

RESEARCH ARTICLE

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Key Points:

- Hillslope N loss was similar to clear cut harvest
- Riparian removal protected streams from N loss
- N impacts were minimal beyond 5 km in headwater streams

Supporting Information:

- Supporting Information S1
- Data Set S1

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Riparian zones attenuate nitrogen loss following bark beetle-induced lodgepole pine mortality

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Abstract A North American bark beetle infestation has killed billions of trees, increasing soil nitrogen and raising concern for N loss impacts on downstream ecosystems and water resources. There is surprisingly little evidence of stream N response in large basins, which may result from surviving vegetation uptake, gaseous loss, or dilution by streamflow from unimpacted stands. Observations are lacking along hydrologic flow paths connecting soils with streams, challenging our ability to determine where and how attenuation occurs. Here we quantified biogeochemical concentrations and fluxes at a lodgepole pine-dominated site where bark beetle infestation killed 50–60% of trees. We used nested observations along hydrologic flow paths connecting hillslope soils to streams of up to third order. We found soil water NO₃ concentrations increased 100-fold compared to prior research at this and nearby southeast Wyoming sites. Nitrogen was lost below the major rooting zone to hillslope groundwater, where dissolved organic nitrogen (DON) increased by 3–10 times (mean 1.65 mg L⁻¹) and NO₃-N increased more than 100-fold (3.68 mg L⁻¹) compared to preinfestation concentrations. Most of this N was removed as hillslope groundwater drained through riparian soils, and NO₃ remained low in streams. DON entering the stream decreased 50% within 5 km downstream, to concentrations typical of unimpacted subalpine streams (~0.3 mg L⁻¹). Although beetle outbreak caused hillslope N losses similar to other disturbances, up to 5.5 kg ha⁻¹y⁻¹ riparian and in-stream removal limited headwater catchment export to <1 kg ha⁻¹y⁻¹. These observations suggest riparian removal was the dominant mechanism preventing hillslope N loss from impacting streams.

1. Introduction

Montane forests are among the world's most reliable sources of clean water [Brown *et al.*, 2005], but they are increasingly disturbed by drought, fire, and insect infestation. Western North America has experienced rapid and extensive forest mortality due to infestation by several species of native bark beetles, and climate change is expected to enhance infestations [Mitton and Ferrenberg, 2012]. Over the last two decades, bark beetles have infested more than 20 million ha in western North America, similar to the extent of wildfire [Meddens *et al.*, 2012]. Absence of immediate soil disturbance differentiates beetle mortality from more well-studied disturbances (e.g., harvest and fire), challenging our ability to predict impacts on the quality of water resources [Edburg *et al.*, 2012; Mikkelsen *et al.*, 2012, 2013].

Extensive literature from other forest disturbances (e.g., harvest, wind throw, and fire) indicates N is usually lost from hillslope soils and often impacts streams [Bormann *et al.*, 1968; Swank *et al.*, 1981; Bernhardt *et al.*, 2003; Houlton *et al.*, 2003; Jones and Post, 2004; Mast and Clow, 2008]. Nitrogen loss may also occur from N-limited western conifer forests if disturbance creates sufficiently large root gaps to prevent uptake by surviving vegetation [Knight *et al.*, 1991; Parsons *et al.*, 1994]. However, N lost from hillslope soils may not reach the stream if it is taken up by plants or removed via denitrification in riparian buffer zones [Hill, 1996; Vidon and Hill, 2004; Hefting *et al.*, 2005; Ranalli and Macalady, 2010]. Nitrogen reaching the channel may be rapidly attenuated by stream-hyporheic processing, particularly in small headwater streams [Triska *et al.*, 1993; Peterson *et al.*, 2001; Bernhardt *et al.*, 2003]. Within the stream, particulate nitrogen (PN) may represent an important flux following disturbance, though data are sparse [Webster *et al.*, 1990; Kreutzweiser and Capell, 2001; Condon, 2013]. Both dissolved and particulate concentrations are needed to determine whether solutes have been removed or processed into particulate forms [Bernhardt *et al.*, 2003; Brooks *et al.*, 2007; Meixner *et al.*, 2012].

In the recent bark beetle infestation, several mechanisms have been proposed to explain why increased N inputs to the forest floor and N concentrations in soils [Huber, 2005; Morehouse *et al.*, 2008; Clow *et al.*, 2011; Griffin *et al.*, 2011; Griffin and Turner, 2012] have not impacted stream water chemistry in large basins [Clow *et al.*, 2011; Mikkelsen *et al.*, 2013; Rhoades *et al.*, 2013]. First, N may be recycled by soil microbial communities, which appear to be resilient so long as sufficient carbon substrate remains available [Ferrenberg *et al.*, 2014; Kaňa *et al.*, 2015]. Second, surviving vegetation may take up available N if it is scarce, as in many western conifer forests [Fahey *et al.*, 1985]. Vegetation uptake has been observed with thinning treatments [Parsons *et al.*, 1994], predicted by models of bark beetle infestation [Rhoades *et al.*, 2013], and hypothesized in other bark beetle studies [Zimmermann *et al.*, 2000; Clow *et al.*, 2011; Edburg *et al.*, 2012; Mikkelsen *et al.*, 2013]. Finally, N-contaminated stream water from infested catchments may be diluted by mixing with streams from uninfested catchments, obscuring large-scale response [Clow *et al.*, 2011; Mikkelsen *et al.*, 2013]. Evaluating these alternative mechanisms of N attenuation has been limited by a lack of observations along hydrologic flow paths linking soils with large-basin outlets.

Across the majority of forests impacted by the recent North American bark beetle infestation, snowmelt is the dominant hydrologic input [Biederman *et al.*, 2015] and driver of aqueous biogeochemical fluxes [Liu *et al.*, 2008]. Because snowmelt rates rarely exceeds infiltration capacity, meltwater typically recharges shallow hillslope groundwater with short residence times (hours to days), moves laterally down gradient in the subsurface, and serves as the primary source of streamflow [Campbell *et al.*, 1995; Boyer *et al.*, 1997; Lohse *et al.*, 2009; Peters *et al.*, 2011; Brooks *et al.*, 2015]. En route to the stream, water drains across riparian soils (i.e., riparian groundwater), influencing stream chemistry [Hooper *et al.*, 1998; Bishop *et al.*, 2004]. Stream water may have longer residence times than suggested by channel velocity due to exchange with the hyporheic zone, facilitating biogeochemical retention and processing, particularly in small streams [Alexander *et al.*, 2000; Peterson *et al.*, 2001; Acuña *et al.*, 2014]. Currently, published observations consist of N concentrations and fluxes primarily for soils and the outlets of large basins, limiting our understanding of where and how N is attenuated between these extremities of the hydrologic flow path.

The primary objective of this study was to identify where on the landscape N attenuation occurred within nested headwater catchments in which all contributing areas were impacted by similarly high degrees of forest mortality in order to constrain processes associated with limited N export previously reported in large basins. Specifically, we addressed three hypotheses. H1: N would not be lost from hillslope soils due to uptake by surviving vegetation. Such N loss prevention which has been observed following forest thinning [Parsons *et al.*, 1994] would imply that thinning is an appropriate proxy for bark beetle disturbance. In the event that N was lost from the hillslopes (H1 rejected), we hypothesized H2: N would be removed as hillslope water drained through soils of intact riparian buffer zones. Riparian N removal would suggest denitrification and/or uptake by riparian plants, which are not beetle hosts. If significant N loss to the stream did occur, we hypothesized (H3) stream-hyporheic processing would significantly reduce N export within headwater catchments (i.e., within the 5 km channel length of the largest headwater catchment studied here). To evaluate H3, we measured both dissolved and particulate N forms in stream water. N removal or retention by riparian (H2) and stream-hyporheic processes (H3) have not been explored in the context of the bark beetle epidemic despite the prominent role of these mechanisms in N attenuation reported elsewhere [Bormann *et al.*, 1968; Triska *et al.*, 1993; Hill, 1996; Peterson *et al.*, 2001; Bernhardt *et al.*, 2003; Hood *et al.*, 2003]. If none of these mechanisms (H1–H3) was sufficient to prevent N export from our heavily infested headwater study catchments, this would lend indirect support for the idea that dilution by water from unimpacted headwater catchments obscures impacts in larger basins further downstream.

2. Study Site

The 725 ha Chimney Park site is located 3 km southeast of Fox Park, Wyoming in the Medicine Bow National Forest, along the eastern edge of the central Rocky Mountains at 41°4'N, 106°7'W (Figure 1). Chimney Park and other nearby sites have been extensively studied in a body of work focused on nitrogen cycling and the effects of disturbance in lodgepole pine ecosystems [Fahey *et al.*, 1985; Knight *et al.*, 1985, 1991; Fahey and Yavitt, 1988; Parsons *et al.*, 1994]. Prior reports indicate annual N wet deposition in this area of 2.5 kg ha⁻¹ [Fahey *et al.*, 1985] to 3.7 kg ha⁻¹ [Burns, 2003]. The climate is characterized by cold winters with continuous snow cover typically lasting from October to May or June and mean annual air temperatures of 1–3°C. Mean

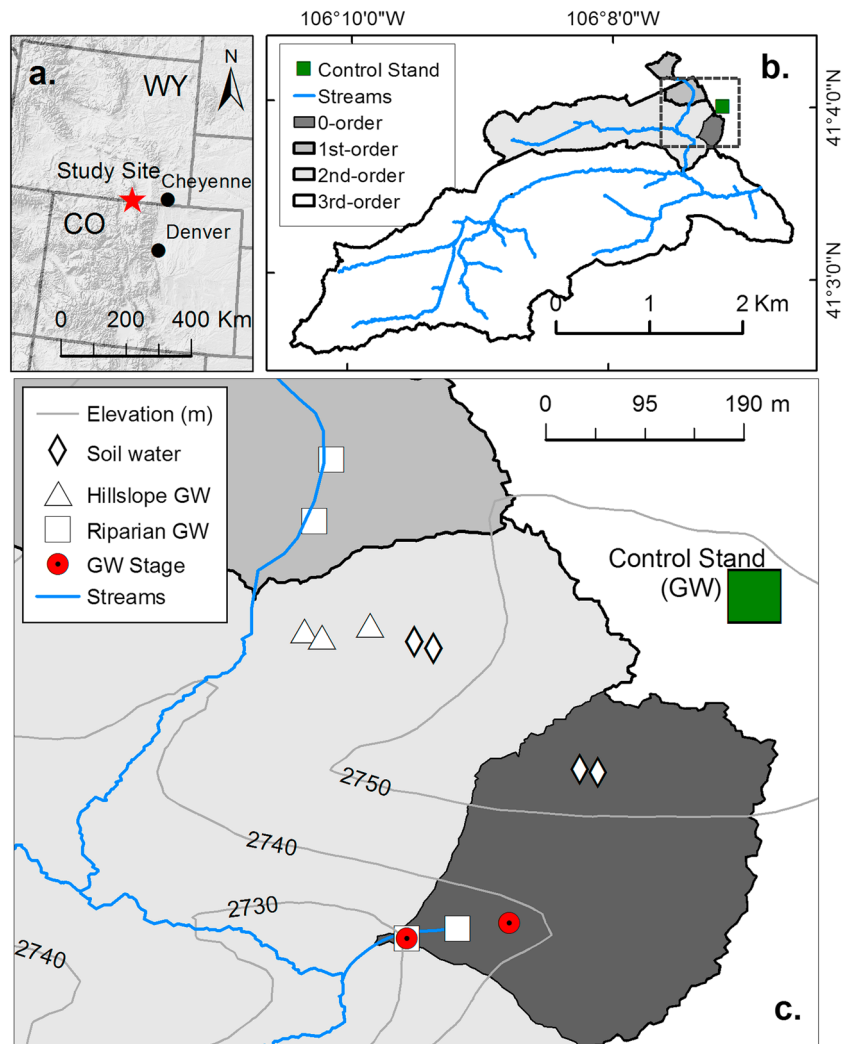


Figure 1. Site maps showing (a) the location of the beetle-impacted study site along the Front Range of the Rocky Mountains in southern Wyoming, U.S., (b) a site map showing nested catchments with streams of zero–third order (catchments indicated by progressively lighter shades), and (c) solution sampling locations along the hydrologic flow path including soil water lysimeters, hillslope groundwater (GW) wells, riparian groundwater wells, and the stream network. Groundwater stage (red circles) was measured in hillslope and riparian wells in the zero-order catchment. Soil water was sampled in six profiles (only four markers shown due to proximity) from the mineral soil at depths of 5, 25, and 60 cm.

annual precipitation is 650 mm, of which about 400 mm is snowfall. The site contains an AmeriFlux network eddy covariance tower (US-CPk; amerflux.lbl.gov) and a cluster of precipitation gages deployed by the National Center for Atmospheric Research (<http://www.ral.ucar.edu/projects/winter>).

The study site is located on a broad plateau at an elevation of 2750 m in gentle terrain with slopes averaging 5–9%. Soils are well-drained, shallow sandy loam Typic Haplocryalfs derived from residuum of granite, amphibolite, and felsic gneiss [Parsons *et al.*, 1994], with a consolidated, low-permeability layer below a depth of 120–180 cm (observed in this study and reported by Knight *et al.* [1985]). Overstory is dominated by lodgepole pine (*Pinus contorta*) aged 90–120 years since the previous stand-replacing disturbance [Knight *et al.*, 1985], with >90% of roots found in the top 40 cm of soil and 75% in the top 20 cm [Pearson *et al.*, 1984]. In the intensively studied hillslopes of the zero-order and first-order catchments (Figure 1), forest height averaged 11.1 m, mean diameter at breast height was 14 cm, and tree density was 2500 stems ha⁻¹. In addition to lodgepole pine, there is <10% abundance of ponderosa pine (*Pinus ponderosa*) and quaking aspen (*Populus tremuloides*). Understory is comprised of perennial forbs and grasses, with occasional tree and shrub seedlings [Norton *et al.*, 2015]. Relatively level riparian areas adjacent to perennial streams are dominated by

Table 1. Physical Characteristics of the Study Catchments

Catchment	Area (ha)	Tree Mortality (%)	Main Channel Length (m)	Main Channel Average Slope (%)	Average Hillslope Slope (stdev) (%)	Average Riparian Width (m)
Zero order	10	50	75	9.4	7.6 (5.5)	10
First order	15	62	725	1.3	5.3 (4.3)	20
Second order	136	61	3257	1.8	7.9 (6.5)	40
Third order	725	52	4581	2.5	8.3 (6.5)	40

phreatophytes including diverse sedges, grasses, and autumn willow (*Salix serissima*), none of which is directly affected by bark beetles.

The region suffered a severe outbreak of several indigenous pine beetle species beginning around 2004 [Meddens and Hicke, 2014]. Chimney Park was infested by mountain pine beetle (*Dendroctonus Ponderosae*) primarily in 2007–2008. Tree mortality averaged 50–62% across the catchments studied here but reached up to 80% on the intensively studied hillslopes. Observations were made in the fourth and fifth years after outbreak (2011 and 2012). Most of the killed trees had passed the red mortality phase, during which dead needles are retained and trees appear red in color, and entered the grey phase, when needles have fallen. Recent research at this site has quantified bark beetle impacts on snow accumulation [Biederman et al., 2014b], catchment-scale evapotranspiration and streamflow [Biederman et al., 2014a], land-atmosphere exchange of carbon dioxide and water [Reed et al., 2014], and soil biogeochemical cycling [Borkhuu et al., 2015; Norton et al., 2015]. Table S1 summarizes several biogeochemical parameters of needlefall, organic, and mineral soils measured by Norton et al. [2015] in 2009, 2 years after beetle outbreak in a lodgepole stand ~500 m northeast of our study catchment boundary (not shown). The C/N ratios of needlefall and the organic layer were 69 and 30, respectively, typical of N limitation in the forest floor of lodgepole pine ecosystems [Fahey et al., 1985]. Mineral soil C/N ratio averaged 14.

3. Methods

3.1. Experimental Overview

We address the study hypotheses by quantifying biogeochemical concentrations and fluxes along hydrological flow paths spanning: soil water, hillslope groundwater, riparian groundwater, and streams of zero to third order. Observations of soil water and groundwater were made within study hillslopes that were in turn nested within catchments of zero, first, second, and third order, where riparian groundwater and stream water were sampled (Figure 1 and Table 1). The zero-order catchment was a convergent area drained by an ephemeral stream that flowed only during the snowmelt period. To investigate spatial patterns that emerged from preliminary stream chemistry results, we made additional observations from the outlet of a third-order stream (2012 only) as well as intermediate reach locations for synoptic sampling. We additionally sampled hillslope groundwater from a lodgepole stand that appeared to be regenerating from experimental harvest (circa 1985) and was not infested by bark beetles. This 20 × 40 m control stand was located on relatively level terrain ~300 m east from the study hillslope of the second-order catchment (Figure 1c).

3.2. Catchment Characteristics

Forest mortality in each catchment was quantified using a QuickBird image (Satellite Imaging Corporation) acquired in August 2011 (Table 1). True color imagery was used to train and evaluate a maximum likelihood classifier with green band, Normalized Difference Vegetation Index, and Red-Green Index variables [Coops et al., 2006], and results were consistent with ground-based field surveys [Biederman et al., 2014a]. Contributing area, average hillslope slope, stream network, stream order [Strahler, 1952], and length and average slope of the main channel (Table 1) were determined using a 1 m airborne laser swath map and the TauDEM toolkit [http://hydrology.uwrl.usu.edu/taudem/taudem5.0] in ARC-GIS 10.1 software. Average width of the riparian zone (including both sides of the channel) was determined from satellite imagery (Table 1). While most riparian zones were clearly distinguished from hillslopes by level terrain and riparian vegetation, the zero-order catchment had a less distinctive riparian zone with slopes similar to the adjacent hillslopes and vegetation that was a mix of lodgepole pine and riparian species. The zero-order catchment riparian width was measured manually onsite.

3.3. Weather and Physical Hydrology

Weather and snowpack observations were made within 500 m of the soil water sampling plots (Figure 1) as described in *Biederman et al.* [2014a, 2014b]. Precipitation was observed as 1 min sums using two Alter-shielded weighing gages (ETI Systems) and a shielded reference weighing gage (T-200B, Geonor Inc.), with a wind correction for snowfall [*Rasmussen et al.*, 2012]. Snow depth was calculated as the daily mean depth of 12 automated snow depth sensors (six each under grey-phase canopy and intercanopy gaps). Volumetric soil moisture was recorded at the same hillslope locations where soil water was sampled (Figure 1c) in six profiles at depths of 10, 30, and 60 cm (EC-5 and 5-TE, Decagon Corporation) and combined to produce time series of volume-weighted soil moisture. Groundwater stage was observed at one hillslope and one riparian groundwater piezometer each in the zero-order catchment. Stream stage was recorded at the outlets of the first-, second-, and third-order catchments, and stage-discharge relationships were developed to enable streamflow calculation across each outlet cross section [*Biederman et al.*, 2014a].

3.4. Hydrochemical Sampling and Analysis

Statistical tests for differences of concentration means were performed using a two-sample *t* test without assuming equal variance in MATLAB R2014a.

Hillslope soil water was sampled approximately weekly beginning during snowmelt and for 3–5 weeks thereafter, until soils were too dry to produce samples using tension lysimeters (Prenart Mini, Prenart Corporation) at depths in the mineral soil of 5 (± 2) cm, 25 (± 5) cm, and 60 (± 10) cm in four profiles. Soil water chemistry did not differ significantly between the two study hillslope locations or between the depths of 25 and 60 cm, which were combined for analysis ($p > 0.05$). Hillslope groundwater, riparian groundwater and streams were sampled every 1–2 weeks from snowmelt onset until the source dried out or became inaccessible due to snow cover (see time series figures for actual frequencies). Hillslope groundwater (depth 110 ± 20 cm) was sampled within a study hillslope of the second-order catchment by three piezometers arranged in a transect perpendicular to the channel and one piezometer in the control stand (Figure 1c). There were no significant differences in chemistry with position along the study hillslope transect, and these samples were combined ($p > 0.05$). Riparian groundwater was sampled from piezometers installed in riparian soils at depths of ~ 100 cm, below which we encountered a low-permeability consolidated layer. There were two riparian piezometers in the zero-order and first-order catchments (Figure 1c). No significant differences were noted within each pairing, and these were combined ($p > 0.05$). During snowmelt, autosamplers (Teledyne Isco Corporation) were used to collect stream water at the outlets of the zero-order catchment (daily in 2011, weekly in 2012) and first- and second-order catchments (daily both years). The third-order stream was sampled manually at the catchment outlet every 2–3 weeks in 2012 only. Intermediate stream reach locations were sampled every few weeks to improve evaluation of chemistry changes with flow distance.

Samples were transported on ice and filtered through 0.70 μm precombusted glass fiber filters within 24 h [*Brooks and Lemon*, 2007; *Perdrial et al.*, 2014]. Stream sample filters were analyzed for particulate organic carbon (POC) and particulate organic nitrogen (PON) concentrations on a continuous flow elemental analyzer (Model 4010, Costech Analytical). Dissolved organic carbon (DOC) and dissolved nitrogen (DN) were analyzed within 2–3 weeks on a TOC/TN analyzer (Shimadzu Corporation) with a method detection limit of 0.05 mg L^{-1} for DOC and DN. The dissolved inorganic nitrogen (DIN) species nitrate (NO_3) and ammonium (NH_4) were analyzed within 1–2 weeks on a SmartChem Discrete Analyzer (Westco Scientific) with detection limits of 0.005 mg L^{-1} and 0.002 mg L^{-1} for $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$, respectively. Dissolved organic nitrogen (DON) was determined by subtraction of DIN from DN. Ratios of DOC to DON (C/N) were calculated on a mass basis.

3.5. Mass Flux Calculation

DN mass flux in streams was calculated from the integrated product of daily streamflow and a daily time series of DN produced by linear interpolation of the DN observations made every 1–2 weeks [*Cohn et al.*, 1992]. For DN flux calculations in hillslope groundwater and the ungauged zero-order catchment, hydrologic flux was estimated using the area-normalized streamflow from the first-order catchment. For this analysis, the snowmelt period began when the snowpack profile was observed to be isothermal at 0°C and the streamflow hydrograph increased for at least 5 consecutive days. The snowmelt period ended 3 weeks after snow disappearance, at which point stream stage had returned to base flow values of < 5 cm in the first-order catchment (Figure 2). Using this definition, snowmelt accounted for 90–94% of annual streamflow.

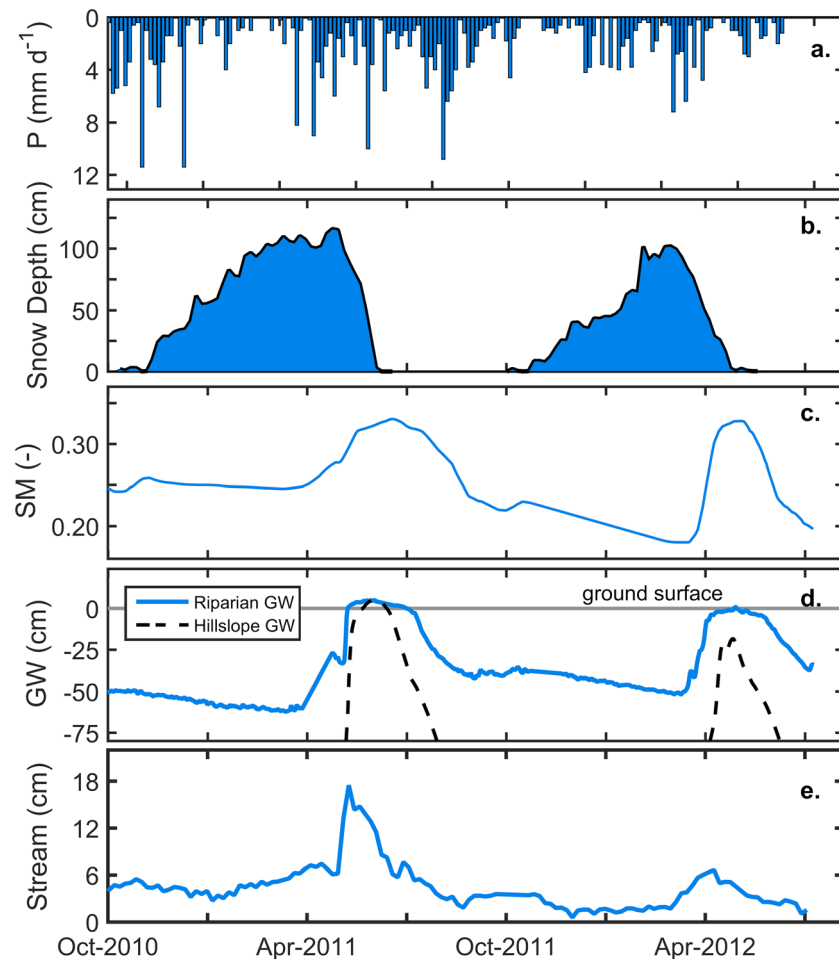


Figure 2. Hydrologic observations including (a) daily precipitation (P), (b) snow depth, (c) volumetric soil moisture (SM), (d) depth to hillslope and riparian groundwater (GW) in the zero-order catchment, and (e) stream stage at the outlet of the first-order catchment. Measurements commenced in 2010 during March (snow depth and streamflow), and late June (soil moisture and groundwater). Soil moisture, groundwater, and streams all reached annual maxima within 1 week of the conclusion of snowmelt. In 2011 larger snowpack was associated with groundwater that reached the ground surface and greater streamflow, while in 2012 the snowpack was smaller, the spring was warmer and drier, groundwater peaked 25 cm below the ground surface, and streamflow was much less [Biederman *et al.*, 2014a].

3.6. Exponential Decay in the Stream Network

All observations of DON and DOC concentration were arranged by distance from the channel head along the primary channel in each stream network. To facilitate description of DOC and DON changes with channel distance, we fit exponential decay models of the form: $\text{concentration} = ae^{-bL}$ where a and b are fitted parameters and L is the channel distance [Melillo *et al.*, 1984]. Exponential decay represents first-order concentration-dependent reaction of dissolved organic matter. This simplifying assumption is made to facilitate quantification of the spatial scale of biogeochemical impacts from forest mortality.

4. Results

4.1. Weather and Physical Hydrologic Response

The 2011 water year was relatively wet, with annual precipitation of 786 mm, while 2012 was drier (448 mm), with both a smaller snowpack and less summer precipitation (Figures 2a and 2b). The Cinnabark Park SNOTEL station 20 km away reported precipitation for water years 2011 and 2012 that was 127% and 74% of the 2004–2012 average, respectively. Mean annual temperatures for 2011 and 2012 were 2.8 and 3.4°C. While the 2011 snowpack was only 15 cm deeper than the 2012 snowpack (Figure 2b), higher precipitation during

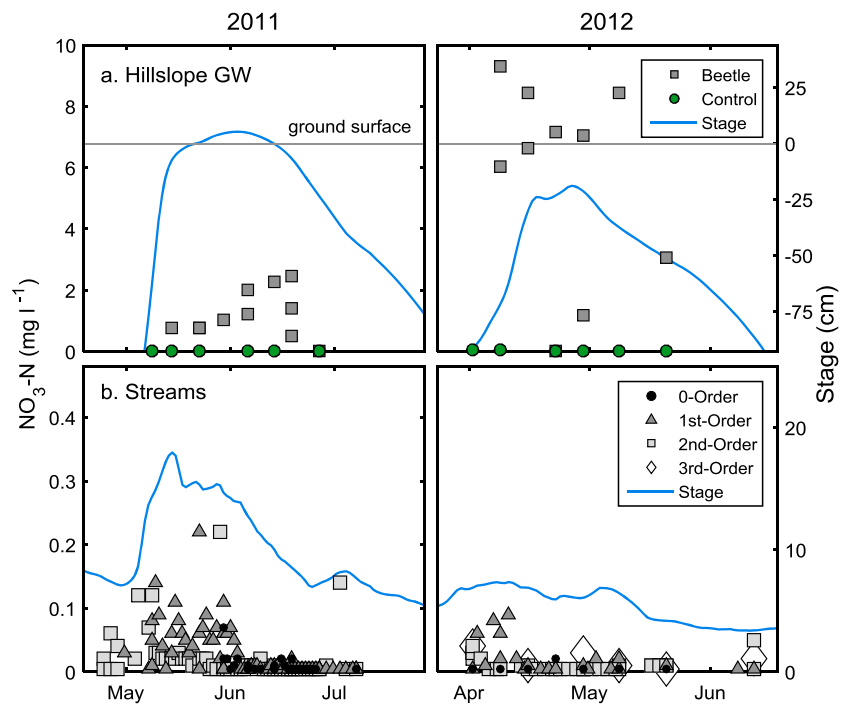


Figure 3. Time series of dissolved nitrate ($\text{NO}_3\text{-N}$) concentration and hydrologic stage for hillslope groundwater (a) and streams (b). Panels in each column (year) show how NO_3 concentrations decreased by an order of magnitude as water drained from hillslopes (Figure 3a) across riparian soils into the stream network (Figure 3b). Note the larger scale for hillslope groundwater (Figure 3a), which had up to one order of magnitude higher nitrate concentrations than streams (Figure 3b). In Figure 3b, stage is for the first-order stream.

snowmelt runoff (Figure 2a) increased spring water inputs relative to 2012. Depth-integrated volumetric soil moisture reached the same peak value of 0.35 in each year but declined thereafter more rapidly in 2012 (Figure 2c). Hillslope groundwater stage reached the surface in 2011 but not 2012 (Figure 2d). Soil moisture content, groundwater and stream stages reached annual peaks within one week (\pm) of the end of snowmelt (Figure 2), and relative stages suggested a hydraulic gradient from groundwater to streams during snowmelt. Both soil water and streams showed the isotopic signature of spring snowpack with little to no evidence of rainfall contributions to flow over the summer.

4.2. Concentration Time Series for Hillslope Groundwater and Streams

Time series of dissolved $\text{NO}_3\text{-N}$ and hydrologic stage (Figure 3a) show that nitrate concentrations varied between 0 and 9 mg L^{-1} in beetle-impacted hillslope groundwater, whereas control stand groundwater remained near detection limits (0.005 mg NL^{-1}), similar to prior observations at this and nearby sites [Fahey et al., 1985; Knight et al., 1991]. $\text{NO}_3\text{-N}$ concentration decreased by an order of magnitude as water moved from hillslopes (Figure 3a) through riparian soils into streams (Figure 3b), which showed similarly low concentrations as riparian groundwater (not shown).

DON and DOC peaked during snowmelt in groundwater and streams (Figures 4 and S1) and C:N ratios ranged from 41 to 53, consistent with allochthonous dissolved organic matter (DOM) flushing from soils [Hornberger et al., 1994; Boyer et al., 1997; Brooks et al., 1999]. DON time series show concentrations were between 0.4 and 4.4 mg L^{-1} in beetle-impacted hillslope groundwater, which was significantly greater than the control stand, where DON varied from 0.1 to 0.6 mg L^{-1} . DON decreased as water moved from beetle-impacted hillslopes (Figure 4a) through riparian soils into streams (Figure 4b), which ranged from 0.1 to 1.2 mg L^{-1} . DON was lower in the larger-order (second and third) streams than the small streams (zero and first) (Figure 4b), despite similar levels of bark beetle impact in all catchments (Table 1). However during the dry year 2012, DON was often lower in the zero-order stream than the first-order stream (Figure 4b). DOC time series indicated no differences between beetle-impacted and control hillslope groundwater or between years, with concentrations varying from 8 to 22 mg L^{-1} (Figure S1). In contrast with reduced N concentrations, DOC increased as

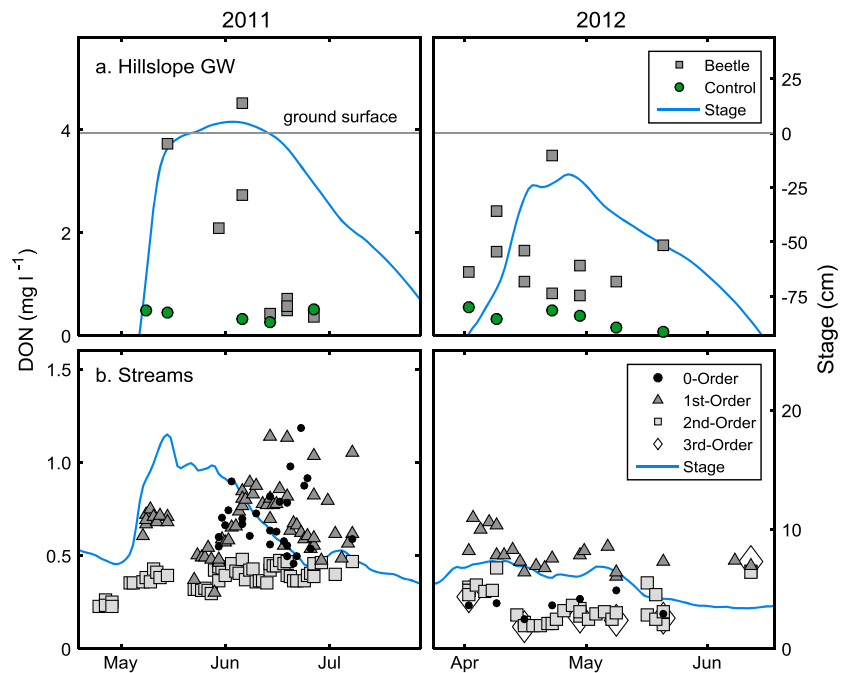


Figure 4. Time series of dissolved organic nitrogen (DON) concentration and hydrologic stage for (a) hillslope groundwater and (b) streams. Panels in each column (year) show how DON concentrations decreased as water drained from hillslopes (Figure 4a) across riparian soils into the stream network and then decreased in streams of progressively larger size (Figure 4b). Note the larger scale for hillslope groundwater (Figure 4a), which had up to one order of magnitude higher DON concentrations than streams (Figure 4b).

water moved from hillslopes through riparian soils into streams. Similar to DON, DOC was typically lower in the larger-order streams.

4.3. Spatial Patterns in Concentrations Along the Hydrologic Flow Path

The greatest N concentrations were found in hillslope groundwater, suggesting significant N loss beyond the major rooting zone (Figure 5a). Hillslope groundwater DN averaged 2.9 mg L^{-1} in 2011 and 8.0 mg L^{-1} in 2012 (Figure 5a). However, only trace NO_3 was detected in riparian groundwater and streams. Mean DON concentrations of $0.2\text{--}0.7 \text{ mg L}^{-1}$ were significantly lower in riparian groundwater and streams than in hillslope groundwater (Table S2). Both DOC and DON declined with depth in soil water, consistent with increased flow path distance from the litter layer and main rooting zone (Figures 5a and 5b), and maintaining C/N ratios of ~ 50 (Figure 5c). In contrast to DON, mean DOC concentration reached its lowest concentration in hillslope groundwater (13.1 mg L^{-1}), resulting in the lowest C/N ratios of any flow path element (means of 14 and 10 in 2011 and 2012, respectively). DOC then increased as water entered the riparian-stream system, where it averaged $21\text{--}26 \text{ mg L}^{-1}$ in riparian groundwater and lower order streams, and $16\text{--}17 \text{ mg L}^{-1}$ in second- and third-order streams.

4.4. Changes in Stream Chemistry With Channel Distance

Channel distance between a stream sampling location and the upstream channel head was a significant predictor of stream DOC during the snowmelt period, which comprised $\sim 90\%$ of annual streamflow. Exponential decay models described 54–55% of DOC variability (Figures 6a and 6b; additional details in Table S3). In the dry year 2012, the DOC model intercept was lower and the decay constant less steep than for 2011, due in part to lower DOC concentrations in the zero-order stream (Figure S1). Channel distance explained 57% of DON variability in 2011 but only 37% during the dry year 2012 (Figures 6c and 6d). Model-predicted stream DOC at 5 km channel distance was $12.1\text{--}12.6 \text{ mg L}^{-1}$, representing a decrease of 52–58% from the intercept values (Table S3), which conceptually represent the DOC concentration of water at a flow distance of zero (i.e., the channel head). Model-predicted DON at 5 km channel distance was 0.27 mg L^{-1} , a 74% decrease from the intercept value.

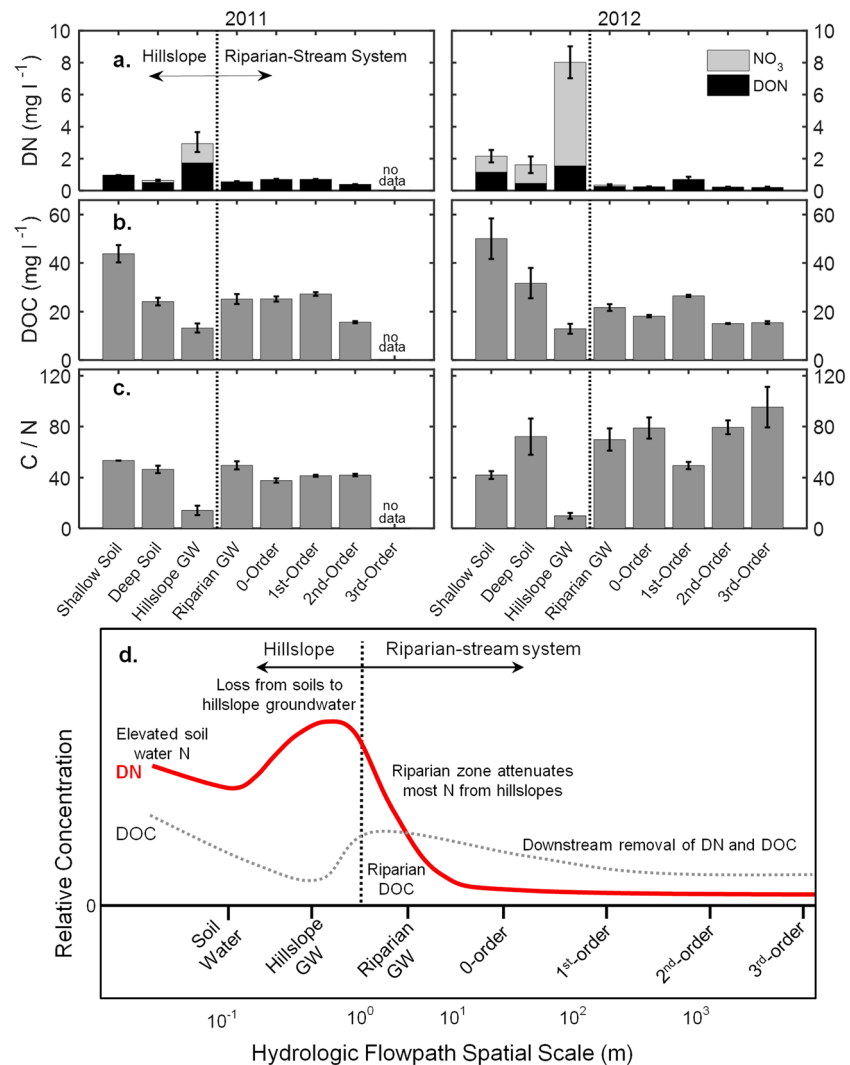


Figure 5. Dissolved concentrations (mean \pm sem) of (a) nitrogen (DON and NO₃-N), (b) DOC, and (c) mass ratios of DOC/DON along a putative hydrologic flow path from soils to hillslope groundwater (GW), through riparian groundwater and into streams of increasing order. (d) A conceptual diagram illustrates how DN and DOC concentrations vary along the flow path. Nitrogen was lost beyond the major rooting zone and accumulated in hillslope groundwater. Most DN was removed as hillslope groundwater moved through DOC-rich riparian soils into the stream, with further N attenuation downstream. In Figure 5a, the total column height and error bar represent the sum of DON and NO₃, which is approximately equal to DN, since NO₂ and NH₄ were negligible.

4.5. Particulate Organic Matter Concentrations in Stream Water

Mean stream concentrations of particulate organic carbon (POC) and nitrogen (PON) were low (less than 1.0 and 0.10 mg L⁻¹, respectively, Table 2), representing < 5% of mean stream organic carbon concentration (dissolved and particulate) and < 15% of the total nitrogen. Well-constrained POC:PON ratios of 10–12 in all streams suggest that particulate organic matter was primarily autochthonous.

5. Discussion

A multiscale analysis from hillslope soils through groundwater, zero-, first-, second-, and third-order streams suggests that riparian systems were a primary site of N attenuation following bark beetle-driven forest mortality. Nitrogen accumulated in hillslope groundwater, but most of this N was removed as water drained across riparian soils, protecting the stream network (Figure 5d). The conceptual flow path proposed here is well supported by numerous observational and modeling studies at this and other sites [Knight *et al.*, 1991;

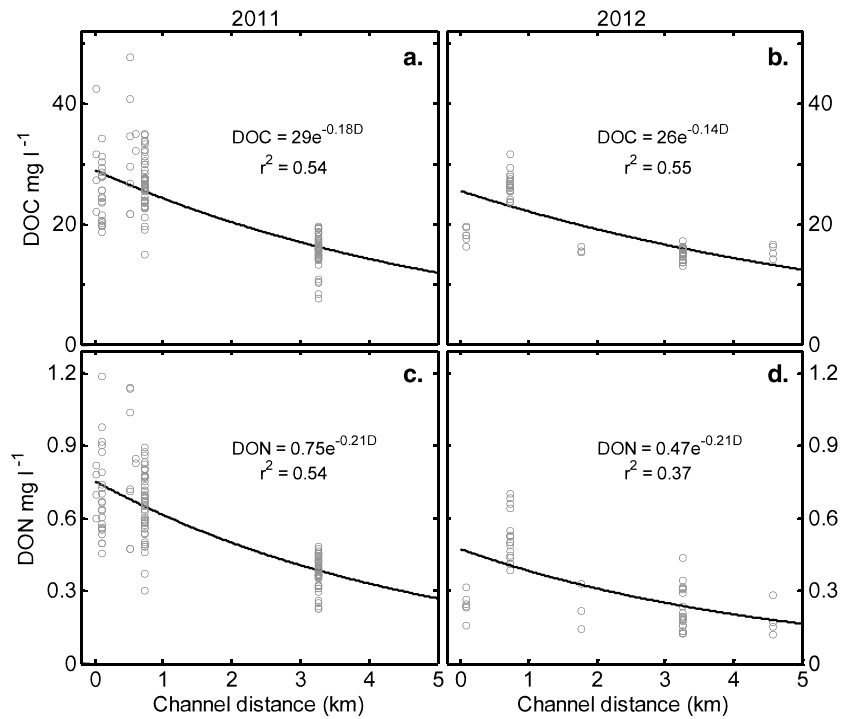


Figure 6. Stream concentrations of (a, b) DOC and (c, d) DON during snowmelt runoff 2011 (Figures 6a and 6c) and 2012 (Figures 6b and 6d) plotted against distance from the channel head. To facilitate quantification of the spatial scale of biogeochemical impacts of forest mortality, concentration data are fit with simple exponential decay models of the form concentration = ae^{-bD} where “a” is a fitted intercept, “b” is a fitted rate constant, e is the base of the natural logarithm, and D is the channel distance. Measurements include all samples taken at catchment outlets as well as three to nine samples per catchment collected at intermediate locations in the reaches above the outlet. The third-order stream was sampled only in 2012 (D = 4.7 km). Curves shown are significant ($p < 0.001$ compared to a constant model).

Hornberger et al., 1994; Boyer et al., 1997; Bishop et al., 2004; Lohse et al., 2009; Brooks et al., 2015]. Most importantly, the differences among flow path elements (i.e., order of magnitude DN differences between hillslope groundwater and streams, Figure 5a) were much greater than differences among instances of a given element. Below, we discuss the implications of these results for our three hypotheses explaining the disconnect between high soil N in beetle-infested hillslopes and low stream N at the outlets of large basins.

Comparison of our results with prior studies at this and nearby sites [Fahey et al., 1985; Knight et al., 1991; Parsons et al., 1994] suggests that bark beetle disturbance increased soil water NO_3 by several orders of magnitude (Table 3) consistent with results from other bark beetle studies [Zimmermann et al., 2000; Hobara et al., 2001; Huber, 2005; Morehouse et al., 2008; Clow et al., 2011; Griffin et al., 2011; Griffin and Turner, 2012; Mikkelsen et al., 2013]. In contrast with increased NO_3 , we found soil water DON concentration, mean organic C/N, and DOC remained similar to undisturbed forests [Fahey et al., 1985], as reported previously for bark beetle disturbance [Clow et al., 2011]. No change in soil water DOC is consistent with findings that soil heterotrophic respiration remained constant [Borkhuu et al., 2015] or decreased [Moore et al., 2013], possibly because decreased root exudation and mycorrhizal turnover may be temporarily balanced by increased litter decomposition [Xiong et al., 2011; Mikkelsen et al., 2013]. Our findings of elevated NO_3 but unchanged DOC

Table 2. Particulate C and N in Streams^a

Stream Order	PC (mg C L ⁻¹)	PN (mg N L ⁻¹)	Particulate C/N
First order	0.82 (0.47)	0.09 (0.07)	9.4 (1.6)
Second order	0.67 (0.32)	0.07 (0.03)	9.9 (1.8)
Third order	0.92 (0.68)	0.09 (0.07)	10.2 (1.4)

^aShown are mean (standard deviation). Sample size $n = 28, 32,$ and 7 for stream orders 1, 2, and 3, respectively.

Table 3. Solution Nitrogen Concentrations by Flow Path Element Observed in This Study and Compared to Earlier Work on N Cycling at This and Nearby Sites^a

Flow Path Element	DON (mg L ⁻¹)	NO ₃ -N (mg L ⁻¹)	NH ₄ -N (mg L ⁻¹)	DN (mg L ⁻¹)	C/N
<i>Top of Mineral Soil (0–10 cm)</i>					
<i>Fahey et al.</i> [1985] control	1.28	0.01	0.04	1.33 ^b	20–70
This study—bark beetle	0.97	1.21	0.06	2.18	42
<i>Soil Water (10–100 cm)</i>					
<i>Parsons et al.</i> [1994] control	–	<0.1	<0.1	–	–
<i>Fahey et al.</i> [1985] control	0.48	0.01	0.03	0.52 ^b	50–70
<i>Knight et al.</i> [1991] control	0.2–0.5 ^b	<0.05	<0.1	0.2–0.5	–
<i>Knight et al.</i> [1991] thinned	0.2–0.9 ^b	<0.1	<0.1	0.2–0.9	–
<i>Parsons et al.</i> , 1994 30-tree harvest	0.4–0.7 ^b	0.4–1.5	<0.1	1.0–1.5 ^b	–
<i>Knight et al.</i> [1991] clearcut	0.5–3.0 ^b	1.6–4.1	<0.1	1.0–6.5	–
This study—bark beetle	0.36	1.0	–	≥1.36^b	53
<i>Hillslope Groundwater (Subsoil, 100–180 cm)</i>					
<i>Fahey et al.</i> [1985] control	0.08	0.01	0.02	0.11 ^b	50–70
<i>Knight et al.</i> [1991] control ^c	0.2–0.5 ^b	<0.05	<0.1	0.2–0.5	–
<i>Knight et al.</i> [1991] thinned	0.2–0.9 ^b	<0.1	<0.1	0.2–0.9	–
<i>Knight et al.</i> [1991] clearcut	0.5–3.0 ^b	1.6–4.1	<0.1	1.0–6.5	–
This study—bark beetle	1.65	3.68	0.09	5.42	12
This study—control	0.38	<0.05	<0.05	0.38	52
<i>Streams—This Study—Bark Beetle Disturbed</i>					
Zero order	0.57	<0.05	0.15	0.72	49
First order	0.64	<0.05	0.12	0.76	42
Second order	0.33	<0.05	0.10	0.43	55
Third order^d	0.26	<0.05	–	≥0.26	65

^aThe studies of Knight and Parsons were conducted at Chimney Park, while Fahey's paper included Chimney Park and three nearby sites. Results from the present study are shown in bold.

^bQuantities were estimated from figures and/or calculated from the reported parameters.

^c*Knight et al.* [1991] composited the observations collected in the mineral soil (40 cm depth) with those from the subsoil (150 cm). We have repeated their data for both flow path elements. Thinning removed 60% of trees.

^dMeasured only in 2012.

support the idea that by the fourth and fifth years following beetle outbreak, DOC limitation reduced the capacity of fast-growing heterotrophs to compete for available N, favoring nitrification, and NO₃ loss to groundwater [Kaňa *et al.*, 2013, 2015]. Increased NO₃ leaching to groundwater could also be facilitated both by temporal asynchrony between snowmelt periods of high soil water NO₃ and potential uptake by short regenerating vegetation that is more likely to be snow-covered than is overstory [Meixner *et al.*, 2001].

Our first hypothesis (H1) that N loss from soils would be prevented by surviving vegetation uptake was rejected because N was lost beyond the major rooting zone [Pearson *et al.*, 1984] and accumulated in hillslope groundwater (Table 3). The elevated NO₃-N we observed in soils and groundwater was similar to clear cuts and large harvest gaps of 30 trees [Knight *et al.*, 1991; Parsons *et al.*, 1994], whereas historical experiments with thinning and smaller harvest gaps showed little difference from controls (Table 3). Meanwhile, control stand groundwater N concentrations remained comparable to pre-outbreak concentrations, indicating that beetle infestation caused the observed impacts (Table 3). Likewise the 2011 estimated DN loss flux in hillslope groundwater, 5.5 kg ha⁻¹ y⁻¹ (Table 4), compares reasonably with the 11.0 kg ha⁻¹ y⁻¹ reported by Knight *et al.* [1991] following clear cut, while our estimate for the control stand (0.7 kg ha⁻¹ y⁻¹) is more similar to their control or thinned stand fluxes (0.3 and 0.4 kg ha⁻¹ y⁻¹, respectively). The clear cut N flux estimate of Knight *et al.* [1991] is about twice as large as in our bark beetle study despite similar observed concentrations. This difference is because Knight's hillslope hydrological model predicted a 277% increase in groundwater drainage from the hillslope, whereas observations following beetle infestation indicated no change in annual hydrologic flux from the hillslopes to streams [Biederman *et al.*, 2014a]. Collectively, comparison of our results with prior studies suggests that severe beetle infestation of this site's managed, even-aged stands created many large root gaps, allowing mobilized N to drain beyond the reach of surviving vegetation. We expect that N loss beyond the root zone could be less in forests with more heterogeneous structure (species, age, and size), where more patchy, uneven beetle infestation favors uptake of water and nutrients by surviving vegetation [Stednick and Jensen, 2007; Rhoades *et al.*, 2013].

Table 4. Annual Dissolved Nitrogen Flux by Flow Path Element

Flow Path Element	DN Flux (kg N ha ⁻¹ y ⁻¹)	
Hillslope groundwater	1985	
<i>Knight et al.</i> [1991] control	0.3 ^a	
<i>Knight et al.</i> [1991] thinned	0.4 ^a	
<i>Knight et al.</i> [1991] clearcut	11.0 ^a	
This study—bark beetle	2011	2012
	5.5^b	0.7^b
Streams—this study		
Zero order	0.7^b	<0.1^b
First order	0.7	<0.1
Second order	0.9	0.2
Third order	–	0.1

^aHydrologic fluxes were estimated using a stand-scale hydrological model.
^bHydrologic fluxes for the hillslope groundwater and zero-order stream were estimated using the area-normalized streamflow of the first-order catchment [Biederman et al., 2014a].

Our second hypothesis (H2), that N lost from beetle-impacted hillslopes would be removed as water drained across intact riparian zones, was supported by large reductions in both concentration and fluxes of DN between hillslope groundwater and streams (Tables 3 and 4 and Figure 5). Only 13–16% of N lost from the hillslopes was measured in streams (Table 4), including very little NO₃ (Figure 5 and Table 3). For 2011 in the first-order catchment, a period of dense observations, we calculated DN removal to be 5 g m⁻² yr⁻¹ within the riparian zone (Table 4), consistent with mixing of limiting reactants, adjacency of different redox zones including the hillslope, stream, and hyporheic, and prevalence of plants and microorganisms [Hill, 1996; Mulholland and Hill, 1997; Dahm et al., 1998; McClain et al., 2003; Vidon and Hill, 2004; Lohse et al., 2009]. Temperate forest riparian sites have shown gross plant N uptake rates as large as 12 to 18 g m⁻² yr⁻¹ [Hefting et al., 2005]. The relatively short growing season at our high-elevation site and resulting lower uptake suggests that here, denitrification in the riparian zone may have removed significant NO₃ from N-rich hillslope groundwater [Osborne and Kovacic, 1993; Hill, 1996; Hefting et al., 2005]. Mean riparian groundwater DOC exceeded 20 mg L⁻¹, and DOC increased between the hillslope and the stream, (Figure 5b), which is consistent with a riparian zone that provided the reduced conditions ideal for denitrification [McClain et al., 2003; Lohse et al., 2009; Peters et al., 2011].

We found mixed evidence for our third hypothesis, (H3), that stream-hyporheic processing would rapidly attenuate N that reached the stream, and annual N loss fluxes showed no pattern with catchment scale (Table 4). Our ability to evaluate this hypothesis was limited because most of the N lost from the hillslopes was removed in the riparian zone, and therefore, biogeochemical impacts of the bark beetle infestation on streams were small across catchment scales. Declining DOC and DON concentrations with channel distance (Figure 6) were fit by exponential decay models conceptually representing idealized plug flow, a simplification which ignores lateral water inputs. We assumed that because all contributing areas within the study site suffered relatively uniform and simultaneous tree mortality (Table 1), (1) biogeochemical inputs to the hillslope groundwater driving streamflow would be similar across catchments and (2) declining stream concentrations in larger catchments therefore reflected biogeochemical removal occurring over longer residence times. Because lateral inputs of hillslope groundwater to higher-order streams likely had greater DOC and DON concentrations than water arriving from upstream, we expect the exponential models (Figure 6) conservatively estimate rates of concentration decline with flow distance in the stream. We used channel distance as a first-order estimate of residence time in the channel network, although actual residence time varies with flow velocity and hyporheic exchange [Peterson et al., 2001]. These assumptions allowed us to combine data from multiple flow paths (Figure 6) and evaluate how biogeochemical impacts of bark beetle infestation varied with spatial scale along an idealized hydrologic flow path, the focus of this paper.

Although local data for control streams are lacking, stream DN and PON found here (Table 2 and Table 3) were comparable to subalpine streams draining nearby Niwot Ridge, Colorado [Hood et al., 2003]. At our bark beetle site, DOC and DON concentrations were both 2–5 times greater than at Niwot but showed similar C/N ratios (40–70). Because we found no evidence of DOC loss from hillslope soils, our larger stream DOC and DON concentrations may reflect a greater flush of organic matter from this site's riparian zones

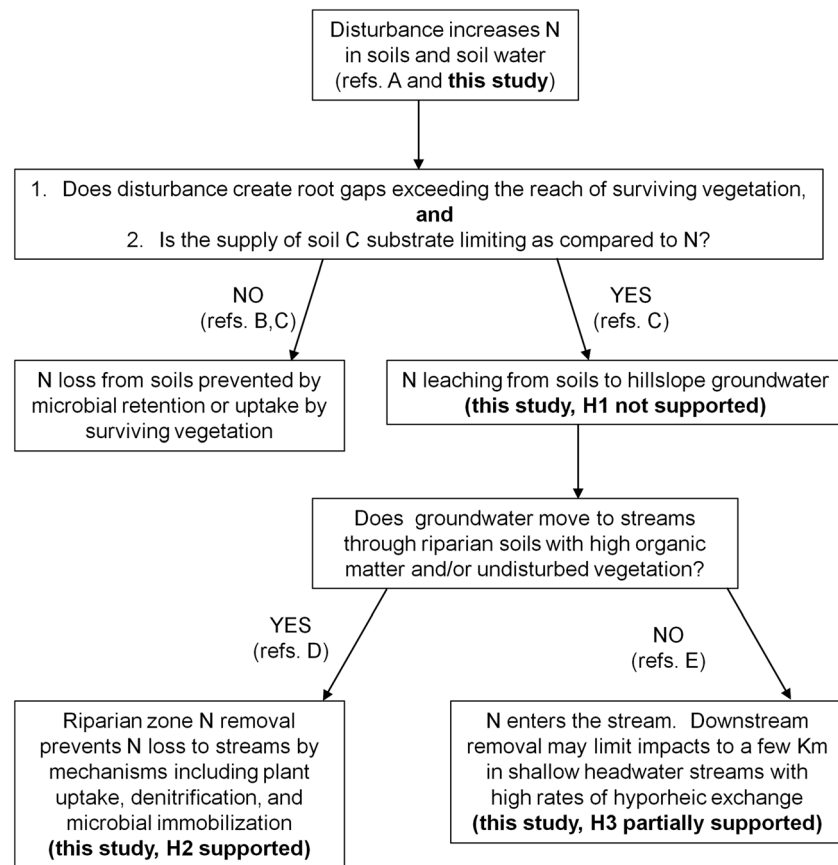


Figure 7. Conceptual model of mechanisms regulating the spatial scale of N loss following forest disturbance based on synthesis of this and prior work. A-[Morehouse et al., 2008; Clow et al., 2011; Griffin et al., 2011; Norton et al., 2015]. B-[Rhoades et al., 2013]. C-[Knight et al., 1991; Parsons et al., 1994; Kaňa et al., 2015]. D-[Hill, 1996; Hedin et al., 1998; McClain et al., 2003; Vidon and Hill, 2004; Hefting et al., 2005; Näsholm et al., 2009]. E-[Triska et al., 1993; Peterson et al., 2001; Bernhardt et al., 2003].

[Hornberger et al., 1994; Hooper et al., 1998; Bishop et al., 2004]. Particulate C and N concentrations remained relatively small and invariant across scales (Table 2) and DIN was not detected; hence, any downstream attenuation of DOC and DON (Figure 6) indicated removal rather than conversion to particulate forms. POC:PON ratios of 10–12 suggested stream particulates were primarily autochthonous, in spite of increased hillslope litter accumulation [Norton et al., 2015]. Flushing of allochthonous particulate matter to streams was unlikely due to low intensities of snowmelt and summer rainstorms (<6 mm d⁻¹) (Figure 2) [Webster et al., 1990] or the gentle slopes and intact vegetation of the riparian zones [Kreutzweiser and Capell, 2001].

To facilitate the transferability of this study to other disturbed catchments, we have developed a conceptual model that synthesizes our results with existing research on biogeochemical impacts of forest disturbance (Figure 7). It is clear that bark beetle disturbance increases N concentrations in soils [Morehouse et al., 2008; Clow et al., 2011; Griffin et al., 2011; Norton et al., 2015; this study]. Nitrogen mobilization and loss to hillslope groundwater appears to require two conditions: (1) disturbance kills contiguous groups of trees and creates root gaps, such as in clear cut harvest or beetle infestation of even-aged stands [Knight et al., 1991; Parsons et al., 1994; this study], while N could be retained by surviving vegetation if disturbance is more scattered, as with thinning treatments or beetle infestation of heterogeneous stands [Knight et al., 1991; Parsons et al., 1994; Rhoades et al., 2013] and (2) carbon substrate is limiting compared to soil N, allowing nitrifiers to compete with faster-growing heterotrophs. As hillslope groundwater moves toward the stream, impacts depend on the degree of N removal in riparian buffer zones. Nitrogen removal is more likely if water drains through riparian zones with undisturbed, active vegetation, organic-rich, saturated soils with variable redox conditions for denitrification, and hydrologic flow paths that include adequate residence time in riparian soils [Hill, 1996; Hedin et al., 1998; McClain et al., 2003; Vidon and Hill, 2004; Hefting et al., 2005; Näsholm et al., 2009].

this study]. Disturbance effects on local water balance and hydrologic flow paths could affect biogeochemical mobilization and processing [Mikkelsen *et al.*, 2013; Bearup *et al.*, 2014], but compensating evaporative mechanisms have limited the net impacts on physical hydrology [Mikkelsen *et al.*, 2013; Biederman *et al.*, 2014a]. Nitrogen reaching streams is likely to be attenuated in the channel network, especially in small streams with high rates of hyporheic exchange [Triska *et al.*, 1993; Peterson *et al.*, 2001; Bernhardt *et al.*, 2003].

6. Conclusions

Observations along putative hydrologic flow paths showed a large N pulse to hillslope groundwater that exceeded the retention capacity of soils and surviving vegetation. Streams were mainly protected from the groundwater N input by riparian removal, although further concentration declines were observed with flow distance in the channel network. Our results provide new evidence that large N loss from soils following bark beetle infestation was attenuated by riparian and in-stream processing within a heavily infested headwater catchment ($<10 \text{ km}^2$), demonstrating alternative mechanisms for the weak basin-scale response.

In Western conifer forests impacted by bark beetles, nitrogen loss from hillslopes to streams likely depends on a combination of soil substrate and microbial conditions, hydrologic flux, formation of root gaps between surviving trees, and hydrological flow paths through the riparian zone. Our results show that N loss can be high, similar to clear-cutting, when bark beetles infest the even-aged, managed stands commonly found across western North America, but for a more natural distribution of forest structure and heterogeneous disturbance, N loss is likely to be less pronounced.

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References

- Acuña, V., T. Datry, J. Marshall, D. Barceló, C. N. Dahm, A. Ginebreda, G. McGregor, S. Sabater, K. Tockner, and M. A. Palmer (2014), Why should we care about temporary waterways?, *Science*, *343*(6175), 1080–1081, doi:10.1126/science.1246666.
- Alexander, R. B., R. A. Smith, and G. E. Schwarz (2000), Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico, *Nature*, *403*(6771), 758–761, doi:10.1038/35001562.
- Bearup, L. A., R. M. Maxwell, D. W. Clow, and J. E. McCray (2014), Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds, *Nat. Clim. Change*, *4*(6), 481–486, doi:10.1038/nclimate2198.
- Bernhardt, E. S., G. E. Likens, D. C. Buso, and C. T. Driscoll (2003), In-stream uptake dampens effects of major forest disturbance on watershed nitrogen export, *Proc. Natl. Acad. Sci. U.S.A.*, *100*(18), 10,304–10,308, doi:10.1073/pnas.1233676100.
- Biederman, J. A., A. A. Harpold, D. J. Gochis, B. E. Ewers, D. E. Reed, S. A. Papuga, and P. D. Brooks (2014a), Increased evaporation following widespread tree mortality limits streamflow response, *Water Resour. Res.*, *50*, 5395–5409, doi:10.1002/2013WR014994.
- Biederman, J. A., P. D. Brooks, A. A. Harpold, E. Gutmann, D. J. Gochis, D. E. Reed, and E. Pendall (2014b), Multi-scale observations of snow accumulation and peak snowpack following widespread, insect-induced lodgepole pine mortality, *Ecohydrology*, *7*(1), 150–162, doi:10.1002/eco.1342.
- Biederman, J. A., A. J. Somor, A. A. Harpold, E. D. Gutmann, D. D. Breshears, P. A. Troch, D. J. Gochis, R. L. Scott, A. J. H. Meddens, and P. D. Brooks (2015), Recent tree die-off has little effect on streamflow in contrast to expected increases from historical studies, *Water Resour. Res.*, *51*, 9775–9789, doi:10.1002/2015WR017401.
- Bishop, K., J. Seibert, S. Koher, and H. Laudon (2004), Resolving the double paradox of rapidly mobilized old water with highly variable responses in runoff chemistry, *Hydrol. Process.*, *18*(1), 185–189, doi:10.1002/hyp.5209.
- Borkhuu, B., S. D. Peckham, B. E. Ewers, U. Norton, and E. Pendall (2015), Does soil respiration decline following bark beetle induced forest mortality? Evidence from a lodgepole pine forest, *Agric. For. Meteorol.*, *214–215*, 201–207, doi:10.1016/j.agrformet.2015.08.258.
- Bormann, F. H., G. E. Likens, D. W. Fisher, and R. S. Pierce (1968), Nutrient loss accelerated by clear-cutting of a forest ecosystem, *Science*, *159*(3817), 882–884, doi:10.1126/science.159.3817.882.
- Boyer, E. W., G. M. Hornberger, K. E. Bencala, and D. M. McKnight (1997), Response characteristics of DOC flushing in an alpine catchment, *Hydrol. Process.*, *11*(12), 1635–1647, doi:10.1002/(SICI)1099-1085(19971015)11:12<1635::AID-HYP494>3.0.CO;2-H.
- Brooks, P. D., and M. M. Lemon (2007), Spatial variability in dissolved organic matter and inorganic nitrogen concentrations in a semiarid stream, San Pedro River, Arizona, *J. Geophys. Res.*, *112*, G03S05, doi:10.1029/2006JG000262.
- Brooks, P. D., D. M. McKnight, and K. E. Bencala (1999), The relationship between soil heterotrophic activity, soil dissolved organic carbon (DOC) leachate, and catchment-scale DOC export in headwater catchments, *Water Resour. Res.*, *35*(6), 1895–1902, doi:10.1029/1998WR900125.
- Brooks, P. D., P. A. Haas, and A. K. Huth (2007), Seasonal variability in the concentration and flux of organic matter and inorganic nitrogen in a semiarid catchment, San Pedro River, Arizona, *J. Geophys. Res.*, *112*, G03S04, doi:10.1029/2006JG000275.
- Brooks, P. D., J. Chorover, Y. Fan, S. E. Godsey, R. M. Maxwell, J. P. McNamara, and C. Tague (2015), Hydrological partitioning in the critical zone: Recent advances and opportunities for developing transferable understanding of water cycle dynamics, *Water Resour. Res.*, *51*, 6973–6987, doi:10.1002/2015WR017039.
- Brown, A. E., L. Zhang, T. A. McMahon, A. W. Western, and R. A. Vertessy (2005), A review of paired catchment studies for determining changes in water yield resulting from alterations in vegetation, *J. Hydrol.*, *310*(1–4), 28–61, doi:10.1016/j.jhydrol.2004.12.010.
- Burns, D. A. (2003), Atmospheric nitrogen deposition in the Rocky Mountains of Colorado and southern Wyoming—A review and new analysis of past study results, *Atmos. Environ.*, *37*(7), 921–932.
- Campbell, D. H., D. W. Clow, G. P. Ingersoll, M. A. Mast, N. E. Spahr, and J. T. Turk (1995), Processes controlling the chemistry of two snowmelt-dominated streams in the Rocky Mountains, *Water Resour. Res.*, *31*(11), 2811–2821, doi:10.1029/95WR02037.
- Clow, D. W., C. Rhoades, J. Briggs, M. Caldwell, J. William, and M. Lewis (2011), Responses of soil and water chemistry to mountain pine beetle induced tree mortality in Grand County, Colorado, USA, *Appl. Geochem.*, *26*, S174–S178, doi:10.1016/j.apgeochem.2011.03.096.

- Cohn, T. A., D. L. Caulder, E. J. Gilroy, L. D. Zynjuk, and R. M. Summers (1992), The validity of a simple statistical model for estimating fluvial constituent loads: An Empirical study involving nutrient loads entering Chesapeake Bay, *Water Resour. Res.*, *28*(9), 2353–2363, doi:10.1029/92WR01008.
- Condon, K. E. (2013), Quantifying Catchment-Scale Particulate Organic Matter (POM) Loss Following Fire, Relative to Background POM Fluxes.
- Coops, N. C., M. Johnson, M. A. Wulder, and J. C. White (2006), Assessment of QuickBird high spatial resolution imagery to detect red attack damage due to mountain pine beetle infestation, *Remote Sens. Environ.*, *103*(1), 67–80, doi:10.1016/j.rse.2006.03.012.
- Dahm, C. N., N. B. Grimm, P. Marmonier, H. M. Valett, and P. Vervier (1998), Nutrient dynamics at the interface between surface waters and groundwaters, *Freshw. Biol.*, *40*(3), 427–451, doi:10.1046/j.1365-2427.1998.00367.x.
- 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*(8), 416–424, doi:10.1890/110173.
- Fahey, T. J., and J. B. Yavitt (1988), Soil solution chemistry in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming, USA, *Biogeochemistry*, *6*(2), 91–118, doi:10.1007/BF00003033.
- Fahey, T. J., J. B. Yavitt, J. A. Pearson, and D. H. Knight (1985), The nitrogen cycle in lodgepole pine forests, southeastern Wyoming, *Biogeochemistry*, *1*(3), 257–275.
- Ferrenberg, S., J. E. Knelman, J. M. Jones, S. C. Beals, W. D. Bowman, and D. R. Nemerugut (2014), Soil bacterial community structure remains stable over a 5-year chronosequence of insect-induced tree mortality, *Front. Microbiol.*, *5*, 681, doi:10.3389/fmicb.2014.00681.
- Griffin, J. M., and M. G. Turner (2012), Changes to the N cycle following bark beetle outbreaks in two contrasting conifer forest types, *Oecologia*, *170*(2), 551–565, doi:10.1007/s00442-012-2323-y.
- Griffin, J. M., M. G. Turner, and M. Simard (2011), Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone, *For. Ecol. Manage.*, *261*(6), 1077–1089, doi:10.1016/j.foreco.2010.12.031.
- Hedin, L. O., J. C. von Fischer, N. E. Ostrom, B. P. Kennedy, M. G. Brown, and G. P. Robertson (1998), Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil–stream interfaces, *Ecology*, *79*(2), 684–703, doi:10.1890/0012-9658(1998)079[0684:TCONAO]2.0.CO;2.
- Hefting, M. M., J.-C. Clement, P. Bienkowski, D. Dowrick, C. Guenat, A. Butturini, S. Topa, G. Pinay, and J. T. Verhoeven (2005), The role of vegetation and litter in the nitrogen dynamics of riparian buffer zones in Europe, *Ecol. Eng.*, *24*(5), 465–482, doi:10.1007/s10533-008-9277-5.
- Hill, A. R. (1996), Nitrate removal in stream riparian zones, *J. Environ. Qual.*, *25*(4), 743–755, doi:10.2134/jeq1996.00472425002500040014x.
- Hobara, S., N. Tokuchi, N. Ohte, K. Koba, M. Katsuyama, S. J. Kim, and A. Nakanishi (2001), Mechanism of nitrate loss from a forested catchment following a small-scale, natural disturbance, *Can. J. For. Res. Rev. Can. Rech. For.*, *31*(8), 1326–1335, doi:10.1139/cjfr-31-8-1326.
- Hood, E., M. W. Williams, and N. Caine (2003), Landscape controls on organic and inorganic nitrogen leaching across an alpine/subalpine ecotone, Green Lakes Valley, Colorado Front Range, *Ecosystems*, *6*(1), 31–45, doi:10.1007/s10021-002-0175-8.
- Hooper, R. P., B. Aulenbach, D. A. Burns, J. J. McDonnell, J. E. Freer, C. Kendall, and K. J. Beven (1998), Riparian control of stream-water chemistry: implications for hydrochemical basin models, in *Hydrology, Water Resources and Ecology in Headwaters*, pp. 451–458, IAHS Press.
- Hornberger, G. M., K. E. Bencala, and D. M. McKnight (1994), Hydrological controls on dissolved organic carbon during snowmelt in the Snake River near Montezuma, Colorado, *Biogeochemistry*, *25*(3), 147–165, doi:10.1007/bf00024390.
- Houlton, B. Z., C. T. Driscoll, T. J. Fahey, G. E. Likens, P. M. Groffman, E. S. Bernhardt, and D. C. Buso (2003), Nitrogen dynamics in ice storm-damaged forest ecosystems: Implications for nitrogen limitation theory, *Ecosystems*, *6*(5), 431–443, doi:10.1007/s10021-002-0198-1.
- Huber, C. (2005), Long lasting nitrate leaching after bark beetle attack in the highlands of the Bavarian Forest National Park, *J. Environ. Qual.*, *34*(5), 1772–1779, doi:10.2134/jeq2004.0210.
- Jones, J. A., and D. A. Post (2004), Seasonal and successional streamflow response to forest cutting and regrowth in the northwest and eastern United States, *Water Resour. Res.*, *40*, W05203, doi:10.1029/2003WR002952.
- Kaňa, J., K. Tahovská, and J. Kopáček (2013), Response of soil chemistry to forest dieback after bark beetle infestation, *Biogeochemistry*, *113*(1–3), 369–383, doi:10.1007/s10533-012-9765-5.
- Kaňa, J., K. Tahovská, J. Kopáček, and H. Šantrůčková (2015), Excess of organic carbon in mountain spruce forest soils after bark beetle outbreak altered microbial N transformations and mitigated N-saturation, *PLoS One*, *10*(7), e0134165, doi:10.1371/journal.pone.0134165.
- Knight, D. H., T. J. Fahey, and S. W. Running (1985), Water and nutrient outflow from contrasting lodgepole pine forests in Wyoming, *Ecol. Monogr.*, *55*(1), 29–48, doi:10.2307/1942524.
- Knight, D. H., J. B. Yavitt, and G. D. Joyce (1991), Water and nitrogen outflow from lodgepole pine forest after 2 levels of tree mortality, *For. Ecol. Manage.*, *46*(3–4), 215–225, doi:10.1016/0378-1127(91)90233-I.
- Kreutzweiser, D. P., and S. S. Capell (2001), Fine sediment deposition in streams after selective forest harvesting without riparian buffers, *Can. J. For. Res.*, *31*(12), 2134–2142, doi:10.1139/x01-155.
- Liu, F., R. Parmenter, P. D. Brooks, M. H. Conklin, and R. C. Bales (2008), Seasonal and interannual variation of streamflow pathways and biogeochemical implications in semi-arid, forested catchments in Valles Caldera, New Mexico, *Ecohydrology*, *1*, 239–252, doi:10.1002/eco.22.
- Lohse, K. A., P. D. Brooks, J. C. McIntosh, T. Meixner, and T. E. Huxman (2009), Interactions between biogeochemistry and hydrologic systems, *Annu. Rev. Environ. Resour.*, *34*, 65–96, doi:10.1146/annurev.enviro.33.031207.111141.
- Mast, M. A., and D. W. Clow (2008), Effects of 2003 wildfires on stream chemistry in Glacier National Park, Montana, *Hydrol. Process.*, *22*(26), 5013–5023, doi:10.1002/hyp.7121.
- McClain, M. E., et al. (2003), Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems, *Ecosystems*, *6*(4), 301–312, doi:10.1007/s10021-003-0161-9.
- Meddens, A. J., and J. A. Hicke (2014), Spatial and temporal patterns of Landsat-based detection of tree mortality caused by a mountain pine beetle outbreak in Colorado, USA, *For. Ecol. Manage.*, *322*, 78–88, doi:10.1016/j.foreco.2014.02.037.
- Meddens, A. J. H., J. A. Hicke, and C. A. Ferguson (2012), Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States, *Ecol. Appl.*, *22*(7), 1876–1891, doi:10.1890/11-1785.1.
- Meixner, T., M. Fenn, and M. Poth (2001), Nitrate in polluted mountainous catchments with Mediterranean Climates, *Sci. World*, *1*(S2), 564–571, doi:10.1100/tsw.2001.324.
- Meixner, T., P. Brooks, J. Hogan, C. Soto, and S. Simpson (2012), Carbon and nitrogen export from semiarid uplands to Perennial rivers: Connections and missing links, San Pedro River, Arizona, USA, *Geogr. Compass*, *6*(9), 546–559, doi:10.1111/j.1749-8198.2012.00510.x.
- Melillo, J. M., R. J. Naiman, J. D. Aber, and A. E. Linkins (1984), Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams, *Bull. Mar. Sci.*, *35*(3), 341–356.
- Mikkelsen, K., E. Dickenson, R. Maxwell, J. McCray, and J. Sharp (2012), Water-quality impacts from climate-induced forest die-off, *Nat. Clim. Change*, doi:10.1038/NCLIMATE1724.

- Mikkelsen, K., L. A. Bearup, R. M. Maxwell, J. D. Stednick, J. E. McCray, and J. O. Sharp (2013), Bark beetle infestation impacts on nutrient cycling, water quality and interdependent hydrological effects, *Biogeochemistry*, *115*, 1–21, doi:10.1007/s10533-013-9875-8.
- Mitton, J. B., and S. M. Ferrenberg (2012), Mountain pine beetle develops an unprecedented summer generation in response to climate warming, *Am. Nat.*, *179*(5), E163–E171, doi:10.1086/665007.
- Moore, D. J., N. A. Trahan, P. Wilkes, T. Quaife, B. B. Stephens, K. Elder, A. R. Desai, J. Negron, and R. K. Monson (2013), Persistent reduced ecosystem respiration after insect disturbance in high elevation forests, *Ecol. Lett.*, *16*(6), 731–737, doi:10.1111/ele.12097.
- Morehouse, K., T. Johns, J. Kaye, and A. Kaye (2008), Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests, *For. Ecol. Manage.*, *255*(7), 2698–2708, doi:10.1016/j.foreco.2008.01.050.
- Mulholland, P. J., and W. R. Hill (1997), Seasonal patterns in streamwater nutrient and dissolved organic carbon concentrations: Separating catchment flow path and in-stream effects, *Water Resour. Res.*, *33*(6), 1297–1306, doi:10.1029/97WR00490.
- Näsholm, T., K. Kielland, and U. Ganeteg (2009), Uptake of organic nitrogen by plants, *New Phytol.*, *182*(1), 31–48, doi:10.1111/j.1469-8137.2008.02751.x.
- Norton, U., B. E. Ewers, B. Borkhuu, N. R. Brown, and E. Pendall (2015), Soil nitrogen five years after bark beetle infestation in lodgepole pine forests, *Soil Sci. Soc. Am. J.*, *79*(1), 282, doi:10.2136/sssaj2014.05.0223.
- Osborne, L. L., and D. A. Kovacic (1993), Riparian vegetated buffer strips in water-quality restoration and stream management, *Freshwater Biol.*, *29*(2), 243–258, doi:10.1111/j.1365-2427.1993.tb00761.x.
- Parsons, W. F. J., D. H. Knight, and S. L. Miller (1994), Root gap dynamics in lodgepole pine forest: Nitrogen transformations in gaps of different size, *Ecol. Appl.*, *4*(2), 354–362, doi:10.2307/1941939.
- Pearson, J. A., T. J. Fahey, and D. H. Knight (1984), Biomass and leaf area in contrasting lodgepole pine forests, *Can. J. For. Res.*, *14*(2), 259–265, doi:10.1139/x84-050.
- Perdrial, J. N., et al. (2014), Stream water carbon controls in seasonally snow-covered mountain catchments: Impact of inter-annual variability of water fluxes, catchment aspect and seasonal processes, *Biogeochemistry*, *118*(1–3), 273–290, doi:10.1007/s10533-013-9929-y.
- Peters, N., J. Bohlke, P. Brooks, T. Burt, M. Gooseff, D. Hamilton, P. Mulholland, N. Roulet, and J. Turner (2011), Hydrology and biogeochemistry linkages, in *Treatise on Water Science*, vol. 2, edited by P. Wilderer, pp. 271–304, Elsevier, Oxford.
- Peterson, B. J., et al. (2001), Control of nitrogen export from watersheds by headwater streams, *Science*, *292*(5514), 86–90, doi:10.1126/science.1056874.
- Ranalli, A. J., and D. L. Macalady (2010), The importance of the riparian zone and in-stream processes in nitrate attenuation in undisturbed and agricultural watersheds—A review of the scientific literature, *J. Hydrol.*, *389*(3–4), 406–415, doi:10.1016/j.jhydrol.2010.05.045.
- Rasmussen, R., et al. (2012), How well are we measuring snow? The NOAA/FAA/NCAR winter precipitation test bed, *Bull. Am. Meteorol. Soc.*, *93*(6), 811–829, doi:10.1175/bams-d-11-00052.1.
- Reed, D. E., B. E. Ewers, and E. Pendall (2014), Impact of mountain pine beetle induced mortality on forest carbon and water fluxes, *Environ. Res. Lett.*, *9*(10), 105004, doi:10.1088/1748-9326/9/10/105004.
- Rhoades, C. C., et al. (2013), Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response, *Proc. Natl. Acad. Sci. U.S.A.*, *110*(5), 1756–1760, doi:10.1073/pnas.1221029110.
- Stednick, J. D., and R. Jensen (2007), Effects of pine beetle infestations on water yield and water quality at the watershed scale in northern Colorado, Report to CWRRI.
- Strahler, A. N. (1952), Hypsometric (area-altitude) analysis of erosional topography, *Geol. Soc. Am. Bull.*, *63*(11), 1117–1141, doi:10.1130/0016-7606(1952)63[1117:haoet]2.0.co;2.
- Swank, W. T., J. B. Waide, D. A. Crossley, and R. L. Todd (1981), Insect defoliation enhances nitrate export from forest ecosystems, *Oecologia*, *51*(3), 297–299, doi:10.1007/bf00540897.
- Netherlands Triska, F. J., J. H. Duff, and R. J. Avanzino (1993), The role of water exchange between a stream channel and its hyporheic zone in nitrogen cycling at the terrestrial—Aquatic interface, in *Nutrient Dynamics and Retention in Land/Water Ecotones of Lowland, Temperate Lakes and Rivers*, edited by A. Hillbricht-Ilkowska and E. Pieczyńska, pp. 167–184, Springer.
- Vidon, P. G., and A. R. Hill (2004), Landscape controls on nitrate removal in stream riparian zones, *Water Resour. Res.*, *40*, W03201, doi:10.1029/2003WR002473.
- Webster, J. R., S. W. Golladay, E. F. Benfield, D. J. D'Angelo, and G. T. Peters (1990), Effects of forest disturbance on particulate organic matter budgets of small streams, *J. North Am. Benthol. Soc.*, *120*–140, doi:10.2307/1467446.
- Xiong, Y. M., J. J. D'Atri, S. L. Fu, H. P. Xia, and T. R. Seastedt (2011), Rapid soil organic matter loss from forest dieback in a subalpine coniferous ecosystem, *Soil Biol. Biochem.*, *43*(12), 2450–2456, doi:10.1016/j.soilbio.2011.08.013.
- Zimmermann, L., K. Moritz, M. Kennel, and J. Bittersohl (2000), Influence of bark beetle infestation on water quantity and quality in the Grosse Ohe catchment (Bavarian forest national park), *Silva Gabreta*, *4*, 51–62.