaerially exposing carbon from wet soils and killing trees. In high-severity blowdown patches, the mass of carbon affected per unit area can be close to the total aboveground tree carbon at the site (Table 1 and supporting information Table 3), and carbon redistribution can approach half the total biomass in even low-severity blowdown patches. The great majority of carbon redistributed during blowdowns is in the form of trees that are toppled (Table 1), altering primarily live biomass to dead biomass and shifting the net ecosystem carbon balance toward greater decomposition.

[29] Also relevant to understanding the effects of blowdowns on carbon redistribution are changes with time following disturbance. Comparing forest stands of diverse age and disturbance history, *Bradford et al*. [2008] found that ecosystem carbon stocks, live biomass increment, and total decomposition all increase with time since disturbance, with the greatest change occurring during the first 100 years after a disturbance. Net ecosystem carbon balance, however, decreases after disturbance. This likely reflects the fact that trees comprise greater than 80% of live biomass and tree primary production equals nearly 70% of total production, so that trees killed and left to decompose — as in a blowdown — can create negative net ecosystem carbon balance [*Bradford et al*., 2008].

[30] Lack of knowledge regarding recurrence intervals of blowdowns limits estimates of carbon redistribution relative to net primary productivity or total decomposition on an annual basis, as well as estimates of the importance of blowdowns relative to other forms of disturbance that can alter net ecosystem carbon balance. Stand-replacing fires recur at intervals of 100–500 years for a given small area (< 1 km^2) in subalpine forests of the southern Rocky Mountains, spruce beetle outbreaks recur at intervals of 70–100 years, and mountain pine beetle outbreaks recur at intervals of 50–100 years [*Veblen*, 2000]. The greater susceptibility of older trees to blowdown suggests an average recurrence interval > 100 years within a given small area of forest. As a first-order approximation, a recurrence interval of 100 years for a high-severity blowdown equates to 2.2 Mg C/ha/yr for wood alone, whereas a recurrence interval of 200 years equates to 1.1 Mg C/ha/yr, and a very conservative estimate of a 400-year recurrence interval equates to 0.6 Mg C/ha/yr.

[31] The effects of the blowdowns documented here on carbon mass per unit area can also be compared to other types of disturbance. Wildfires, like blowdowns, can vary substantially in spatial extent and severity, resulting in complete or partial mortality of trees within a given forest stand. *Pfeifer et al*. [2011] found that aboveground tree carbon in lodgepole pine of central Idaho was reduced 31–83% following a mountain pine beetle outbreak. At a larger spatial scale (~84,000 km^2), the 2005 Hurricane Katrina caused an average 20% tree mortality in the most severely damaged forests in the southeastern United States [*Chapman et al*., 2008], although *Uriarte and Papaik* [2007] infer up to 70% mortality for southern New England forests affected by a hurricane with a Fujita index of F3. Uncertainty regarding the recurrence interval of blowdowns complicates direct comparison of the magnitude of their effect on carbon pools relative to other types of disturbance through time, but the effect per unit area appears to be comparable to insect infestations, less severe wildfires, and the most severe hurricanes.

4.4. Blowdowns and Carbon Redistribution in a Warming Climate

[32] Various factors appear to be responsible for an increase in background mortality rates within old-growth forests in the western United States [*van Mantgem et al*., 2009]. Many of these factors, such as water deficits, drought stress, and pathogens, weaken trees and make them more susceptible to blowdowns. Blowdowns in the Southern Rockies are relatively frequent events that may become more frequent and/or severe in future as a result of warming climate and complex interactions with other forms of disturbance.

[33] Warming climate may result in more severe storms and shifts in storm tracks [*Fowler and Hennessy*, 1995; *Karl et al*., 1995; *Mearns et al*., 1995; *Easterling et al*., 2000]. Although local-scale winds are below the resolution of many climate models, increasing temperatures correlate with increased intensity of atmospheric convective processes, including severe winds [*Dale et al*., 2001]. As spring time becomes warmer, snowpacks melt more rapidly, rainfall replaces snow at lower elevations, and peak stream flow occurs earlier in the season at many sites across the western United States [*Mote et al*., 2005; *Regonda et al*., 2005; *Stewart et al*., 2005]. Strong winds occurring late in the winter or early in the spring are thus more likely to occur when soils are wet and saturated, rather than frozen. Drought-stressed trees can also be weakened and more susceptible to

blowdowns and other disturbances [*Hanson and Weltzin*, 2000], and climate models indicate that droughts will become more prolonged and intense in the western United States [*Easterling et al*., 2000].

[34] Blowdowns may also become more common as different types of disturbance interact. Beetle-infested trees are widespread in the Southern Rockies. These trees can be more susceptible to blowdown because the beetles weaken and eventually kill the trees, and because tree mortality from beetles opens up once-contiguous forest canopies [*Klutsch et al*., 2009; *Hicke et al*., 2012] so that trees that did not grow to be wind-firm become exposed to winds. Warmer temperatures promote beetle infestations by favorably influencing the life cycle of the insects and via drought-related declines in the tree's ability to withstand the insects [*Veblen*, 2000; *Bentz et al*., 2010].

[35] Some of the forest stands in northern Colorado affected by blowdowns during the past 15 years have subsequently burned more severely than unaffected stands during wildfires [*Kulakowski and Veblen*, 2007]. Fire-injured trees can also be more susceptible to attack by beetles and to blowdown [*Veblen*, 2000]. The fire season is likely to start earlier in the spring and last longer into the autumn in the western U.S. in future [*Flannigan et al*., 2000].

[36] Consideration of the potential effects of changing climate and interactions between blowdowns and other forms of forest disturbance indicates the potential for complex, nonlinear changes in forest disturbance regime in future [*Turner*, 2010] (Figure 2). If warmer climate makes forests more susceptible to fires, insects, and blowdowns, increased frequency and intensity of each of these three major types of disturbance could increase the frequency and intensity of the other two types of disturbance [*Schmid and Hinds*, 1974; *Veblen et al*., 1989; *Veblen*, 2000; *Kulakowski and Veblen*, 2007]. Interactions among different types of disturbance and forest dynamics are not well quantified for diverse forest ecosystems [*Turner*, 2010; *Edburg et al*., 2012; *Hicke et al*., 2012; *Kasischke et al*., 2013], however, and the net effect on organic carbon distribution of changes in overall disturbance regime remains unknown.

5. Conclusions

[37] Most subalpine forests in the southern Rocky Mountains are strongly shaped by natural disturbances with long (> 100–600 years) return intervals, particularly at higher elevations [*Veblen*, 2000; *Kulakowski and Veblen*, 2003; *Sibold et al*., 2006]. However, data from unmanaged old-growth forests across the western United States indicate that background mortality rates have increased rapidly in recent decades, likely as a result of climate warming that creates increasing water deficits and drought stress on trees, along with enhanced growth and reproduction of insects and pathogens that attack trees [*van Mantgem et al*., 2009]. Under these circumstances, enhanced understanding of the magnitude and frequency of blowdowns, and the manner in which these disturbances interact with other disturbances and alter carbon dynamics, becomes important.

[38] The carbon balance of a forest ecosystem is fundamentally linked to the cycle of disturbance and recovery [*Frolking et al*., 2009; *McKinley et al*., 2011]. Blowdowns can be an important component of this cycle because they create a rapid, large transfer of biomass from living to dead material. As this dead material decomposes, the forest can become a carbon source to the atmosphere [*Harmon et al*., 1990; *Janisch and Harmon*, 2002; *Turner*, 2010], not least because most forest biomass is contained within plants, and particularly within the wood of canopy trees and the mass of downed trees not yet incorporated into soil organic matter [*Frolking et al*., 2009; *McKinley et al*., 2011; *Wohl et al*., 2012]. Decomposition of downed wood is quite slow in the relatively arid environment of Colorado subalpine forests, although most of the change in carbon stocks and fluxes occurs within the first 100 years following stand-replacing disturbance [*Bradford et al*., 2008]. Growth of new trees stores carbon even while decomposition of dead trees releases carbon, and average forest carbon stocks are relatively stable over large spatial and long temporal scales, in part because a single disturbance is unlikely to affect an entire landscape simultaneously [*McKinley et al*., 2011]. The potential for significantly increased frequency and severity of disturbance, however, raises the possibility that average forest carbon stocks could change during the next few decades. Given the large amounts of carbon that patch blowdowns can transfer from living to dead biomass, and the initially higher rates of carbon flux following disturbance, increased frequency and/or severity of blowdowns in old-growth subalpine forests of the southern Rockies could significantly alter terrestrial carbon sources.

[39] Patch blowdowns in the southern Rocky Mountains of Colorado during the winter of 2011–2012 represent a type of forest disturbance that may increase in extent and/or frequency under a warmer, drier climate. The blowdowns redistributed from 106 to 308 Mg of organic carbon per hectare in the form of displaced soil and downed trees in old-growth forests. These values represent a substantial proportion of the total carbon in such forests.

[40] The effects of this carbon redistribution are not straightforward. Moist, organic-rich soil exposed through tree uprooting can result in carbon loss through oxidation and erosion [*Trumbore and Czimczik*, 2008; *Wohl et al*., 2012]. Mortality of toppled trees can also result in carbon loss through wood decomposition. Trees recruited into a river, however, can facilitate the formation of logjams and floodplain deposition and storage of organic carbon. Development of a floodplain and retention of instream wood strongly depend on valley geometry. Only relatively wide, low gradient valley segments are likely to store significant quantities of organic matter over periods of hundreds to thousands of years [*Wohl et al*., 2012; *Wohl and Beckman*, 2013a]. Consequently, the effects of patch blowdowns on carbon redistribution partly depend on the geomorphic setting in which the blowdown occurs. Increased disturbance and mortality of old-growth subalpine forests in the region may result in greater instream and floodplain retention of organic carbon in wider valley segments. Although these segments constitute only 25% of the total river length within Rocky Mountain National Park, they store an estimated 75% of the carbon within the channel network [*Wohl et al*., 2012]. Forest mortality resulting from blowdowns on the uplands and along the remainder of the river network is likely to create a larger carbon source than blowdowns in wide valley segments.

[41] Numerous studies have quantified the amount of carbon lost from a system following disturbance, but relatively

few examine how disturbances shape carbon storage in complex ways that reflect site-specific conditions, such as stream and valley geometry. The 2011–2012 blowdowns examined here illustrate how disturbance type and interactions create very different postevent site conditions at diverse sites, with unique consequences for the landscape and carbon dynamics. When asking how a disturbance redistributes carbon in a forested landscape, to quote *McKinley et al*. [2011, p. 1917], "The answer is: it depends."

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References

Alexander, R. R. (1964), Minimizing windfall around clear cuttings in spruce-fir forests, *For. Sci.*, *10*, 130–142.

Alexander, R. R. (1987), Ecology, silviculture and management of the Engelmann spruce-subalpine fir type in the central and southern Rocky Mountains. USDA Forest Service, Agricultural Handbook No. 659.

Amiro, B. D., et al. (2010), Ecosystem carbon dioxide fluxes after disturbance in forests of North America, *J. Geophys. Res.*, *115*, G00K02, doi:10.1029/2010JG001390.

Ancelin, P., B. Courbaud, and T. Fourcaud (2004), Development of an individual tree-based mechanical model to predict wind damage within forest stands, *For. Ecol. Manage.*, *203*, 101–121.

Arthur, M. A., and T. J. Fahey (1992), Biomass and nutrients in an Engelmann spruce-subalpine fir forest in north central Colorado: Pools, annual production, and internal cycling, *Can. J. For. Res.*, *22*, 315–325.

Aufdenkampe, A. K., E. Mayorga, P. A. Raymond, J. M. Melack, S. C. Doney, S. R. Alin, R. E. Aalto, and K. Yoo (2011), Riverine coupling of biogeochemical cycles between land, oceans, and atmosphere, *Front. Ecol. Environ.*, *9*, 53–60.

Baker, W. L., P. H. Flaherty, J. D. Lindemann, T. T. Veblen, K. S. Eisenhart, and D. W. Kulakowski (2002), Effect of vegetation on the impact of a severe blowdown in the southern Rocky Mountains, USA, *For. Ecol. Manage.*, *168*, 63–75.

Battin, T. J., L. A. Kaplan, S. Findlay, C. S. Hopkinson, E. Marti, A. I. Packman, J. D. Newbold, and F. Sabater (2008), Biophysical controls on organic carbon fluxes in fluvial networks, *Nat. Geosci.*, *1*, 95–100.

Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold (2010), Climate change and bark beetles of the western United States and Canada: Direct and indirect effects, *BioScience*, *60*, 602–613.

Binkley, D., U. Olsson, R. Rochelle, T. Stohlgren, and N. Nikolov (2003), Structure, production, and resource use in some old-growth spruce/fir forests in the Front Range of the Rocky Mountains, USA, *For. Ecol. Manage.*, *172*, 271–279.

Bradford, J. B., R. A. Birdsey, L. A. Joyce, and M. G. Ryan (2008), Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests, *Global Change Biol.*, *14*, 2882–2897.

Brummer, C. J., T. B. Abbe, J. R. Sampson, and D. R. Montgomery (2006), Influence of vertical channel change associated with wood accumulations on delineating channel migration zones, Washington, USA, *Geomorphology*, *80*, 295–309.

Burns, S. F. (1981), Windthrow in a mountain beech forest, Craigieburn Range, New Zealand. Preliminary report to the Forest Research Institute, Ilam, N. Z. (cited in *Schaetzl et al*., 1990).

Burns, S. F., and P. J. Tonkin (1987), Erosion and sediment transport by windthrow in a mountain beech forest, New Zealand, in *Erosion and Sedimentation in the Pacific Rim*, edited by R. C. Beschta et al., pp. 279–290, IAHS 165, Wallingford, U. K.

Chambers, J. Q., J. I. Fisher, H. Zeng, E. L. Chapman, D. B. Baker, and G. C. Hurtt (2007), Hurricane Katrina's carbon footprint on U.S. Gulf Coast forests, *Science*, *318*, 1107.

Chapman, E. L., J. Q. Chambers, K. F. Ribbeck, D. B. Baker, M. A. Tobler, H. Zeng, and D. A. White (2008), Hurricane Katrina impacts on forest trees of Louisiana's Pearl River basin, *For. Ecol. Manage.*, *256*, 883–889.

Cole, J. J., et al. (2007), Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget, *Ecosystems*, *10*, 171–184.

Collins, B. D., D. R. Montgomery, K. L. Fetherston, and T. B. Abbe (2012), The floodplain large-wood cycle hypothesis: A mechanism for the physical and biotic structuring of temperate forested alluvial valleys in the North Pacific coastal ecoregion, *Geomorphology*, *139-140*, 460–470.

Cremeans, D. W., and P. J. Kalisz (1988), Distribution and characteristics of windthrow microtopography on the Cumberland Plateau of Kentucky, *Soil Sci. Soc. Am. J.*, *52*, 816–821.

Dale, V. H., et al. (2001), Climate change and forest disturbances, *BioScience*, *51*(9), 723–734.

Davidson, E. A., and I. V. Janssens (2006), Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, *Nature*, *440*(9), 165–173.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns (2000), Climate extremes: Observations, modeling, and impacts, *Science*, *289*, 2068–2074.

Edburg, S. L., J. A. Hicke, P. D. Brooks, E. G. Pendall, B. E. Ewers, U. Norton, D. Gochis, E. D. Gutmann, and A. J. H. Meddens (2012), Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes, *Front. Ecol. Environ.*, *10*, 416–424.

Flaherty, P. H. (2000), Effects of pre-disturbance forest vegetation on the impacts of a catastrophic blowdown in a Rocky Mountain subalpine landscape. MS thesis, University of Wyoming, Laramie.

Flannigan, M. D., B. J. Stocks, and B. M. Wotton (2000), Climate change and forest fires, *Sci. Total Environ.*, *262*, 221–229.

Forest Products Laboratory (2010), Wood Handbook: Wood as an Engineering Material, USDA Forest Products Laboratory General Tech Report FPL-GTR-190, Madison, Wisc.

Fowler, A. M., and K. J. Hennessy (1995), Potential impacts of global warming on the frequency and magnitude of heavy precipitation, *Nat. Hazards*, *11*, 283–303.

Frolking, S., M. W. Palace, D. B. Clark, J. Q. Chambers, H. H. Shugart, and G. C. Hurtt (2009), Forest disturbance and recovery: A general review in the context of spaceborne remote sensing of impacts on aboveground biomass and canopy structure, *J. Geophys. Res.*, *114*, G00E02, doi:10.1029/2008JG000911.

Gallaway, J. M., Y. E. Martin, and E. A. Johnson (2009), Sediment transport due to tree root throw: Integrating tree population dynamics, wildfire and geomorphic response, *Earth Surf. Processes Landforms*, *34*, 1255–1269.

Glidden, D. (1982), *Winter Wind Studies in Rocky Mountain National Park*, Rocky Mountain Nature Association, Estes Park, Colo.

Hanson, P. J., and J. F. Weltzin (2000), Drought disturbance from climate change: Response of United States forests, *Sci. Total Environ.*, *262*, 205–220.

Harmon, M. E., W. K. Ferrell, and J. F. Franklin (1990), Effects on carbon storage of conversion of old-growth forests to young forests, *Science*, *247*, 699–702.

Harmon, M. E., B. Bond-Lamberty, J. Tang, and R. Vargas (2011), Heterotrophic respiration in disturbed forests: A review with examples from North America, *J. Geophys. Res.*, *116*, G00K04, doi:10.1029/2010JG001495.

Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler (2012), Effects of bark beetle-caused tree mortality on wildfire, *For. Ecol. Manage.*, *271*, 81–90.

Hilimire, K., J. C. B. Nesmith, A. C. Caprio, and R. Milne (2013), Attributes of windthrown trees in a Sierra Nevada mixed-conifer forest, *West. J. Appl. For.*, *28*, 85–88.

Janisch, J. E., and M. E. Harmon (2002), Successional changes in live and dead wood carbon stores: Implications for net ecosystem productivity, *Tree Physiol.*, *22*, 77–89.

Jeffries, R., S. E. Darby, and D. A. Sear (2003), The influence of vegetation and organic debris on flood-plain sediment dynamics: Case study of a low-order stream in the New Forest, England, *Geomorphology*, *51*, 61–80.

Karl, T. R., R. W. Knight, and N. Plummer (1995), Trends in high-frequency climate variability in the twentieth century, *Nature*, *377*, 217–220.

Kasischke, E. S., B. D. Amiro, N. N. Barger, N. H. F. French, S. J. Goetz, G. Grosse, M. E. Harmon, J. A. Hicke, S. Liu, and J. G. Masek (2013), Impacts of disturbance on the terrestrial carbon budget of North America, *J. Geophys. Res. Biogeosci.*, *118*, 303–316, doi:10.1002/jgrg.20027.

Klutsch, J. G., J. F. Negrón, S. L. Costello, C. C. Rhoades, D. R. West, J. Popp, and R. Caissie (2009), Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dedroctonus ponderosae* Hopkins) outbreak in Colorado, *For. Ecol. Manage.*, *258*, 641–649.

Kulakowski, D., and T. T. Veblen (2002), Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest, *J. Ecol.*, *90*, 806–819.

Kulakowski, D., and T. T. Veblen (2003), Subalpine forest development following a blowdown in the Mount Zirkel Wilderness, Colorado, *J. Veg. Sci.*, *14*, 653–660.

Kulakowski, D., and T. T. Veblen (2007), Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests, *Ecology*, *88*, 759–769.

Law, B. E., D. Turner, J. Campbell, O. J. Sun, S. Van Tuyl, W. D. Ritts, and W. B. Cohen (2004), Disturbance and climate effects on carbon stocks and fluxes across western Oregon USA, *Global Change Biol.*, *10*, 1429–1444.

Lenart, M. T., D. A. Falk, F. N. Scatena, and W. R. Osterkamp (2010), Estimating soil turnover rate from tree uprooting during hurricanes in Puerto Rico, *For. Ecol. Manage.*, *259*, 1076–1084.

Lindemann, J. D., and W. L. Baker (2001), Attributes of blowdown patches from a severe wind event in the southern Rocky Mountains, USA, *Landscape Ecol.*, *16*, 313–325.

Martin, T. J., and J. Ogden (2006), Wind damage and response in New Zealand forests: A review, *N. Z. J. Ecol.*, *30*, 295–310.

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.

Mearns, L. O., F. Giorgi, L. McDaniel, and C. Shields (1995), Analysis of daily variability of precipitation in a nested regional climate model: Comparison with observations and doubled CO_2 results, *Global Planet. Change*, *10*, 55–78.

Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lettenmaier (2005), Declining mountain snowpack in western North America, *Bull. Am. Meteorol. Soc.*, *86*, 39–49.

Nelson, D. W., and L. E. Sommers (1982), Total carbon, organic carbon, and organic matter, in *Methods of Soil Analysis, part 2, Chemical and Microbiological Properties*, 2nd ed., edited by A. L. Sparks, pp. 539–579, American Society of Agonomy, Inc, Madison, Wisc.

Nicoll, B. C., A. Achim, S. Mochan, and B. A. Gardiner (2005), Does steep terrain influence tree stability? A field investigation, *Can. J. For. Res.*, *35*, 2360–2367.

NRCS (1996), Method 6E1c, in Soil Survey Laboratory Methods. Soil Survey Investigations Report No. 42, version 3.0. USDA, NRCS, National Soil Survey Center.

NRCS (2006), Soil survey of Rocky Mountain National Park, Colorado, available online at http://soildatamart.nrcs.usda.gov/Manuscripts/CO651/0/Soil%20Survey%20of%20Rocky%20Mountain%20National%20Park,%20CO.pdf

Peterson, C. J. (2000), Catastrophic wind damage to North American forests and the potential impact of climate change, *Sci. Total Environ.*, *262*, 287–311.

Peterson, C. J. (2007), Consistent influence of tree diameter and species on damage in nine eastern North America tornado blowdowns, *For. Ecol. Manage.*, *250*, 96–108.

Pfeifer, E. M., J. A. Hicke, and A. J. H. Meddens (2011), Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States, *Global Change Biol.*, *17*, 339–350.

Regonda, S. K., B. Rajagopalan, M. Clark, and J. Pitlick (2005), Seasonal shifts in hydroclimatology over the western United States, *J. Clim.*, *18*, 372–384.

Reid, L. M. (1981), Sediment production from gravel-surfaced forest roads, Clearwater Basin, Washington. Fisheries Research Institute Report, No. FRI-UW-8108.

Rich, R. L., L. E. Frelich, and P. B. Reich (2007), Wind-throw mortality in the southern boreal forest: Effects of species, diameter and stand age, *J. Ecol.*, *95*, 1261–1273.

Richards, P. J., J. M. Hohenthal, and G. S. Humphreys (2011), Bioturbation on a south-east Australian hillslope: Estimating contributions to soil flux, *Earth Surf. Processes Landforms*, *36*, 1240–1253.

Schaetzl, R. J., S. F. Burns, D. L. Johnson, and T. W. Small (1989a), Tree uprooting: Review of impacts on forest ecology, *Vegetatio*, *79*, 165–176.

Schaetzl, R. J., D. L. Johnson, S. F. Burns, and T. W. Small (1989b), Tree uprooting: Review of terminology, process, and environmental implications, *Can. J. For. Res.*, *19*, 1–11.

Schaetzl, R. J., S. F. Burns, T. W. Small, and D. L. Johnson (1990), Tree uprooting: Review of types and patterns of soil disturbance, *Phys. Geogr.*, *11*, 277–291.

Schmid, J. M., and T. E. Hinds (1974), Development of spruce-fir stands following spruce beetle outbreaks, USDA Forest Service Research Paper RM-131, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo., 16 pp.

Sibold, J. S., T. T. Veblen, and M. E. González (2006), Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range, *J. Biogeogr.*, *33*, 631–647.

Stewart, I. T., D. R. Cayan, and M. D. Dettinger (2005), Changes toward earlier streamflow timing across western North America, *J. Clim.*, *18*, 1136–1155.

Swanson, F. J., R. L. Fredriksen, and F. M. McCorison (1982), Material transfer in a western Oregon forested watershed, in *Analysis of Coniferous Forest Ecosystems in the Western United States*, edited by R. L. Edmonds, pp. 233–266, Hutchinson Ross Publishing Co., Stroudsburg, Pa.

Trumbore, S. E., and C. I. Czimczik (2008), An uncertain future for soil carbon, *Science*, *321*, 1455–1456.

Turner, M. G. (2010), Disturbance and landscape dynamics in a changing world, *Ecology*, *91*(10), 2833–2849.

Urata, T., M. Shibuya, A. Koizumi, H. Torita, and J. Y. Cha (2012), Both stem and crown mass affect tree resistance to uprooting, *J. For. Res.*, *17*, 65–71.

Uriarte, M., and M. Papaik (2007), Hurricane impacts on dynamics, structure and carbon sequestration potential of forest ecosystems in southern New England, USA, *Tellus*, *59A*, 519–528.

Van Mantgem, P. J., et al. (2009), Widespread increase of tree mortality rates in the western United States, *Science*, *323*, 521–524.

Veblen, T. T. (2000), Disturbance patterns in southern Rocky Mountain forests, in *Forest Fragmentation in the Southern Rocky Mountains*, edited by R. L. Knight et al., pp. 3–54, University Press of Colorado, Boulder, Colo.

Veblen, T. T., and J. A. Donnegan (2005), Historical range of variability for forest vegetation of the national forests of the Colorado Front Range. Final report, Agreement No. 1102-0001-99-033, USDA Forest Service, Rocky Mountain Region, Golden, Colo., 151 pp.

Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus (1989), Blowdown and stand development in a Colorado subalpine forest, *Can. J. For. Res.*, *19*, 1218–1225.

Veblen, T. T., K. S. Hadley, and M. S. Reid (1991), Disturbance and stand development of a Colorado subalpine forest, *J. Biogeogr.*, *18*, 707–716.

Veblen, T. T., D. Kulakowski, K. S. Eisenhart, and W. L. Baker (2001), Subalpine forest damage from a severe windstorm in northern Colorado, *Can. J. For. Res.*, *31*, 2089–2097.

Wohl, E. (2011), Threshold-induced complex behavior of wood in streams, *Geology*, *39*, 587–590.

Wohl, E., and N. Beckman (2013a), Controls on the longitudinal distribution of channel-spanning logjams in the Colorado Front Range, USA, *River Res. Appl.*, doi:10.1002/rra.2624, in press.

Wohl, E., and N. D. Beckman (2013b), Leaky rivers: Implications of the loss of longitudinal fluvial disconnectivity in headwater streams, *Geomorphology*, *205*, 27–35.

Wohl, E., and D. Cadol (2011), Neighborhood matters: Patterns and controls on wood-distribution in old-growth forest streams of the Colorado Front Range, USA, *Geomorphology*, *125*, 132–146.

Wohl, E., and J. R. Goode (2008), Wood dynamics in headwater streams of the Colorado Rocky Mountains, *Water Resour. Res.*, *44*, W09429, doi:10.1029/2007WR006522.

Wohl, E., K. Dwire, N. Sutfin, L. Polvi, and R. Bazan (2012), Mechanisms of carbon storage in mountainous headwater rivers, *Nat. Commun.*, *3*, 1263, doi:10.1038/ncomms2274.

Zeng, H., J. Q. Chambers, R. I. Negrón-Juárez, G. C. Hurtt, D. B. Baker, and M. D. Powell (2009), Impacts of tropical cyclones on U.S. forest tree mortality and carbon flux from 1851 to 2000, *Proc. Natl. Acad. Sci. U. S. A.*, *106*, 7888–7892.