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Special Section:

Disturbance Hydrology

Key Points:

- Streamflow did not increase as predicted
- Three empirical methods produced consistent results
- Weak, variable streamflow response is consistent with recent process literature

Supporting Information:

- Supporting Information S1

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Recent tree die-off has little effect on streamflow in contrast to expected increases from historical studies

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Abstract Recent bark beetle epidemics have caused regional-scale tree mortality in many snowmelt-dominated headwater catchments of western North America. Initial expectations of increased streamflow have not been supported by observations, and the basin-scale response of annual streamflow is largely unknown. Here we quantified annual streamflow responses during the decade following tree die-off in eight infested catchments in the Colorado River headwaters and one nearby control catchment. We employed three alternative empirical methods: (i) double-mass comparison between impacted and control catchments, (ii) runoff ratio comparison before and after die-off, and (iii) time-trend analysis using climate-driven linear models. In contrast to streamflow increases predicted by historical paired catchment studies and recent modeling, we did not detect streamflow changes in most basins following die-off, while one basin consistently showed decreased streamflow. The three analysis methods produced generally consistent results, with time-trend analysis showing precipitation was the strongest predictor of streamflow variability ($R^2 = 74\text{--}96\%$). Time-trend analysis revealed post-die-off streamflow decreased in three catchments by 11–29%, with no change in the other five catchments. Although counter to initial expectations, these results are consistent with increased transpiration by surviving vegetation and the growing body of literature documenting increased snow sublimation and evaporation from the subcanopy following die-off in water-limited, snow-dominated forests. The observations presented here challenge the widespread expectation that streamflow will increase following beetle-induced forest die-off and highlight the need to better understand the processes driving hydrologic response to forest disturbance.

1. Introduction

Reliable water supply is a critical ecosystem service of forested headwater catchments throughout western North America [Millenium Ecosystem Assessment, 2005; NRC, 2008]. Since the mid-1990s, warmer temperatures, drought, and management legacies have facilitated an epidemic of bark beetles in the western U.S. and Canada [Raffa et al., 2008; Williams et al., 2010], killing billions of trees and rivaling the extent of wildfire [Westerling et al., 2006; Hicke et al., 2012; Meddens et al., 2012]. Nearly a century of forest hydrology research has shown that die-off usually increases streamflow [Bates and Henry, 1928; Bosch and Hewlett, 1982; Stednick, 1996; Andréassian, 2004; Brown et al., 2005]. However, after nearly two decades of the current North American bark beetle epidemic, we lack published, observational evidence of streamflow impacts in the headwater basins critical for surface water supplies.

Because this bark beetle epidemic is unprecedented in the modern hydrological record, expectations for annual streamflow change have been influenced by the rich literature on experimental harvest, mostly in small paired catchments of $< 2 \text{ km}^2$ [Bosch and Hewlett, 1982; Stednick, 1996; Andréassian, 2004; Brown et al., 2005]. These reviews suggest that harvest will increase annual streamflow subject to several nuances: (i) mean annual precipitation must exceed 450–500 mm, below which most precipitation is consumed by evaporative losses; (ii) disturbance must remove at least $\sim 20\%$ of the basal area; (iii) increased streamflow is expected in the years immediately following treatment, but the duration of the effect may vary from 5 to 50

years or more; (iv) streamflow increase may be limited when disturbance is spatially diffuse, such as by thinning or shelterwood harvest, due to increased transpiration (the water lost via stomata during photosynthesis) by surviving vegetation distributed across the catchment. The focus of this paper is on annual streamflow in large basins of interest for water resources. We do not address the response of peak flows or other streamflow dynamics to forest disturbance, which have been addressed in other recent literature [Alila *et al.*, 2009; Green and Alila, 2012; Kuraš *et al.*, 2012].

In the present North American bark beetle outbreak, the only multibasin observations show an equal mix of increased and decreased annual streamflow in an unpublished report from the first few years following outbreak [Stednick and Jensen, 2007]. However, there remains an expectation of increased streamflow [USDA Forest Service, 2011; Mikkelsen *et al.*, 2013a; Pugh and Gordon, 2013] originating from several sources. First, two historical studies compared large basins (200–5000 km²) following previous beetle outbreaks in the central Rocky Mountains and reported 14–26% greater annual streamflow in Colorado [Love, 1955; Bethlahmy, 1974] and Montana [Potts, 1984]. These two papers are frequently cited (increasingly so in recent years), highlighting both significant research interest and a need for observations from the current outbreak. Scant local observations prevented these authors from testing their hypothesis that precipitation variability could obscure the forest die-off effects, as has been subsequently demonstrated with the benefit of modern climate data sets [Zhang *et al.*, 2012; Burt *et al.*, 2015]. Second, most basin-scale assessments of the current outbreak have employed models or remote sensing products, which predict reduced evaporative losses with reduced vegetation density, resulting in estimates of more water available for streamflow [Knight *et al.*, 1991; Bewley *et al.*, 2010; Pomeroy *et al.*, 2012; Bright *et al.*, 2013; Maness *et al.*, 2013; Mikkelsen *et al.*, 2013b; Livneh *et al.*, 2015; Vanderhoof and Williams, 2015]. The third source of expectations for increased streamflow is mechanistic studies documenting reduced interception [Boon, 2012; Pugh and Small, 2012; Pugh and Gordon, 2013; Biederman *et al.*, 2014b] and transpiration [Hubbard *et al.*, 2013], which are usually described as the key mechanisms of hydrologic response to forest disturbance [Stednick and Jensen, 2007; NRC, 2008; USDA Forest Service, 2011; Pugh and Gordon, 2013].

A growing body of studies documents that forest mortality can increase evaporative processes from the subcanopy, counteracting reductions in interception and overstory transpiration that are expected to increase streamflow. Eddy covariance observations have shown a mix of relatively small increases and decreases in stand-scale evaporative loss following bark-beetle die-off [Brown *et al.*, 2013; Biederman *et al.*, 2014a; Frank *et al.*, 2014]. Because snowmelt is the dominant hydrologic input in western North America, snow processes strongly regulate hydrologic impacts of disturbance in this region [Troendle and King, 1985; MacDonald and Stednick, 2003; USDA Forest Service, 2011]. It is often assumed that the presence of canopy will increase seasonal sublimation because snowpack is thought to be less vulnerable than intercepted snow in the canopy. However, interactions among forest geometry, terrain, and solar radiation drive seasonal snowpack sublimation that can be either higher or lower than canopy interception losses [Musselman *et al.*, 2008; Rinehart *et al.*, 2008; Gustafson *et al.*, 2010; Schelker *et al.*, 2013]. Accordingly, there appears to be a trade-off between interception and snowpack shading that minimizes evaporative losses (and maximizes snowmelt volumes) in forests of intermediate density [Veatch *et al.*, 2009; Broxton *et al.*, 2014]. Hence, peak snowpack can decline or remain unchanged in cases of severe disturbance [Schmid *et al.*, 1991; Biederman *et al.*, 2014b; Harpold *et al.*, 2014]. Canopy arrangement is also important, with alternating clusters of trees and small gaps of up to a few tree heights in size maximizing snowpack through optimization of the interception-shading trade-off [Troendle and King, 1985; Golding and Swanson, 1986]. Because snowmelt is the key driver of annual streamflow, we expect the hydrologic impacts of bark beetle infestation to depend in part upon the severity and stand-scale arrangement of forest mortality.

Here our main objective was to quantify annual streamflow impacts during the decade after die-off in eight headwater basins near the Continental Divide in Colorado, U.S.A. Mean annual precipitation (~800 mm) and affected area (35–50%) were well above the thresholds for expected streamflow increases, while the period of observation should capture maximum response [e.g., Stednick, 1996; Andréassian, 2004]. However, our expectation of increased streamflow was tempered by process literature suggesting variable and counteracting responses and the notable absence of changes reported by water resource managers. To obtain results independent from model assumptions, we employed three established empirical methods, two of which utilized local climate observations unavailable to earlier bark beetle studies in this region. The methods were: (i) double-mass paired catchment analysis; (ii) statistical comparisons of precipitation, streamflow

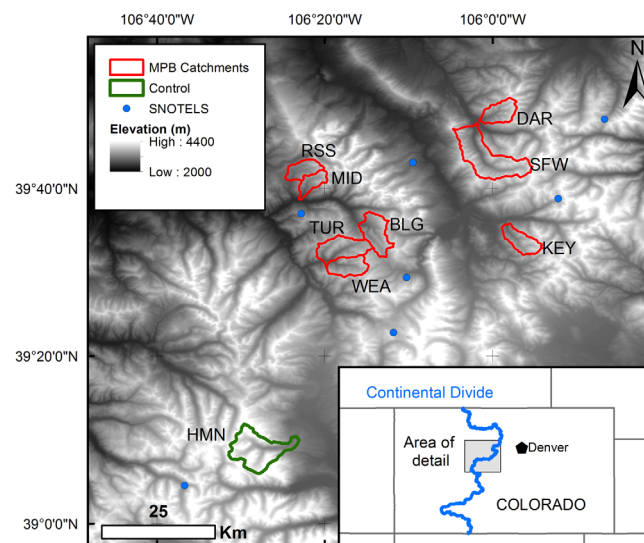


Figure 1. Map of the study region with detail area showing study catchments and nearby SNOTEL stations. See Table 1 for catchment codes and properties.

and runoff ratios ($RR = \text{streamflow} / \text{precipitation}$); and (iii) time-trend analysis, which quantifies changes to the empirical relationship between climate variables and streamflow. A secondary objective was to quantify any changes in subannual dynamics including seasonal distribution of flow between snowmelt and base flow periods, the peak daily flow, and the timing of snowmelt onset and peak flow. Recent work has shown that large-scale disturbance may advance the timing of snowmelt runoff and increase peak flow rates [Zhang and Wei, 2014; Winkler et al., 2015]. However, we focused our analysis on annual streamflow both to minimize impacts of unknown water storage residence times in these large basins

and to support our main objective of determining whether the bark beetle outbreak has impacted surface water supplies over the last decade.

2. Study Catchments

We identified eight catchments in the central Colorado Rockies affected by forest die-off triggered by bark beetles (Figure 1), a region with extensive bark beetle infestation since 1997 [Meddens et al., 2012; Meddens and Hicke, 2014]. These eight catchments were severely affected by a regional outbreak of mountain pine beetle (*Dendroctonus ponderosae*) that occurred in lodgepole pine (*Pinus contorta*) between 2004 and 2007, in addition to ongoing lower-level mortality of subalpine fir (*Abies lasiocarpa*) infested by western balsam bark beetle (*Dryocoetes confusus*). Catchment selection was based on the availability of continuous, long-term (43–49 years) streamflow records from catchments with unimpaired flow (no diversions or upstream regulation), forest cover greater than 60%, availability of tree mortality data, and availability of nearby meteorological data to consistently characterize climate, including snowfall, in mountainous terrain (Table 1; catchments are hereafter referred to using three-letter codes listed in column 1). All eight beetle-infested catchments were in the headwaters of the Colorado River basin within the USDA Forest Service (USFS) National Forest System in the Arapaho, Roosevelt, and White National Forests near the North American continental divide. WEA is a subcatchment (25 km²) contained within TUR (62 km²). We include both here because there are relatively few catchments with long-term records spanning the bark beetle outbreak that do not have significant impoundments or other disturbance, but we point out that streamflow from WEA

Table 1. Study Catchment Properties

Site	USGS Gauge	Area (km ²)	Mean Elevation (m)	Forest Cover (%)	Mean Annual Temperature (°C)	Mean Annual Precipitation (mm)	Mean Annual RR ^a	Affected Area (%)	First Year of Die-Off Period	Last Year Gauged
Black Gore Creek (BLG)	09066000	33	3259	69	−1.7	762	0.59	44	2006	2014
Darling Creek (DAR)	09035800	23	3335	74	−3.1	827	0.43	50	2004	2011
Keystone Gulch (KEY)	09047700	24	3303	84	0.4	730	0.33	49	2007	2014
Middle Creek (MID)	09066300	15	3187	86	0.4	762	0.43	50	2006	2014
Red Sandstone Creek (RSS)	09066400	19	3169	85	−0.1	762	0.54	35	2007	2008
S. Fork Williams (SFW)	09035900	71	3343	63	−1.7	827	0.52	42	2004	2014
Turkey Creek (TUR)	09063400	62	3270	84	−1.1	786	0.40	41	2006	2008
Wearyman Creek (WEA)	09063200	25	3301	81	−1.1	786	0.37	40	2006	2008
Halfmoon (HMN) ^b	07083000	61	3593	30	−2.5	789	0.55	2	NA ^c	2014

^aRR = Runoff ratio (Annual Streamflow/Precipitation).

^bControl catchment.

^cWhere useful for comparing pre- and post-outbreak periods, an artificial die-off date of 2006 was imposed for HMN.

and TUR are not fully independent. Four of the eight gauges were decommissioned between 2008 and 2011, unfortunately reducing the sample size available for future analyses. A nearby control catchment, HMN, had bark beetle effects in $\sim 2\%$ of catchment area, similar to background levels in this ecoregion.

Catchment boundaries were delineated from the National Hydrography Dataset Plus (www.horizon-systems.com/nhdplus) using the Basin Delineator Tool. Catchment elevation and aspect were derived from U.S. Geological Survey (USGS) National Elevation Dataset 30 m resolution data. Land cover in each catchment prior to bark beetle infestation was determined from the USGS coordinated Southwest Regional Gap Analysis Project (SWREGap; <http://earth.gis.usu.edu/swgap>). Spatial analyses were performed in ArcMap 10.2 (ESRI, Inc.), while statistical analyses and modeling were performed in MATLAB 2014a (Mathworks, Inc.).

Bark beetle-affected catchments were relatively similar physiographically. They ranged in size from 15 to 71 km², and mean elevation ranged from approximately 3150–3350 m (Table 1). Aspect was predominantly south and west in six catchments (DAR, KEY, TUR, BLG, MID, RSS) and was predominantly north and east in two catchments (SFW and WEA). Catchments contained minimal man-made structures or other disturbance and were on average 78% covered by forest (Table 1). Dominant cover types from the SWREGap data set were spruce-fir and lodgepole pine forest, with aspen forest in some catchments ($<15\%$), and remaining cover was classified as dry tundra or riparian shrubland. The control catchment (HMN) may have avoided bark beetle infestation due to its lesser forest cover (30%), higher elevation (3593 m), and likely elevation-dependent differences in dominant tree species (i.e., fewer beetle-susceptible lodgepole pine, more spruce and fir). To aid comparisons across basins of different sizes, all reported streamflow values are normalized by basin area.

3. Data Sets

3.1. Streamflow Data

This study used several publicly available data sets. Daily streamflow for each catchment was obtained from the USGS National Water Information System (<http://waterdata.usgs.gov/nwis>). All available streamflow observations were downloaded beginning in 1966, the first year after which observations were continuously available in all catchments, through 2014. Stream condition was unimpaired in each site's most recent USGS Annual Water Data Report (<http://wdr.water.usgs.gov>). In all study catchments, at least 84% of reported daily streamflow values were classified as "good" quality by USGS. Daily values were processed to compute monthly and annual streamflow (Q) using the hydrologic year (October–September) and normalized by catchment area.

3.2. Climate Data

Annual catchment precipitation (P) estimates were based on seven SNOTEL stations identified in the study area with continuous records beginning in 1981 or earlier (Figure 1; <http://www.wcc.nrcs.usda.gov/snow>). SNOTEL stations have weighing precipitation gauges equipped with a single-alter wind shield and are typically placed in small forest clearings. These steps are taken to minimize errors due to wind, and they provide the most reliable long-term precipitation observations near the study catchments and at similar elevations. Annual precipitation for each infested catchment was calculated using the arithmetic mean of the three nearest SNOTEL stations. Average horizontal and vertical distances between catchments and associated SNOTEL stations were 16 ± 1 km and 199 ± 56 m (± 1 standard error), while the standard deviation of annual precipitation among the three stations for a given catchment and year was, on average, 151 mm. Although annual precipitation varies over mountainous terrain, this approach provided temporal consistency, which is more important to our pre/post-outbreak analyses than absolute accuracy. For this reason, we did not use gridded climate estimates such as PRISM (www.prismclimate.org), wherein the stations incorporated change over time as they are deployed or decommissioned. We also evaluated the gridded precipitation and temperature data set of *Livneh et al.* [2013] based on a stable set of NOAA Cooperative Observation stations located mostly at lower elevations. The SNOTEL precipitation observations were more closely related to annual streamflow (average R^2 of 0.83 using SNOTEL as compared to 0.60 using *Livneh et al.* [2013]) although the study conclusions were not sensitive to the choice of precipitation data source. Only one SNOTEL station was found to be suitably close to HMN in distance, elevation, and mean annual precipitation (compared using *Livneh et al.* [2013]; annual precipitation from this station was closely related to HMN streamflow ($R^2 = 0.89$)). Due to known artificial trends in SNOTEL temperature records most likely

related to sensor changes [Oyler *et al.*, 2015], we used the annual temperature (T) estimates of Livneh *et al.* [2013] at the centroid of each catchment, which were available through hydrologic year 2011.

3.3. Forest Mortality Data

Bark beetle-driven forest mortality in each catchment was determined from USDA Forest Service insect and disease aerial survey maps beginning in 1997 [USDA Forest Service, 2010]. We present cumulative affected area through 2009, which is 2 years after the die-off period began in the last catchments (Table 1). A catchment was considered to be in the post-die-off period beginning in the first year that cumulative affected forest exceeded 20% of total catchment area, a threshold that has been reported as a minimum treatment area required for detecting streamflow response following forest cover change in multiple studies [Stednick, 1996; Brown *et al.*, 2005]. This definition is conservative since aerial surveys detect mortality when canopy changes are visible, which is generally the year after mortality actually occurs. This definition led to 2–11 years of post-outbreak streamflow data per catchment, which, given the time course of expected changes following mortality, should capture the peak of any catchment-scale hydrological responses [Brown *et al.*, 2005; Edburg *et al.*, 2012; Pugh and Gordon, 2013]. Hereafter “pre-die-off” refers to the available data record until the year prior to die-off, while “post-die-off” refers to all remaining years in the record. To evaluate the stability of the HMN control catchment in the runoff ratio comparison and time-trend analysis, an artificial die-off year of 2006 was imposed, representing the mean in the infested catchments.

4. Methods

Three methods of empirical analysis were used to evaluate annual streamflow. These are presented in order of increasing complexity and data requirements.

4.1. Double-Mass Paired Catchment Comparison

In double-mass analysis [Searcy and Hardison, 1960] we compared the slope of the relationship between cumulative annual streamflow (Q) since 1966 in each bark beetle catchment against that of the control catchment and used covariance analysis to test whether the relationship changed after bark beetle die-off at the 95% confidence level (i.e., were slopes different, one-way analysis of covariance, ANOCOVA). We also calculated annual residuals between observed streamflow and the prediction based on the pre-die-off relationship. Double-mass analysis was used in two paired catchment studies showing increased streamflow following bark beetle outbreaks in the Rocky Mountains [Love, 1955; Bethlahmy, 1974; Potts, 1984] and in studies of hydrologic effects from timber harvest and related management practices [Leaf, 1975; Zhao *et al.*, 2010; Zhang and Wei, 2012].

4.2. Comparisons of Streamflow, Runoff Ratio and Climate

Analysis of annual streamflow change following bark beetle die-off was conducted beginning in 1981 (beginning of our SNOTEL precipitation record) through a statistical comparison of pre- and post-die-off streamflow, where significant changes in streamflow or runoff ratio were interpreted as a potential bark beetle effect. A significant increase in post-die-off annual streamflow without an accompanying precipitation (P) increase would suggest that beetle-driven forest die-off acted to increase streamflow. Not all streamflow and climate observations were normally distributed [Lilliefors, 1967], therefore mean climate and runoff ratio ($RR = Q/P$) values pre- and post-die-off were compared using the nonparametric Mann-Whitney U test [Mann and Whitney, 1947], which makes no assumption about sample distribution. Examination of discharge autocorrelation plots suggested weak autocorrelation at a lag of 1 year in only one catchment (MID). Because this correlation was weak and the effect was small, no corrective procedures to account for autoregressive error were applied to the Mann-Whitney U test. Post die-off changes in RR were multiplied by post-die-off precipitation to estimate bark beetle effects on streamflow. In addition to annual climate and streamflow, we compared pre- and post-die-off streamflow by season (snowmelt streamflow as taken as the sum of April–July, and base flow as August–March), peak daily flow, and the mean dates of snowmelt onset and peak flow.

4.3. Time-Trend Analysis

A more robust method for quantifying the influence of forest cover changes on streamflow under variable climate is time-trend analysis [Bosch and Hewlett, 1982; Zhao *et al.*, 2010; Guardiola-Claramonte *et al.*, 2011].

Time-trend analysis involves three main steps. First, an empirical model is developed between streamflow and climate (here, precipitation and temperature) in each catchment, with a period of pre-die-off years reserved for independent model evaluation. Next, the model is used to predict streamflow for both pre-die-off evaluation and post-die-off periods, and residuals between observed and predicted values are calculated for each period. Finally, changes in the structure of residuals between the pre- and post-die-off periods indicate any beetle die-off effect. Here two forms of linear model were investigated. Precipitation variation was expected to be the dominant control on streamflow variation [Zhao *et al.*, 2010], and the first model quantified the pre-die-off empirical relationship as:

$$Q=a+bP \quad (1)$$

where a and b are fitted coefficients. Temperature was expected to exert negative control on streamflow due to its exponential relationship to vapor pressure deficit, itself a primary control on evaporative losses [Shuttleworth, 2012], and a temperature term was added to equation (1) to form the second model:

$$Q=a+bP+cT \quad (2)$$

Each model was calibrated to the pre-die-off period from 1981 until 5 years prior to die-off in each catchment. Following calibration, four assumptions of linear regression models were tested: (1) scatter plots confirmed the linear relationship between annual streamflow and precipitation (Supporting Information supporting information Figure S1); (2) residual histograms and the Lilliefors test for normality confirmed normal distribution of residuals; (3) residual homoscedasticity was detected from plots of residuals versus time and residuals versus predicted annual streamflow; and (4) residual independence was assessed from autocorrelation and lag plots. Weak lag-1 autocorrelation was evident in residuals of one study catchment (MID), but addition of variable lag terms to the regression equation did not improve the model or remove residual autocorrelation, and therefore no modifications were made.

The 5-year period between calibration and die-off was reserved as an evaluation period to test the empirical model's ability to provide accurate pre-die-off streamflow predictions. A one-sided t -test ($p<0.05$) was used to determine whether the mean residual during the evaluation period was different from zero. Similarly, a t -test was used to detect post-die-off residuals different from zero, indicating beetle die-off effects on annual streamflow. A bootstrap sampling approach was used to evaluate the sensitivity of the time-trend analysis to the choice of evaluation period, with the model calibration and residual comparisons repeated for all possible consecutive 5 year blocks.

5. Results

Following a description of beetle-driven forest die-off, streamflow analysis results from each method are presented in order of increasing complexity and data requirements.

5.1. Bark Beetle Die-Off

Within 2 years following the peak outbreak period (2004–2007), aerial surveys showed 35–50% of catchment area was affected by beetle-driven die-off (Table 1). Die-off occurred earliest in DAR and SFW (2004), resulting in 8 and 11 years of post-die-off streamflow data, respectively, and more recently (2006 or 2007) in the remaining study catchments, resulting in 9 years post-die-off in BLG and MID and 8 years in KEY. Shorter post-die-off analysis periods were possible for WEA, and TUR (3 years), and RSS (2 years) due to decommissioning of gauges (Table 1). The artificial die-off date of 2006 provided a “post-die-off” period of 9 years in the HMN control.

5.2. Subannual Hydrograph Comparisons

Mean monthly hydrographs did not suggest any consistent change in magnitude or timing of streamflow between the pre- and post-die-off periods (Figure 2). Snowmelt during April–July contributed 64–88% of mean annual streamflow in the bark beetle catchments, and 73% in HMN, similar to prior reports for the Colorado River headwaters [Clow, 2010]. No significant changes were found for annual precipitation between the pre- and post-die-off periods. No significant changes to amount or timing of peak daily streamflow were detected in the post die-off period (Mann-Whitney U-test, all $p>0.10$). Similarly, no

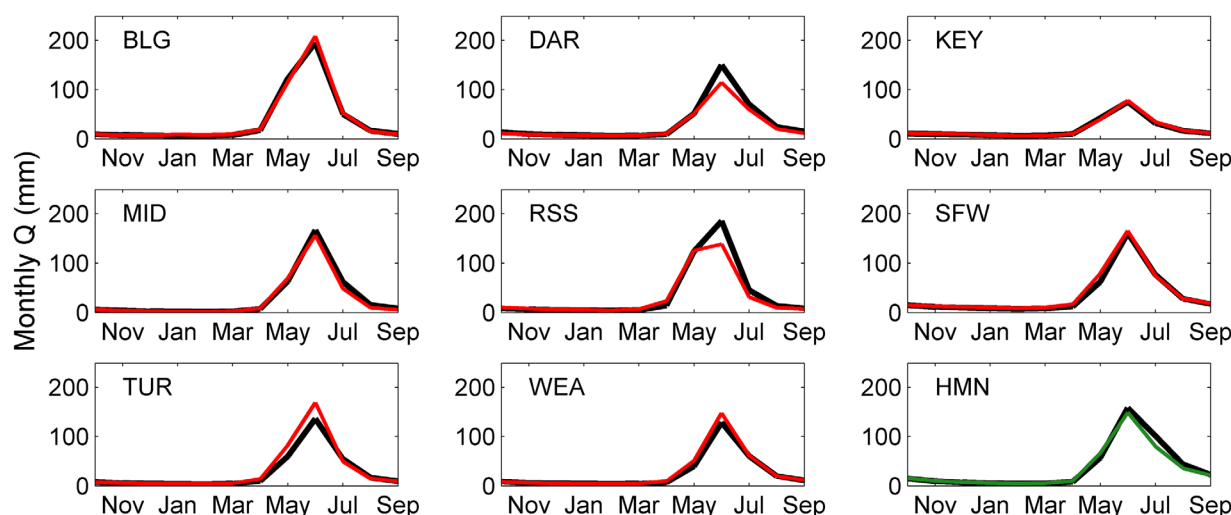


Figure 2. Mean monthly streamflow (Q) normalized by catchment area for pre- (black, since 1966) and post- (red) bark beetle die-off. For comparison with the post-die-off period in other catchments, streamflow for the Halfmoon (HMN) control catchment is shown in green for the period 2006–2014.

changes were detected in peak daily flow or the dates of snowmelt onset (first day of area-normalized flow > 1 mm) or peak flow.

5.3. Double-Mass Paired Catchment Comparison

Double-mass plots of cumulative annual streamflow in each bark beetle catchment against the control catchment showed only two significant and opposite responses to beetle die-off: a 17% streamflow decline in DAR, and a 14% increase in SFW, corresponding to the changes in slope (Figure 3), while the other six catchments showed no detectable change in their streamflow relationship to the control. DAR and SFW have adjacent outlets (Figure 1) and experienced similarly severe and early outbreak (Table 1), but the aspect of DAR was primarily south and west, while SFW faced predominantly north and east. Residuals from all catchments showed patterns of positive and negative periods that appeared to be coherent across study catchments (Figure 4). Double-mass

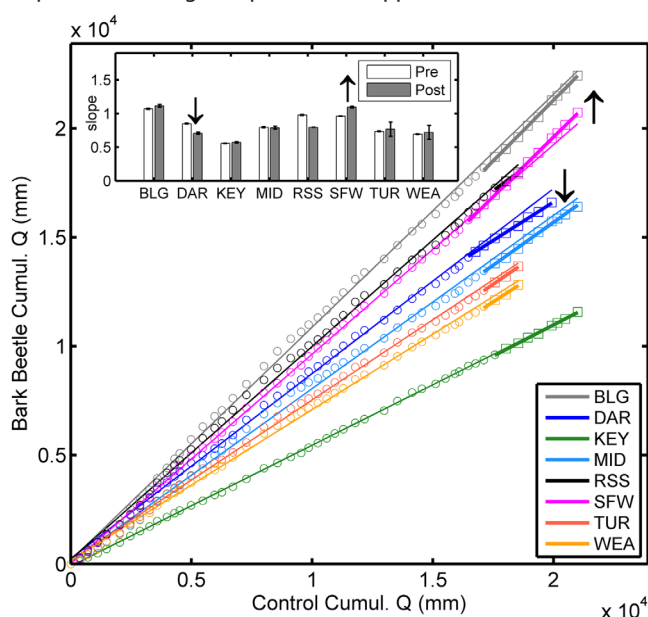


Figure 3. Double-mass plots of cumulative annual streamflow (Q) in each beetle-affected study catchment against cumulative Q in the control catchment (HMN) for years 1966–2014 or the last available year. Square symbols and thick lines indicate the post-die-off period. The inset panel shows slopes (\pm one standard error) pre- and post-die-off. Arrows indicate significantly different slopes ($p < 0.05$). Significant slope changes indicate the die-off effect on annual streamflow.

residuals were significantly related to the annual precipitation differences between a treatment catchment and the control ($Q_{\text{Residual}} = 0.54 \times (P_{\text{catchment}} - P_{\text{control}}) - 2.5$ mm; $R^2 = 0.27$; $p < 0.001$); this relationship was similar during the pre- and post-die-off periods.

5.4. Climate and Streamflow Comparison

Spatial variation of annual precipitation (P) across the bark beetle catchments in a given year was low (range ~ 100 mm) while temporal P variation in each catchment showed a larger range (~ 500 mm; Figure 5). Both annual streamflow normalized by basin area (Q) and runoff ratio ($RR = Q/P$) varied temporally with precipitation. Across all nine catchments P was highly correlated with Q (average $r = 0.91$) and with RR ($r = 0.71$). Annual mean temperature (T) showed similar ranges of spatial variation and within-catchment temporal variation,

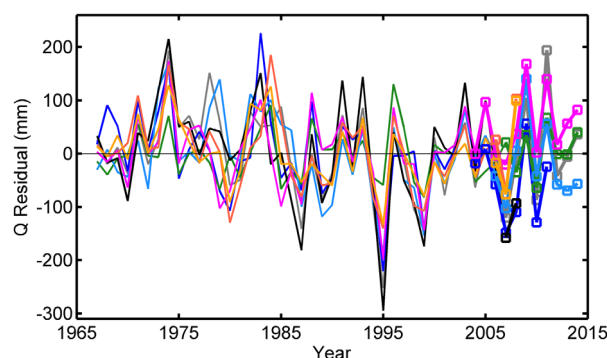


Figure 4. Annual residuals from the pre-die-off double-mass streamflow relationships shown in Figure 3. Square symbols and thick lines indicate the post-die-off period. Colors are as in Figure 3.

and 127 mm, respectively), suggesting that precipitation variation was the dominant control of streamflow variation.

Despite large changes in live tree cover, there were few significant differences between pre- and post-die-off climate and streamflow variables (Table 2, nonparametric Mann-Whitney U-test, $p > 0.05$). A small decline was found in mean annual T post-die-off for MID (-0.3°C). No significant changes were found for annual precipitation. The only significant change in area-normalized streamflow was a decline (-65 mm yr^{-1} in DAR). Since DAR mean P was on average greater by 16 mm post-die-off, the runoff ratio declined from 0.45 to 0.37, resulting in a calculated bark beetle effect of -67 mm yr^{-1} —a 21% reduction—similar to the 17% reduction indicated by the

significant double-mass slope change (Figure 3). Changes in mean snowmelt streamflow (March–June) between pre- and post-die-off periods (all nonsignificant) were nearly equal to the changes in mean annual streamflow (Table 2, $\Delta Q_{\text{SM}} \approx \Delta Q$). Changes in mean base flow (August–March Q) associated with forest-die were undetectable except in DAR, where there was a small but significant decline (-15 mm , $\sim -4\%$ of annual streamflow).

5.5. Time-Trend Analysis

In all catchments the annual precipitation-streamflow relationship (equation (1)) was highly significant ($p < 0.001$). Models described the observations well (Figure 6) and accounted for 74–96% of observed variability in annual streamflow during the calibration period (Table 3, individual model fits are shown in supporting information Figure S1). Model skill, as measured by mean absolute error (MAE), was similar during the calibration and evaluation periods for 7 of the 8 beetle catchments and the control (~ 30 – 60 mm yr^{-1} , Table 3). For SFW, the calibration MAE (21 mm) was lower than for the

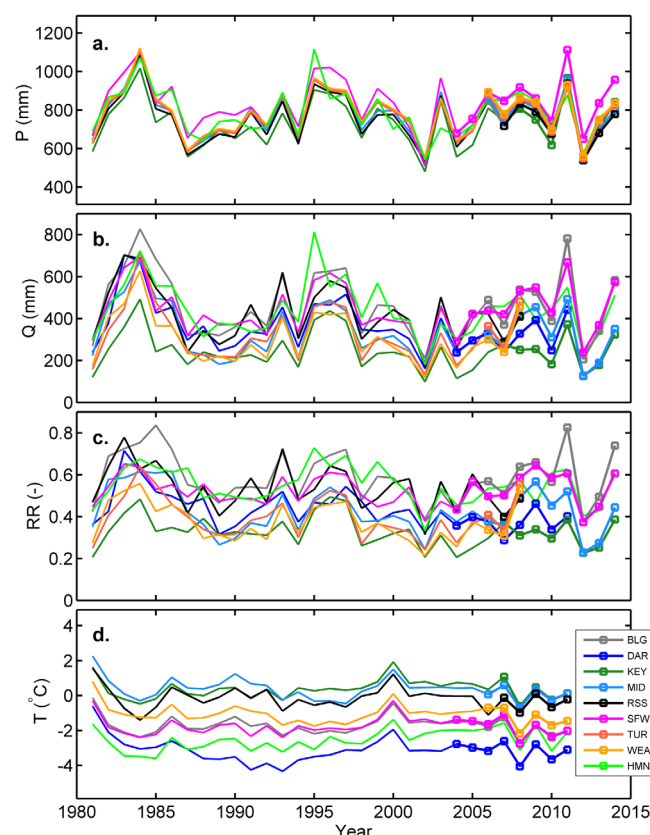


Figure 5. Mean annual (a) precipitation (P), (b) streamflow (Q), (c) runoff ratio ($RR = Q/P$), and (d) temperature (T) for each catchment for 1981–2014 (temperature record ends in 2011). Years with square symbols and thick lines indicate the post-die-off period.

Table 2. Differences Between Mean Pre- and Post-Die-off Climate and Streamflow^a

Site	Air Temperature ΔT_{mean} (°C)	Annual Precipitation ΔP (mm)	Base Flow ΔQ_{BF} ^b (mm)	Snowmelt ΔQ_{SM} (mm)	Annual Streamflow ΔQ (mm)	Runoff Ratio ΔRR	Estimated Bark Beetle Effect ^c (mm)
BLG	−0.3	+50	−2	+61	+59	+0.04	+31
DAR	0.0	+16	−15**	−52	−65*	−0.08**	−67**
KEY	−0.3	+53	+6	+13	+16	0.00	0
MID	−0.4*	+50	−8	+45	+37	+0.03	+23
RSS	−0.4	+20	−4	−71	−74	−0.09	−78
SFW	−0.1	+16	+7	+25	+30	+0.03	+25
TUR	−0.2	+63	−1	+52	+52	+0.04	+34
WEA	−0.2	+63	+1	+31	+32	+0.02	+17
HMN ^d	+0.4	+58	1	+23	+24	+0.00	0

^aPost-die-off mean minus pre-die-off mean (from 1981 to the last year prior to die-off, see Table 1). Pre- and post-die-off period observations significantly different at * $p < 0.10$;

** $p < 0.05$ using the nonparametric Mann-Whitney U test.

^b ΔQ_{SM} = Snowmelt period streamflow, April–July, ΔQ_{BF} = Base flow, August–March. All other values are annual.

^cThe product of post-die-off mean P with change in runoff ratio ($\text{RR} = Q/P$).

^dTo facilitate comparisons, an artificial die-off date of 2006 was imposed for the HMN control.

evaluation period (53 mm). A model form that included a temperature term (equation (2)) did not show any improvement in model skill as compared to equation (1), and temperature was not a significant predictor of annual streamflow in any catchment (see supporting information Table S1). Based on a lack of model improvement, the additional complexity of equation (2) was not warranted, and equation (1) was used for the time trend analysis.

Time trend analysis indicated that bark beetle die-off for a given catchment had either a negative effect or no significant effect on annual streamflow (Table 3). Mean residuals during the evaluation period were not different from zero in any catchment, but post-die-off residuals were significantly less than zero (i.e., streamflow was less than predicted) by 27–100 mm in three catchments (DAR, RSS, $p < 0.05$, and KEY, $p < 0.10$). Bootstrap analysis showed the time-trend results were largely insensitive to the choice of evaluation period (supporting information Figure S2). Similarly, time-trend conclusions were not affected by the inclusion of

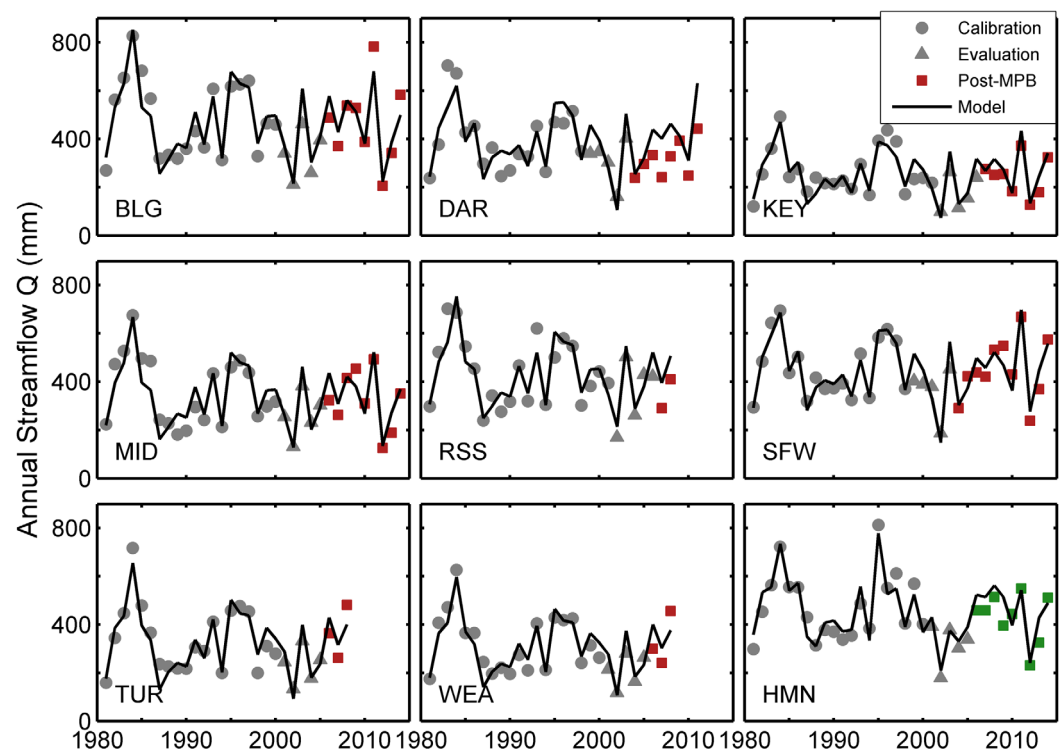

Figure 6. Annual streamflow beginning in 1981 observed and modeled with the empirical model $Q = a + bP$ (equation (1)). Model parameters and statistics are shown in Table 3. Model fits are shown in supporting information Figure S1.

Table 3. Linear Regression Model Coefficients^a, Skill, Statistics and Estimated Bark Beetle Effects on Annual Streamflow (Q), 1981–2014

Site	Intercept a (mm)	Slope b	Calibration MAE ^b (mm)	Evaluation MAE (mm)	R ²	Post-Die-off Streamflow Change ΔQ	
						Mean Residual (mm)	Std. Error (mm)
BLG	−407	1.15	42	48	0.88	−3	(21) ^c
DAR	−328	0.87	53	69	0.74	−89 ^{**c}	(24)
KEY	−267	0.72	31	42	0.86	−27 [*]	(11)
MID	−394	0.98	45	45	0.83	−21	(19)
RSS	−325	0.99	43	42	0.82	−100 ^{**}	(4)
SFW	−308	0.91	21	53	0.96	−3	(16)
TUR	−455	0.99	39	34	0.87	−13	(47)
WEA	−369	0.86	33	44	0.88	−27	(55)
HMN	−322	0.99	37	30	0.89	−36	(19)

^aParameter estimates of equation (1): $Q = a + bP$. Model fits are shown in supporting information Figure S1.

^bMean absolute error (MAE) between observed and modeled annual streamflow.

^c**denotes significant effect at $p < 0.05$. *denotes significant effect at $p < 0.10$.

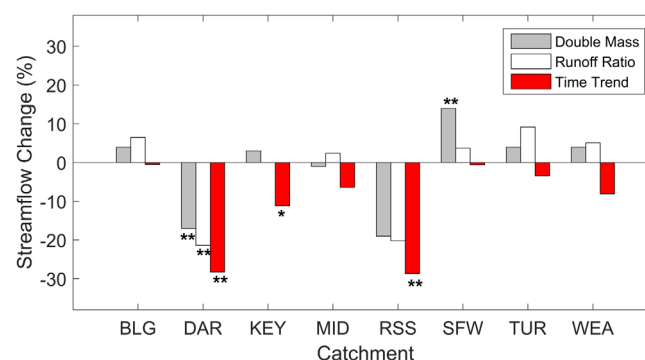
temperature in the regression model (equation (2)) except for KEY, where the negative bark-beetle effect was slightly larger (−30 mm versus −27 mm) but became nonsignificant ($p = 0.20$; supporting information Table S1). In other words, when we accounted for temperature, streamflow in KEY was not significantly less than predicted. In comparison to residuals from the double-mass analysis (Figure 4), time-trend residuals (supporting information Figure S3) were smaller (± 100 mm as compared to ± 200 mm) and showed less coherent behavior among catchments.

5.6. Comparison of Streamflow Response Among Methods

Collectively, the three empirical analysis methods suggested streamflow response to forest die-off was undetectable in most catchments (Figure 7). Of the twenty-four evaluations conducted (three methods in eight catchments), five showed significant streamflow declines of 11–29%, one showed a 14% increase, and 18 showed no effect.

6. Discussion

Using three types of empirical analysis across eight subalpine headwater catchments of the Colorado River, we found annual streamflow changes were mostly undetectable during the decade following bark beetle-driven forest die-off, with one catchment consistently showing a decline (Figure 7). These results do not support expected streamflow increases based on historical paired catchment studies, experimental harvests, recent modeling and remote sensing analyses, and process studies focused on interception and transpiration. Importantly, our findings contrast with reported increases of 14–26% in the two studies from prior outbreaks, which are among the most highly cited papers on basin-scale hydrologic response to bark beetle infestation [Bethlahmy, 1974; Potts, 1984]. These influential studies were conducted in the same central Rocky Mountain region and used the same double-mass paired-catchment method we used, but they did not


Figure 7. Percent change in annual streamflow following bark beetle die-off determined by three empirical methods. **denotes significant effect at $p < 0.05$. *denotes significant effect at $p < 0.10$.

benefit from the modern climate data sets that enabled the runoff ratio and time trend analyses presented here. We therefore discuss the relative merits of the empirical methods employed by this and prior studies, and we evaluate these results in the context of the literature on experimental harvest and emerging process understanding from smaller-scale research.

Our conclusion that bark beetle effects on annual streamflow were primarily undetectable or occasionally negative was mostly insensitive to the choice of empirical analysis method (Figure 7).

Runoff ratio comparison (Table 2) was considered to be the weakest method, because proportionality between streamflow and precipitation incorrectly implies passage through the origin. Instead, observations show that annual precipitation must exceed a minimum evaporative loss threshold before appreciable streamflow occurs [Stednick, 1996; Flerchinger and Cooley, 2000; Biederman et al., 2014a]. In our bark beetle catchments, modeled intercepts for equation (2) averaged -357 mm, while slopes averaged 0.93 (Table 3). Inversion of equation (2) using this average parameterization suggests a minimum evaporative loss threshold of 383 mm (i.e., the intercept of the precipitation axis, supporting information Figure S1), or nearly 50% of mean annual precipitation (Table 1). This minimum precipitation threshold of 383 mm is somewhat similar to the precipitation threshold of 500 mm reported by Bosch and Hewlett [1982] for detection of annual streamflow response to forest cover changes.

While double-mass analysis often produces inferences consistent with other empirical methods [Zhao et al., 2010] and requires only streamflow observations, spatial variability in climate could alter the paired catchment relationship. This is the main uncertainty in the present analysis, where the catchments showing significant cumulative streamflow effects (Figure 3; DAR, SFW) were furthest from the control catchment, ~ 75 km, and ~ 250 m lower in elevation. These differences highlight the difficulty of finding a suitable control in paired-catchment analysis of nonexperimental disturbances. While double-mass analysis indicated a 14% streamflow increase in the die-off period for SFW (Figure 7), both methods that explicitly included precipitation (i.e., runoff ratio and time-trend) found no significant effect in SFW. Our finding that the precipitation difference between a bark beetle catchment and the control predicted double-mass residuals supports the idea that climate differences between catchments, rather than bark beetle effects, could explain the paired-catchment inference of streamflow increase in SFW [Brown et al., 2005; Zhang et al., 2012; Burt et al., 2015]. As a further example, the pre-die-off double-mass residuals in the present study might falsely indicate an increase during the mid-1980s or a decrease during 1995–1999 (Figure 4). Likewise, climate differences could have influenced the results of Bethlahmy [1974] and Potts [1984], who paired much larger basins (500–2000 km²) with likely greater spatial variability in precipitation. This could explain why Bethlahmy did not find maximal streamflow increase until 15 years after outbreak, while the strongest response would be expected within 1–3 years, based on bark beetle hydrologic process impacts [Pugh and Small, 2012; Hubbard et al., 2013; Biederman et al., 2014b] and experimental harvest streamflow [e.g., Bosch and Hewlett, 1982; Stednick, 1996; Andréassian, 2004].

Time-trend analysis was considered the most robust empirical analysis method, because it accounts for a minimum evaporative loss threshold and incorporates the effects of climate variation [Zhao et al., 2010]. SNOTEL-based estimates of catchment precipitation used here could include biases due to gauge undercatch or small elevation differences [Rasmussen et al., 2012]. However, time-trend analysis depends mainly on temporal consistency of the observations, and our confidence in the SNOTEL precipitation observations is supported by their ability to explain 74–96% of the variation in pre-die-off annual streamflow (Figure 6 and Table 3). We had expected to find predictive power in mean annual temperature, an indicator of energy available to drive evaporative losses. However, temperature did not improve the models (supporting information Table S1), possibly due to negative correlation with precipitation (i.e., wetter years tended to be cooler).

The present multidecade study should be considered in the context of regional climate change, which could affect the results in two ways. First, if temperatures were greater in the post-die off period, evaporative losses could increase, potentially counteracting the streamflow increases we expected. While mountain temperatures were thought to have increased during the period of our study at SNOTEL stations across parts of Colorado and the Intermountain West [Clow, 2010; Harpold et al., 2012], it has recently been shown that instrumental bias caused overestimation of temperature trends [Oyler et al., 2015]. Here comparison of pre- and post-die-off periods showed mostly nonsignificant temperature declines in the bark beetle catchments, while the control catchment showed a nonsignificant increase (Table 2). If these small temperature changes had any effect, it would likely be to decrease evaporative losses (and increase streamflow) in the bark beetle catchments while decreasing streamflow in the control, thereby introducing a false positive bark beetle effect on streamflow. Therefore, our finding that streamflow did not increase is conservative. The second possible climate change effect would be an increase in atmospheric evaporative demand enhancing snowpack sublimation, obscuring potential streamflow increases resulting from beetle kill. While we do not have catchment-level snowpack observations, recent studies show the region of the present study catchments (Figure 1) is high enough in elevation with cold enough winter temperatures (-5°C) that

sublimation losses show no trends [Clow, 2010; Harpold *et al.*, 2012]. These studies suggest that the relationship between precipitation and snowmelt volume did not change in the open areas where SNOTEL stations are located. Hence, post-die-off streamflow is likely determined by precipitation and forest ecohydrological process changes.

While process observations were beyond the scope of this study, several factors likely regulate the effects of bark beetle disturbance on net evaporative losses (i.e., interception, snowpack sublimation, transpiration, and evaporation), providing context for the absence of streamflow increases. Whereas harvest studies often used strip or patch cut patterns, which appear to optimize the trade-off between interception and solar shading and maximize peak snowpack [Troendle and King, 1985; Golding and Swanson, 1986], beetle-driven mortality tends to be distributed more evenly across affected stands, allowing penetration of wind and solar radiation to drive increased snowpack sublimation [Biederman *et al.*, 2014b]. Increased transpiration by surviving vegetation, which has been inferred from increased carbon uptake and greater tree ring widths [Veblen *et al.*, 1991; Berg *et al.*, 2006; Brown *et al.*, 2010], may be facilitated by the diffuse nature of beetle mortality. In a study of harvest gap sizes, neighboring lodgepole pines utilized nutrient resources from gaps of less than 15 harvested trees (~ 8 m diameter, twice the radius of lateral roots) [Parsons *et al.*, 1994], implying that increased soil water uptake by surviving vegetation is likely when disturbance is diffuse and produces gaps smaller than the radii of lateral roots. Accordingly, annual streamflow response to bark beetle disturbance was more likely to be positive in basins dominated by even-aged stands [Stednick and Jensen, 2007], which were more likely to have contiguous areas of heavy mortality, producing large gaps where soil moisture surpluses are inaccessible to roots of surviving trees. Streamflow response may also be counteracted by transpiration from the understory, which can respond rapidly after beetle infestation [Norton *et al.*, 2015].

Reliable prediction of how forest mortality will affect streamflow in a given catchment will require process-based understanding of interactions among canopy, topography, and climate distributed across the landscape. Spatially, the evaporative loss responses which integrate to control basin-scale streamflow are likely variable within and across catchments and dependent on aspect, topographic shading, and the location of affected forest stands [Rinehart *et al.*, 2008]. For example, canopy loss on exposed slopes can be expected to increase snowpack sublimation and evaporation, reducing streamflow, while mortality on shaded slopes may reduce transpiration and snow sublimation from the canopy without compensatory response from the subcanopy, increasing streamflow. These trade-offs are likely related to solar radiation patterns controlled by topography and forest geometry [Troendle and King, 1987; Zou *et al.*, 2007; Pomeroy *et al.*, 2012]. The two basins with the greatest significant declines in streamflow were RSS and DAR. With only 2 years of observations post-die-off we are hesitant to draw conclusions about RSS, but DAR had 8 years of observations and showed a significant streamflow decline by all three analysis methods. DAR was one of the first catchments affected by bark beetle, and it had the highest percentages of total area affected (50%), forest area affected (67%), and SW aspect (70%). While a detailed spatial analysis remains a useful topic for future work, here we speculate that severe canopy mortality on slopes with high solar radiation exposure increased evaporative losses from the subcanopy, reducing streamflow.

Our results underscore the challenges of extrapolating point-scale ecohydrological process observations to predict annual water resources in large basins. In the present bark beetle epidemic, initial process-level observations at scales of plots to stands documented reduced interception [Boon, 2012; Pugh and Small, 2012; Biederman *et al.*, 2014b] and transpiration [Hubbard *et al.*, 2013], consistent with increased soil moisture [Clow *et al.*, 2011], leading to predictions of increased streamflow [Pugh and Gordon, 2013]. However, observations of increased snowpack sublimation and soil water evaporation illustrated mechanisms that could counteract streamflow increases [Biederman *et al.*, 2014a, 2014b]. Intermediate-scale observations of ecosystem-scale ET and small catchment streamflow showed that the net effect of these competing process responses could vary in magnitude and direction [Brown *et al.*, 2013; Biederman *et al.*, 2014a; Frank *et al.*, 2014], possibly due to site factors including the spatial arrangement of mortality and interactions of terrain, canopy, and climate. The results of the present study suggest that the integrated effects of competing processes and variable landscapes within large basins may lead to minimal water resources impacts from forest disturbance. Linking spatially variable processes to basin-scale response requires further developments in high-resolution mortality mapping [Meddens *et al.*, 2012; Meddens and Hicke, 2014], laser mapping of terrain and canopy (i.e., LiDAR) [Harpold *et al.*, 2015], and spatially explicit forest models of water and energy partitioning [Broxton *et al.*, 2014].

7. Conclusions

We found that annual streamflow changes following beetle-induced forest mortality were most often undetectable, while one basin with severe mortality and a predominantly southwest aspect consistently showed reduced streamflow. These results contrasted with historical paired catchment studies from earlier beetle outbreaks in the central Rocky Mountain region [Love, 1955; Bethlahmy, 1974; Potts, 1984], which may have been influenced by the researchers' lack of data on spatial and temporal climate variability. A lack of significant streamflow changes contrasts with the experimental harvest literature [i.e., Bosch and Hewlett, 1982; Stednick, 1996; Brown *et al.*, 2005], which suggests significant streamflow increases in basins with ~800 mm annual precipitation and 30–50% of forest area affected. Therefore, experimental harvest may not be an apt proxy for bark beetle disturbance. Finally, the observations presented here do not support expectations of increased streamflow in the wake of the present beetle outbreak based on remote sensing and models, highlighting the importance of empirical work in evaluating the tools used for basin-scale hydrologic prediction.

Acknowledgments

All of the data sets used herein were downloaded from publicly available sources. The gridded temperature forcing data set [Livneh *et al.*, 2013] is available at <ftp://ftp.hydro.washington.edu/pub/blivneh/CONUS/>. SNOTEL data are available at <http://www.wcc.nrcs.usda.gov/snow> for the six stations used: 335, 415, 485, 505, 802, and 842. Streamflow data are available at <http://waterdata.usgs.gov/nwis> for the gauge numbers listed in Table 1. Land cover data for the Southwest Regional Gap Analysis are available at <http://earth.gis.usu.edu/swgap>. Catchment boundaries are available from www.horizon-systems.com/nhdplus. Aerial survey forest health data are available from http://www.fs.usda.gov/detail/r2/forest-grasslandhealth?cid=fsbdev3_041629. The authors wish to thank those individuals and organizations who collected and made these data available. This work was supported by the following awards: NSF EAR9876800, NSF EAR0910831, NSF EAR0724958, and DOE TCC 10-287. A. Harpold was supported by NSF EAR1144894 and USDA NIFA NEV05293. The National Center for Atmospheric Research is sponsored by the National Science Foundation (NSF AGS-0753581). We thank Younes Alila and three anonymous reviewers for their thoughtful comments.

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