Spruce Beetle Outbreak Increases Streamflow from Snow-Dominated Basins in Southwest Colorado, USA

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November 24, 2022

Abstract

Bark beetle outbreaks have impacted over 58 million acres of coniferous forest in the Western US since 2000, an area slightly larger than the state of Utah. Most of these beetle-impacted forests are in semi-arid, snow-dominated headwater catchments that generate a disproportionate fraction of water supplies. Limited previous studies have shown severe beetle-kill can cause mixed increases and decreases in streamflow. This study is the first to empirically explore changes in streamflow following a recent spruce beetle outbreak in southwest Colorado using a paired catchment approach. The period following beetle kill (2014-2019) was 0.95° C warmer and 5.8 cm/year drier than the 21-year period prior to the disturbance's peak (1993-2013). There was no change in streamflow in the control basins after beetle kill. In contrast, post-beetle kill had 34% higher peak flows on average and consistent predictions of >14% increases in streamflow in wetter basins and >20% in drier basins. Our results suggest that higher streamflows are primarily driven by 44% higher runoff efficiencies during the snowmelt period. The increased flows due to beetle kill are occurring at a time when control catchments have unchanged runoff efficiencies. These findings are the first to clearly show streamflow increases following extensive spruce beetle kill in watersheds that contribute water to millions of downstream residents. Moreover, our findings contrast with evidence of unchanged or decreased streamflow following mountain pine beetle kill in nearby parts of Colorado, highlighting the need for better post-disturbance hydrologic predictions in these important montane forests.

Spruce Beetle Outbreak Increases Streamflow from Snow-Dominated Basins in Southwest Colorado, USA

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Key Points:

- Multiple lines of evidence indicate that basin streamflow efficiency increases following widespread tree mortality in subalpine forests.
- Streamflow increases following beetle kill despite decreases in non-impacted (control) streamflow due to climate conditions.
- Streamflow increases contrast with little streamflow response to bark beetle impacts in nearby lodgepole pine forests.

Abstract

Bark beetle outbreaks have impacted over 58 million acres of coniferous forest in the Western US since 2000, an area slightly larger than the state of Utah. Most of these beetle-impacted forests are in semi-arid, snow-dominated headwater catchments that generate a disproportionate fraction of water supplies. Limited previous studies have shown severe beetle-kill can cause mixed increases and decreases in streamflow. This study is the first to empirically explore changes in streamflow following a recent spruce beetle outbreak in southwest Colorado using a paired catchment approach. The period following beetle kill (2014-2019) was 0.95° C warmer and 5.8 cm/year drier than the 21-year period prior to the disturbance's peak (1993-2013). There was no change in streamflow in the control basins after beetle kill. In contrast, post-beetle kill had 34% higher peak flows on average and consistent predictions of >14% increases in streamflow in wetter basins and >20% in drier basins. Our results suggest that higher streamflows are primarily driven by 44% higher runoff efficiencies during the snowmelt period. The increased flows due to beetle kill are occurring at a time when control catchments have unchanged runoff efficiencies. These findings are the first to clearly show streamflow increases following extensive spruce beetle kill in watersheds that contribute water to millions of downstream residents. Moreover, our findings contrast with evidence of unchanged or decreased streamflow following mountain pine beetle kill in nearby parts of Colorado, highlighting the need for better post-disturbance hydrologic predictions in these important montane forests.

Plain Language Summary

Since 2000, bark beetles have damaged over 58 million acres of conifer forest in the Western US. Forest canopy has important but complex effects on snow and water use in mountain basins, which are an important source of streamflow. Previous studies exploring how beetle kill affects streamflow have had mixed results, with some suggesting that beetle kill causes increased streamflow and others finding no significant effects. We use measurements of streamflow and climate in six beetle-impacted basins and two unaffected basins in southwest Colorado to determine if streamflow changed after a spruce beetle outbreak. We found that streamflow in beetle-impacted basins was 14.5%-47.2% higher after beetle kill, while streamflow in basins unaffected by beetle kill did not change. Streamflow increased the most during snowmelt, with less effect of Winter low flows. These findings suggest that beetle kill could have important

impacts on the timing and volume of water resources, and that effects vary between forest types and locations.

1 Introduction

Disturbance of montane forests that supply critical streamflow to downstream resources remains an active area of research (NRC, 2008) with substantial implications on large-scale water availability and carbon budgets (Williams et al., 2016; Zhang et al., 2017). Recent insect outbreaks have caused widespread forest mortality in forested snow dominated catchments in the Western US (Meddens et al., 2012). Bark beetles, in particular spruce beetle (*Dendroctonus rufipennis*) and mountain pine beetle (*Dendroctonus ponderosae*), have affected approximately 58.8 million acres of coniferous forest in the region since 2000 (USFS, 2020). In bark beetle outbreaks, mortality rates are usually highest in newly affected forest stands because negative feedbacks in infection rates limit re-infection of previously impacted stands (Hart et al., 2015). Bark beetle population growth over the last several decades has been attributed to a combination of increased reproduction rates (Mitton & Ferrenberg, 2012) and warmer temperatures (Pettit et al., 2020). Bark beetles and associated secondary fungal infections restrict water uptake and eventually kill host trees over the course of a growing season (Hubbard et al., 2013; Frank et al., 2014). Dead host trees drop their needles over a period of 1-3 years, but in contrast to trees affected by logging and stand-replacing fire, they can remain standing for many years (Rhodes et al., 2020). Consequently, bark beetles cause a reduction rather than complete removal of forest canopy (Edburg et al., 2012). Canopy reduction is spatially and temporally heterogenous, as mortality rates in beetle-impacted forests can vary between outbreaks, and from stand to stand (CSFS, 2019). Cumulative effects on canopy can be large in basins with higher mortality rates, where in some cases, 70%-90% of mature trees are killed (CSFS, 2019).

Following extensive forest canopy reduction due to bark beetles (referred to as beetle kill) and other disturbances, relative changes in canopy and understory evapotranspiration fluxes can combine to increase and decrease streamflow efficiency (amount of streamflow per amount of precipitation), making the overall effect on streamflow challenging to assess (Goeking & Tarboton, 2020; Brown et al., 2005). Most early studies assessing beetle kill impacts on streamflow used relatively simple methods to estimate total annual stream discharge and showed increases in streamflow relative to pre-disturbance observations or control basins (Bethlahmy, 1974; Love, 1955; Bosch & Hewlett, 1982). Recent studies that better account for climate variability, particularly inter-annual variation in precipitation, suggest that the hydrologic effects of beetle kill are mixed (Goeking & Tarboton, 2020.; Brown et al., 2005), with some showing increasing steamflow (Livneh et al., 2015) and others showing minimal effects or decreased streamflow (Biederman et al., 2015; Slinki et al., 2016). Although complex physical hydrology models provide potential to isolate processes to determine cause and effect in complex systems, physical models are less likely to predict the mixed effects of beetle kill on streamflow response seen in recent observational studies (Chen et al., 2015; Livneh et al., 2015). In general, process models try to simulate decreases in overstory transpiration and interception and increased understory transpiration, soil evaporation, and snowpack sublimation (Goeking & Tarboton, 2020). Despite these competing processes, models generally show increased streamflow (Livneh et al., 2015; Penn et al., 2016), less sublimation (Frank et al., 2019; Sexstone et al., 2018), more snowmelt (Chen et al., 2015), and decreased evapotranspiration (Frank et al., 2014; Knowles & Molotch, 2019). This contrasts with a growing body of observations supporting increases in snowpack sublimation (Biederman et al. 2014a) and compensating ET losses (Brown et al., 2014) causing reduced or minimal changes in streamflow volumes after beetle kill (Slinski et al., 2016). There remains an active research effort to understand how model simplifications, such as unaddressed measurement uncertainty and neglecting fine-scale spatial heterogeneity in snow and evapotranspiration, may bias these compensating vapor losses (Mazzoti et al., 2020; Krogh et al., 2020; Frank et al., 2019; Millar et al., 2017; Broxton et al., 2015; Chen et al., 2015; Moeser et al., 2020), and limit our ability to predict post-disturbance streamflow response.

In forested snow dominated catchments, forest canopy structure plays an important, but complex role in snowpack and related vaporization processes like sublimation and interception (Knowles et al., 2015; MacDonald & Stednick, 2003; Molotch et al., 2009; Varhola et al., 2010). Forest canopy intercepts snowfall, which can sublimate more readily from increased surface area and turbulence compared to the snowpack on the ground (Frank et al., 2019). Canopy also reduces shortwave radiation by shading the snowpack and reducing subcanopy wind speeds (Bernier, 1990; Pomeroy & Dion, 1996) that both increase following canopy loss and affect snowpack ablation from melt and sublimation (Biederman et al., 2014a). Modeled sublimation rates in the northern Colorado were predicted to decrease slightly after beetle kill (-0.03 mm d-1) because an increase in snowpack sublimation partially compensated for decreasing canopy-intercepted snow sublimation (Sexstone et al., 2018). However, these modeling results largely ignore the differences in forest structure due to forest species, forest gaps, and other factors that may lead to highly variable snowpack response to beetle kill (Broxton et al., 2015; Mazzotti et al., 2020). For example, Boon (2007) observed higher maximum SWE and similar ablation rates in a lodgepole pine stand impacted by mountain pine beetles (MPB) in British Columbia. In northern Colorado, accumulations of SWE were greater in MPB-impacted stands relative to unimpacted stands, but melted more rapidly (Pugh & Small, 2012), or were compensated by snowpack sublimation (Biederman et al., 2014a), resulting in unchanged SWE. In contrast, beetle-impacted spruce forests in the same region had reduced canopy sublimation (interception losses) that exceeded increases in snowpack sublimation, resulting in greater peak SWE (Frank et al., 2019). Previous studies showing mixed snowpack response to beetle kill may not be surprising given the variation between study areas' pre-disturbance vegetation structure (e.g. tree species, forest cover, etc.) and local physiographic conditions (Molotch et al., 2009), as well as how the post-disturbance forest structure changes with respect to topography (Moeser et al, 2020).

In addition to snowpack effects from beetle kill, compensating vapor losses during the growing season remain a key to predicting forest water balance and streamflow response. While canopy transpiration ceases from beetle-killed trees (Hubbard et al., 2013), total ecosystem evapotranspiration (ET) rates may be unchanged due to compensatory ET from the sub-canopy or remaining trees (Reed et al., 2016; Biederman et al., 2014b) as they respond to decreased competition for resources with rapid growth (Brown et al., 2014; Millar et al., 2017). Biederman et al (2014b) observed isotopic evidence of increased soil evaporation following beetle kill in WY. In addition, ET can significantly decrease following beetle kill then rebound after 20-30 years and exceed pre-beetle ET rates as the canopy becomes re-established (Vanderhoof & Williams, 2015). Following severe spruce beetle outbreaks, re-establishment of canopy-forming spruce trees, and associated increase in canopy transpiration rates is difficult to predict (Pettit et al., 2019). Additionally, beetle kill may facilitate a shift in forest type, favoring fir- or aspen-dominated regrowth (Bretfeld et al., 2016; DeRose & Long, 2010), which would result in different canopy and subcanopy transpiration rates than re-establishment of spruces (LaMalfa & Ryle, 2008). Transpiration from conifer forests is a primary term in the water budget that is expected to respond to climate change (McCabe & Wolock, 2020; Lehner et al., 2017).

In this study, we explore how an ongoing spruce beetle outbreak in headwater basins in southwest Colorado, USA impacts the magnitude and timing of streamflow. Since the early 2000s, a new spruce beetle outbreak has affected over 1.8 million acres of forest in the Southern Rocky Mountains, mostly in southwest Colorado's Hinsdale, Gunnison, Rio Grande, Mineral, and Saguache counties (CSFS, 2019). Mortality rates of 50-90% are common in affected areas (CSFS, 2019), which contain the headwaters of economically and ecologically important rivers, including the Rio Grande and large tributaries of the Colorado River like the Gunnison and San Juan Rivers. Consequently, streamflow impacts from beetle kill could have regional implications for water resources, flood management, and water managers' responses to climate change (Bennett et al., 2019; Booker et al., 2005; Hurd & Coonrod, 2007). Despite the outbreak's scale and regional importance, its impacts on streamflow efficiency and timing remain unknown. To address this knowledge gap, we utilize an expanded paired-catchment approach (i.e. multiple control and impacted basins) to compare streamflow before and after beetle kill in eight snow dominated montane catchments to answer the following questions:

1. How does climate differ pre- and post-beetle kill?
2. How does streamflow efficiency and predicted streamflow compare pre- and post- beetle kill?
3. Does seasonal streamflow response suggest changes in streamflow result from snow season or growing season processes?

We use 27 years of ground-based streamflow, snow, and climate observations to determine change between a pre-beetle (1993-2013) and post-beetle period (2014-2019) in eight beetle kill-impacted basins and two unimpacted control basins. We use a modified version of the Biederman et al., (2015) methods applying three empirical streamflow comparisons: statistical divergence from control conditions, multiple linear regression, and non-parametric runoff ratio comparison. Additionally, we add estimates of seasonal streamflow amount and timing to infer the causes of widespread streamflow increases following change.

2 Methods

2.1. Study Area

The study was conducted for eight basins in southwest Colorado. These included two control basins, the Uncompahgre (c-UN) and San Miguel (c-SM) river basins, and six basins with extensive beetle-related spruce mortality: Lake Fork (LF), Cochetopa Creek (CC), Tomichi Creek (TO), Vallecito Creek (VA), the Rio Grande River (RG), and the Conejos River (CN) (Table 1).

Basin selection prioritized catchments in which bark beetles had impacted at least 50% of spruce forest cover, that contained no major man-made reservoirs or diversions, and had at least 25 years of stream gauge and precipitation data. Basins range in mean elevation from 3038 to 3436 meters above sea level, and all include alpine, subalpine, and montane riparian ecosystems. Basin-wide mean precipitation, temperatures, and potential evapotranspiration (PET) were found using the NLDAS gridded data product (Xia et al. 2012). Mean annual precipitation and mean annual temperature ranged from 402 mm/yr to 917 mm/yr and from 1.3 °C to 3.4 °C, respectively.

Table 1. Basin attributes, where "c-" denotes control basin. See section 2.1 for basin names and abbreviations.

Basin	Area (km^2)	Mean Elevation (m)	Area Above 3600m (%)	Spruce Forest Cover (%)	Spruce Forest Affected (%)	Total Area Affected (%)	USGS gage	SNOTEL station
c-UN	386	3038	25.5	21.4	2.2	0.47	9146200	713
c-SM	800	3044	15.4	18.3	2.5	0.46	9172500	586
LF	878	3317	37.9	30.1	63.7	19.2	9124500	762
CC	865	3108	9.7	18.8	55.0	10.3	9118450	762
TO	383	3120	3.2	22.0	75.4	16.6	9115500	701
VA	188	3436	52.4	32.7	55.1	18.0	9352900	843
RG	3419	3232	18.0	38.5	87.4	33.6	8220000	327
CN	730	3196	10.5	39.0	69.4	27.0	8246500	580

Table 2. Basin climate including Aridity Index (AI), where "c-" denotes control basin.

Basin	Mean Annual Precipitation (mm)	Mean Annual Runoff (mm)	Mean Annual Temperature (*C)	Mean AI	Pre-Beetle Mean AI	Post-Beetle Mean AI
c-UN	687	379	3.36	0.595	0.579	0.659
c-SM	618	259	3.28	0.529	0.533	0.515
LF	737	230	1.30	0.624	0.616	0.653
CC	402	39	2.34	0.297	0.297	0.296
TO	510	145	1.95	0.435	0.408	0.260
VA	917	661	1.49	0.730	0.778	0.600
RG	638	216	1.80	0.501	0.493	0.541
CN	675	346	2.60	0.435	0.449	0.393

2.2. Beetle Impact Extent

The extent of beetle kill in spruce forests was determined using insect detection survey polygons produced by the US Forest Service starting between 1997 and 2000, depending on the basin (USFS, 2020). Because spruce trees are slow to grow and regenerate, we assumed any area characterized as impacted since the beginning of data collection in 2009 would remain impacted through 2019 (the final year of the study). In 2012, the USFS began to include impact severity data. All areas impacted before 2012 were counted, but after 2012, only those areas with "moderate" or more severe infestations were included. In many cases, uncounted low severity areas were counted in the following years due to increased severity. Cumulative impact areas were determined for each catchment starting in 2009 (including 1997-2009) due to inconsistencies in survey coverage between catchments prior to 2009, and for every subsequent year through 2019. 2014 was identified as the first year of the "after beetle impact" period because it was the peak of the epidemic in the study region (I.e., the year with the largest area newly identified as beetle impacted by aerial surveys), and because it was the first year in which the mean percentage of spruce forest impacted within the beetle-affected basins (excluding the much more heavily impacted Rio Grande basin) exceeded 20%, a cutoff identified as critical by Adams et al. (2012) for causing changes in streamflow. Spruce-fir forest type cover was determined using the LANDFIRE vegetation type dataset from 2008 (LANDFIRE, 2008). New versions of the dataset were not used because beetle-induced mortality may cause impacted stands to be excluded from the spruce-fir forest vegetation type coverage.

The average fraction of basin area covered by spruce-fir forest type was 27.6% and ranged from 18.8% (CC) to 38.9% (CN) (table 1). The cumulative fraction of the total area affected by spruce beetles within all impacted basins was 20.8%, and cumulative fraction of spruce forest affected by spruce beetles within all study basins was 78.2%. RG was the most heavily impacted, with the fraction of total area impacted and fraction of spruce forest impacted 33.6% and 87.4% respectively (Table 1 and Figure 1).

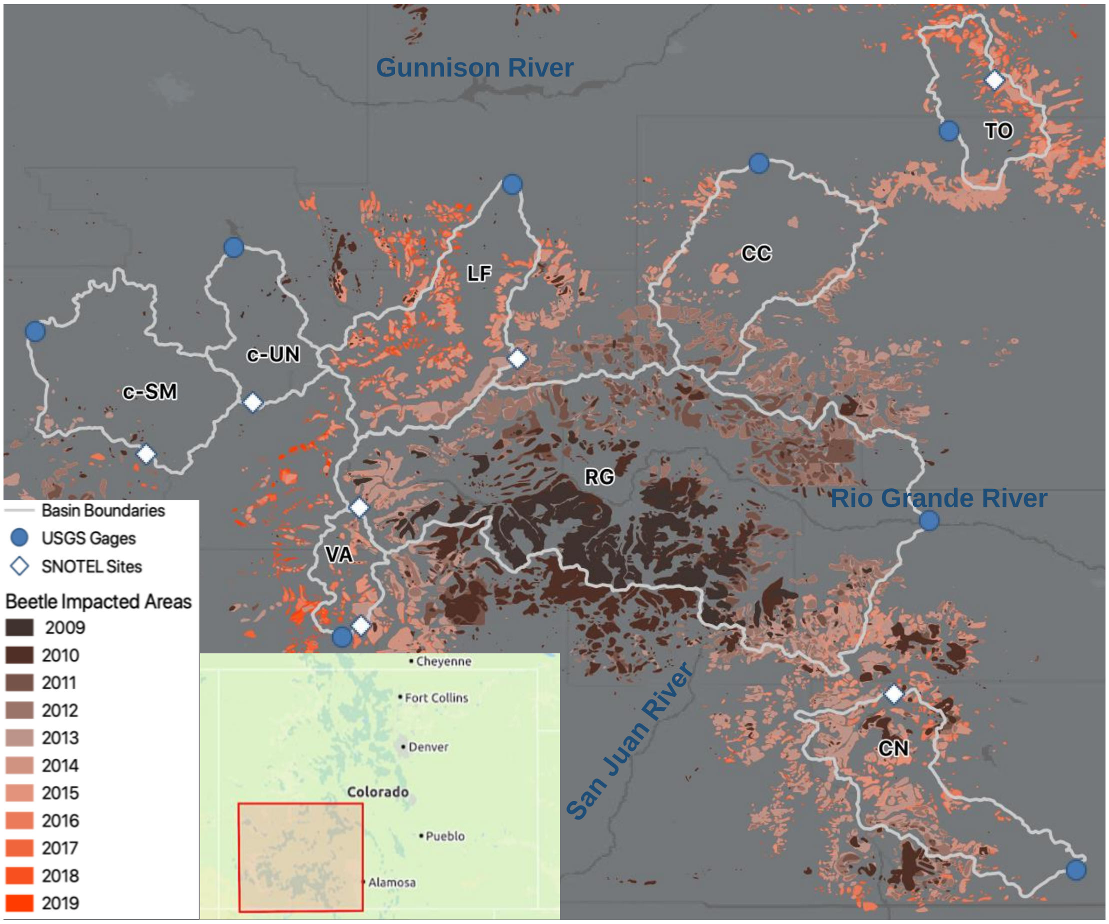


Figure 1. Map showing new area impacted by beetle kill each year in the study region, study basin boundaries, and USGS gauge and SNOTEL site locations.

2.3. Climate Variables

All streamflow analyses used temperature, SWE and/or precipitation (P) data from the SNOTEL sensor network. Potential evapotranspiration (PET) values used to characterize basin aridity index (P/PET) were from the NLDAS dataset (Xia et al., 2012). All but one study basin contained a SNOTEL site with adequate record length, so site 762 was used for basin CC, which is 25 km away. There were too few SNOTEL sites with records of adequate length, quality, and proximity to study basins to average precipitation values across multiple sites. SWE varies widely across the study basins, and due to siting preferences SNOTEL sites usually represent the high end of SWE persistence in the area (Serreze et al., 1999) and show strong correlations with streamflow (Schaefer & Johnson, 1992). Therefore, SNOTEL data does not represent a basin-scale precipitation amount. The goal of this study was to assess changes in runoff efficiency and resulting streamflow through time, and individual SNOTEL sites provide better temporal consistency than most gridded data products, which incorporate data from new meteorological stations as they become available. However, to ensure SNOTEL data did not introduce elevation or site-specific anomalies into results, analyses were initially performed using SNOTEL climate data, then again with a secondary gridded dataset, NOAAs nClimGrid, which has been homogenized to account for topographic and network variability making it useable for conducting trend analysis (Vose et al., 2014). Precipitation data from SNOTEL and nClimGrid were similarly correlated with annual streamflow (R^2 = 0.70 and R^2 = 0.68 for SNOTEL and nClimGrid respectively). We corrected a known sensor-related discontinuity in SNOTEL temperature data (Oyler et al., 2015) using an empirically derived correction for affected years (Harms et al., 2016) and site-specific sensor installation information. SNOTEL site histories were examined to avoid other discontinuities in precipitation and SWE data collection.

2.4. Changes in Streamflow

Streamflow data were harvested from the US Geological Survey's stream discharge gauging network starting in water year 1993, when the TO gauge began reporting, through 2019. Streamflow was normalized to runoff in mm by basin area. To allow for comparison between the spruce beetle impacted basins discussed here and basins impacted by pine beetle in central Colorado in the mid-2000's, we use a multi-evidence approach similar to Biederman et al. (2015) in our analyses of changes to runoff efficiency and total streamflow (Q). The multiple Q change detection methods used here vary from simple paired basin runoff analysis, to more involved methods that estimate runoff efficiency (the amount of streamflow generated from a certain amount of precipitation) by including precipitation (P) and seasonal temperature (T) variables. Estimates of runoff efficiency can then be used to predict the change in annual Q between pre- and post-beetle periods (hereafter predicted Q). Predicted Q provides a more robust assessment of changing streamflows than raw measured Q, because predicted Q accounts for variation in precipitation and temperature between study periods and individual years. Pre- and post-beetle predicted Qs were compared using a nonparametric Mann-Whitney U test for difference.

2.4.1. Runoff Ratios

The relationship between precipitation and runoff generation was assessed through statistical comparison of annual runoff ratios (Q/P) over the water year from October 1 to September 30. Because SNOTEL precipitation values are from specific sites and not averaged over the whole basin area, Q/P values presented are site specific ratios rather than whole basin ratios, while the Q/P derived from nClimGrid estimate values for the whole basin. For each basin, annual Q/P and snowmelt Q/P were averaged for the pre-beetle (1993-2013) and post-beetle (2014-2019) periods. Annual Q/P was assessed by water year, and snowmelt Q/P was calculated as runoff occurring during the snowmelt season (April through July) divided by precipitation contributing to peak SWE (October through April). Predicted Q was found by multiplying mean pre- and post-beetle annual Q/P values by mean annual P. While Q/P outside the snowmelt season could provide important information about runoff efficiency during summer rain events, we were unable to specifically assess non-snowmelt Q/P, because the period between summer snowmelt and autumn snowpack accumulation was extremely variable in length and sometimes shorter than a month. Instead, we chose to examine late summer and winter low flows (discussed below).

2.4.2. Control Divergence Paired Catchment Analysis

Control divergence (CD) analysis assumes that for each water year, climatic conditions in a control basin are predictive of conditions in impacted basins. We used an analysis of covariance (ANCOVA) to identify variation in Q between pre- and post-beetle periods for each basin, while controlling for variation in Q observed in the control basin c-UN. In this manner, changes in Q between pre- and post-beetle periods can be largely isolated from regional variation in annual climate variables that cause variation in flow from the control catchment, and no additional calculation is necessary to determine predicted Q. A second control watershed, c-SM was compared to c-UN to support the assumption that beetle kill caused any apparent changes in predicted Q. Because the post-beetle period was only 6 years, we performed a sensitivity analysis to ensure single extreme years were not responsible for apparent changes in predicted Q by shifting the window of post-beetle years back a year and systematically excluding one post-beetle year at a time from the analysis.

2.4.3. Time-Trend Analysis

Time-trend analysis is a more complex approach for detecting beetle-induced streamflow changes that accounts for the influence of both precipitation and temperature on generation of stream runoff (Biederman et al., 2015; Bosch & Hewlett, 1982). An empirical multiple linear regression model for the relationship between climate variables and streamflow is developed for each basin and calibrated using a subset of years before beetle impacts (water years 1993 – 2007). This model relies on annual precipitation and spring-summer (March – August) temperature as key controls of runoff generation (Biederman et al., 2015), such that:

$$Q = a + bP + cT$$

That calibrated model is then applied to the remaining water years before beetle impacts (2008 – 2013) and the years after beetle impacts (2014 – 2019) using each basin's annual climate data. Mean residuals (between observed and predicted Q values) for the pre- and post-beetle periods were differenced to determine change in predicted Q. A shift in residual mean suggests a change in streamflow due to factors other than climate, and in this case was interpreted as a beetle-induced change in streamflow. The validity of assumptions associated with linear regression models were tested for each basin's climate-runoff model. We confirmed a linear relationship between runoff and precipitation, the Lilliefors test indicated a normal distribution of residuals, and scatterplots of residuals versus runoff and water year confirmed residual homoscedasticity.

2.5 Changes in High and Low Flows

Magnitude and timing of annual peak runoff (peak flows) and seasonal minimum runoff (low flows) were both assessed using a 7-day moving average. Low flows were examined only for September to capture summer-like baseflow conditions after the summer monsoon rains dissipate and before herbaceous vegetation senesces fully, and in January, the month with the lowest average flow overall. Peak flows were assessed annually. Flow parameters were found for each basin in each year and averaged for the pre- and post-beetle periods. Flow parameters were compared using a nonparametric Mann-Whitney U test for difference.

3 Results

3.1 Pre- and Post-Beetle Climate

Precipitation in the study region is consistently snow-dominated and bimodal, with peak SWE and summer monsoon rains representing 60%-70% and 21%-29% of annual precipitation across the studied SNOTEL sites on average. Precipitation and snowfall were highly variable from year to year throughout the study period. Water years 2018 and 2019 exemplified this variability, with maximum annual SWE values of 57% and 142% of long-term average respectively. Basins were water limited based on aridity index (P/PET) values that ranged from 0.30 in CC to 0.73 in VA.

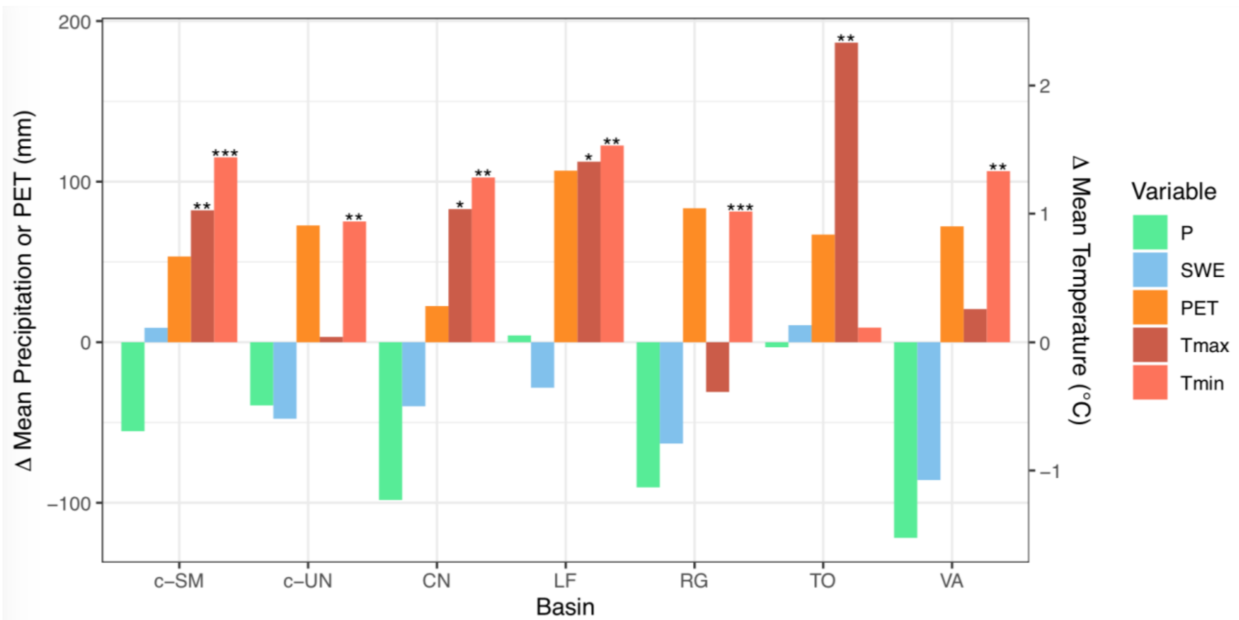


Figure 2. Changes in mean annual precipitation (P), peak SWE, annual potential evapotranspiration (PET), mean daily high temperatures (Tmax) and mean daily low temperature (Tmin) from pre-beetle to post-beetle periods as measured by SNOTEL sites. Analyses for CC used the same SNOTEL data as LF. Significant changes are denoted by * ($p<0.05$), ** ($p<0.01$), and *** ($p<0.001$).

Average annual air temperature is significantly higher post-beetle (2014-2019) compared to pre-beetle (1993-2013) at all SNOTEL sites, including those in control basins, with an average increase of 0.95 °C across SNOTEL sites (figure 2). This increase in observed temperature is consistent with estimated regional warming trends (McCabe et al., 2020; Woodhouse et al., 2016; NOAA, 2020). Increases in PET in all basins mirror the higher air temperatures but lack statistical significance (a short and variable post-beetle period reduces statistical power). Similarly, consistent but statistically insignificant post-beetle decreases in annual P and peak SWE are observed in most basins. Decreases in post-beetle precipitation and increases in temperature and PET would generally be expected to decrease runoff efficiency based on typical Budyko-type relations (Zhang et al., 2008). From year to year, agreement between measures of basin climate conditions were high (>R^2 = 0.70, table 3) for both SNOTEL and nClimGrid data, indicating that regional consistency in precipitation and temperature patterns was adequate for comparison between control and impacted basins.

Table 3. Mean correlation coefficients for annual climate variables between all basins and between impacted basins and controls.

Basin	SNOTEL Precipitation	SNOTEL Temperature	nClimGrid Precipitation	nClimGrid Temperature
All	0.83	0.70	0.87	0.95
c-SM	0.82	0.80	0.86	0.96
c-UN	0.84	0.83	0.87	0.95

3.2 Streamflow Analysis

3.2.1 Runoff Ratios

Using SNOTEL precipitation data, mean annual post-beetle Q/P increased significantly in all impacted basins except LF (Figure 3). Mean Q/P in control basins were 0.35 pre-beetle and 0.36 post beetle, with no significant changes in either control basin. In contrast, the average Q/P in impacted basins increases from 0.34 pre-beetle to 0.41 post-beetle. Resulting predicted Q also increased by 21%, despite less precipitation (not significant) in the post-beetle kill period. Snowmelt season Q/P also increased significantly in all impacted basins except LF, averaging 0.36 before and 0.47 after beetle kill, which contrasts with insignificant changes in control basins (0.36 pre-beetle and 0.39 post beetle). Reported values are for SNOTEL-based results. The significance and direction of post-beetle changes in Q/P were not sensitive to data sources (see supplemental notes for results based on nClimGrid data).

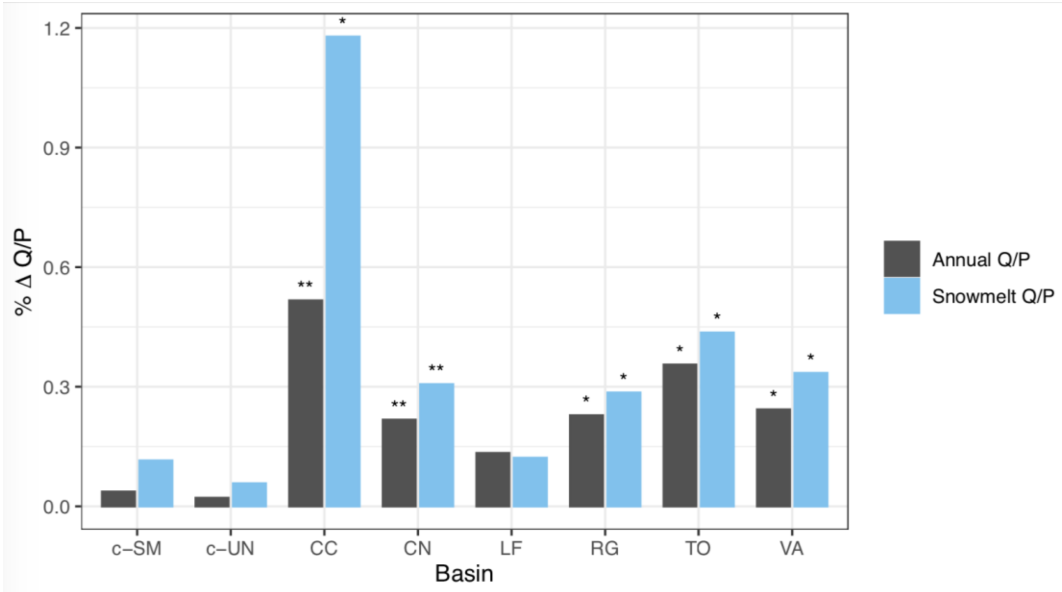
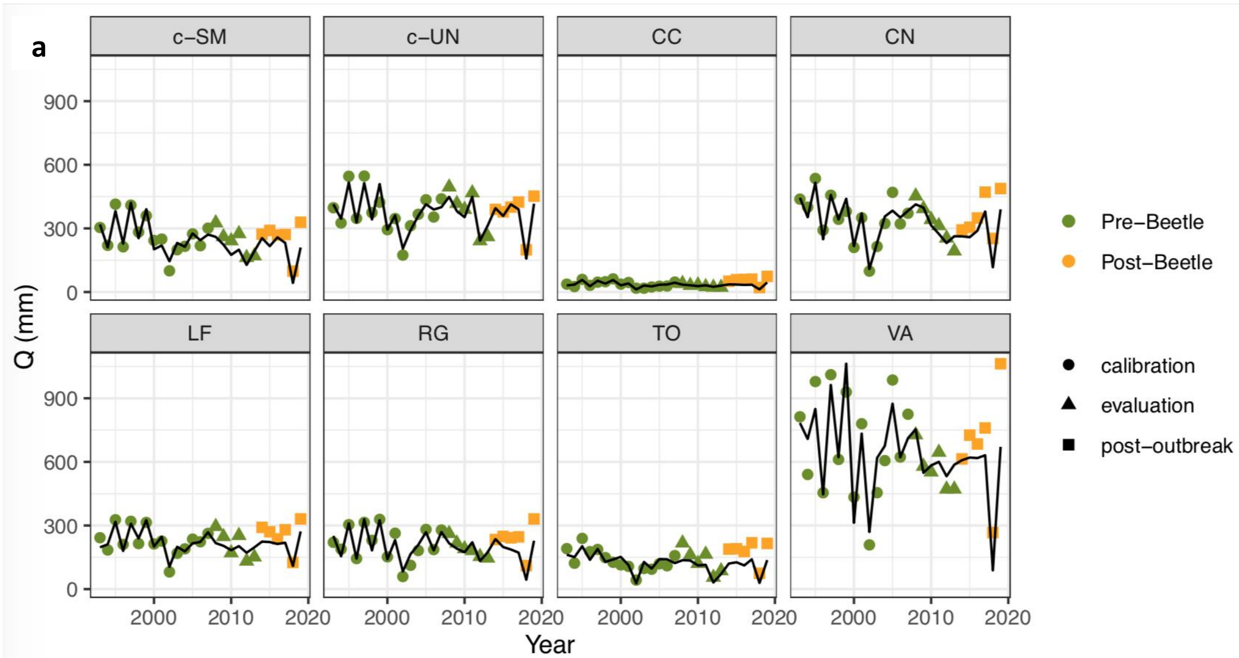


Figure 3. Relative change in annual and snowmelt runoff ratios (Q/P) between pre- and post-beetle periods using SNOTEL data. Significant changes are denoted by * ($p<0.05$) and ** ($p<0.01$)

3.2.2 Time-Trend Analysis

Annual precipitation and mean spring/summer (March to August) temperatures were effective in predicting variation in runoff during the calibration period (1993-2007), with a mean adjusted R^2 value of 0.81 using SNOTEL data (ranging from 0.63 to 0.88 across basins). Models that used annual mean T or neglected T altogether were slightly less effective (R^2 = 0.80 and R^2 = 0.79, respectively). Model skill decreased slightly from the calibration period to the evaluation period (2008-2013), with MAEs of 28 mm and 35 mm respectively. Positive post-beetle residuals represent a 28% increase in predicted Q across impacted basins on average, and changes were significant for all impacted basin except LF. No significant changes to residual mean were observed for the control basins c-UN and c-SM using SNOTEL data (see supplemental notes for results based on nClimGrid data).



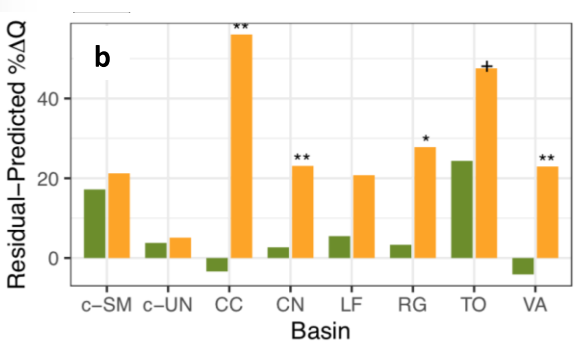


Figure 4. a) observed annual runoff (Q) pre-beetle (green) and post-beetle (orange) with black line showing model-predicted Q, calibrated from a subset of pre-beetle years (1993 – 2007). b) mean residuals from the pre-beetle evaluation period (2008 – 2013) and post-beetles period (2014 – 2019). Significant changes denoted by ** ($p < 0.01$), * ($p < 0.05$), and + ($p<0.1$).

3.2.3 Control Divergence Paired Catchment Analysis

An analysis of covariance suggested that after accounting for non-beetle-related interannual variation (using discharge from control basin c-UN), predicted Q in beetle impacted basins increased by 6%-16% in high discharge basins and 33% -51% in low discharge basins. Predicted Q did not change in the control basin c-SM post-beetle. The largest relative changes were in CC and the smallest relative changes were in VA. The significance of increases did not change in a sensitivity analysis, but the effects on one impacted basin, CN, were notably smaller than in the primary analysis (4.8% versus 8.3% increase post-beetle).

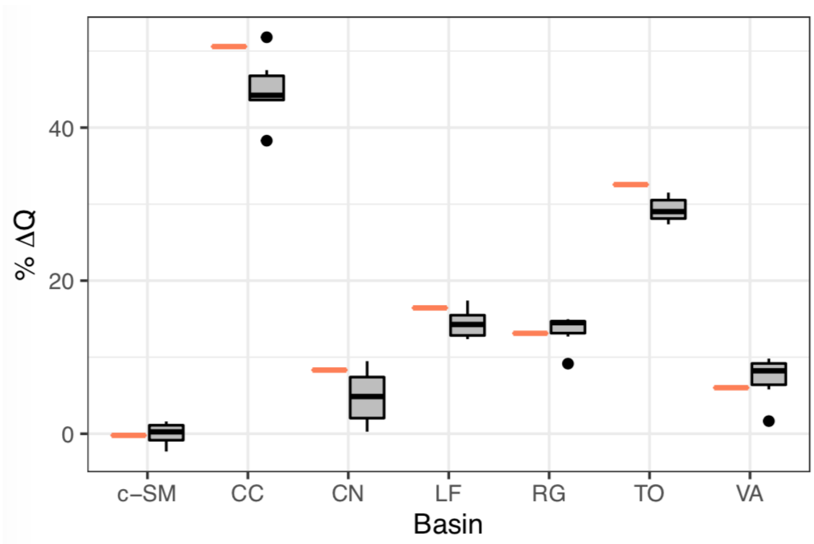


Figure 5. Relative change in water yields from pre- to post-beetle periods as predicted by ANCOVA (red lines) and distribution of values returned by sensitivity analysis (grey box plots). Black dots denote outliers.

3.2.4 Comparing Methods of Water Yield Analysis

Change in predicted Q derived from time-trend (TT), control divergence (CD), and runoff ratio (Q/P) analyses agreed on increasing Q and its order of magnitude in the impacted basins. VA was a possible exception, as the CD method predicted a much smaller, but still significant increase in Q than the Q/P and TT methods (6.0%, 27.4% and 27.1% respectively). Absolute change in mean annual measured Q was included as a reference in figure 6, but was not considered a primary method for analysis because it neglects variation in climate variables like precipitation. In impacted basins, absolute change in mean Q was similar in direction and magnitude to other methods despite increased temperature and aridity. In control basins, small changes in predicted Q lacked statistical significance, including a small decrease in measured Q.

Correlation between the different methods was high across basins, with the highest correlation between CD and TT analyses (R^2 =0.86) and lowest between CD and Q/P (R^2 =0.73). Agreement between methods on the magnitude of changes varies between basins. The CD method generally suggested smaller relative changes in predicted Q for high discharge basins (CN, RG, VA) than other methods, while the TT method had the opposite pattern. Agreement between methods was poorest for the basins with the highest (VA) and lowest (CC) mean annual discharge. The basins in which TT and Q/P methods predicted very different (>10%) changes in Q (CC and RG) had the highest elevation SNOTEL sites.

Substituting gridded climate data (nClimGrid) for SNOTEL data in Q/P and TT methods results in similar significant increases in predicted Q for most basins. For the control basin c-SM, TT analysis using SNOTEL data suggests no significant change, while gridded data shows a 21% increase in predicted Q. For VA, SNOTEL-based Q/P analysis predicts a 27% increase in Q, while gridded data shows a 11% increase lacking statistical significance.

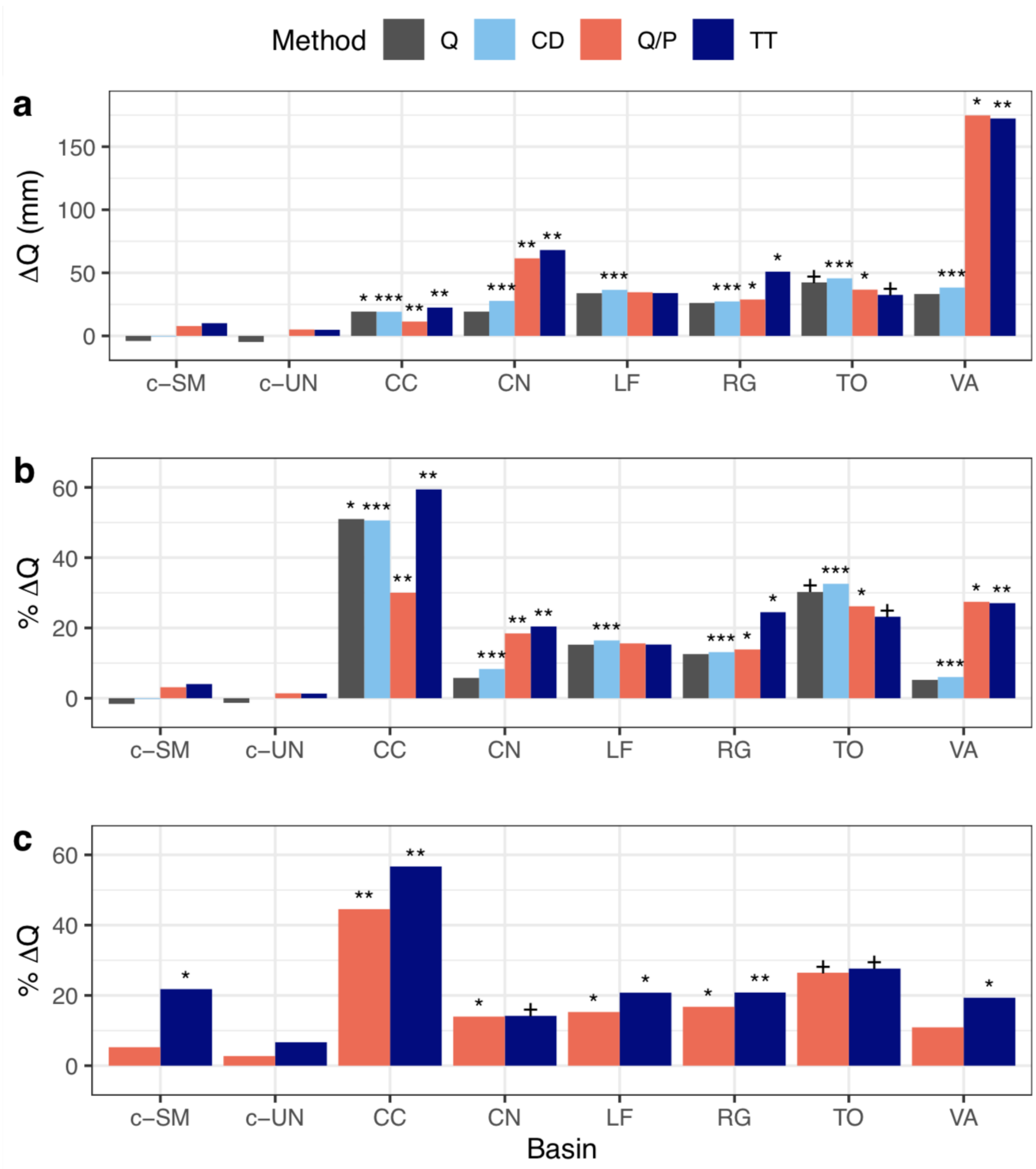


Figure 6. a) Absolute change and b) percent change in predicted Q during pre- to post-beetle periods from double mass (CD), runoff ratio (Q/P), and time-trend (TT) analyses using SNOTEL data, and c) percent change in predicted Q using gridded climate date for Q/P and TT analyses. Difference in mean annual measured Q shown in grey for reference. Significant changes denoted by *** ($p<0.001$), ** ($p < 0.01$), * ($p < 0.05$), and + ($p<0.1$).

3.2.5 Changes in Peak and Low Flows

The magnitude of annual runoff peak flows increased significantly post-beetle kill, as compared to the pre-beetle kill period, in all impacted basins except CN. Increases occurred in maximum annual 7-day Q and when normalized for peak SWE (divided by maximum annual SWE in mm) (figure 8). Averaged between impacted basins, the normalized peak flows (Q/SWE) increased from 9.1 mm/m before to 12.3 mm/m after beetle kill. No significant changes in normalized peak flows are observed in control basins, where pre- and post-beetle values were 7.5 mm/m and 8.6 mm/m. The average day of year on which peak runoff occurred (Qpeak DOY) was 160 (June 8th) before and 158 (June 6th) after beetle kill. Changes in peak runoff timing were not significant for raw values or when normalized for peak SWE except for CC (figure 7).

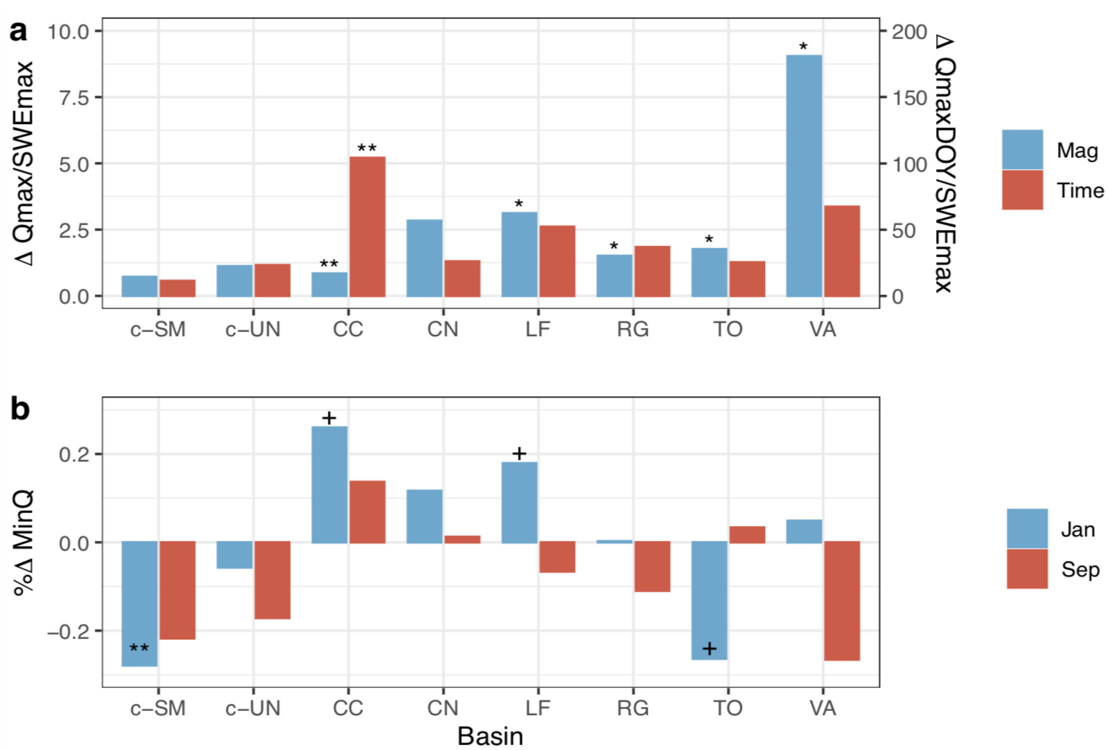


Figure 7. a) Change in SWE-normalized magnitude (mag) and timing (time) of mean annual peak streamflows from pre- to post-beetle periods. b) Relative change in mean annual (Jan) low flows and mean growing season (Sep) low flows from pre- to post-beetle periods. Significant changes denoted by ** ($p < 0.01$), * ($p < 0.05$), and + ($p<0.1$).

Low flows exhibit limited and inconsistent increases and decreases in the impacted basins (Figure 8b). Basin average low flows for September and January were 0.26 mm/day and 0.14

mm/day respectively before beetle kill, and 0.30 mm/day and 0.13 mm/day after beetle kill. One control basin, c-SM, saw a significant decrease in January low flows that are consistent with reduced groundwater recharge during the warmer post-beetle kill period. January low flows increased in CC and CN, and decreased in TO. September low flows did not change significantly in any control or impacted basins.

4 Discussion

Multiple methods of analysis show runoff efficiency and predicted Q increases of >15% after beetle impacts despite warmer temperatures, higher PET, and lower or unchanged Q in unimpacted basins. Increases in predicted Q were persistent across different assumptions and data requirements of the three analytical methods and multiple climate datasets used. Higher runoff efficiency in impacted basins resulted in higher predicted Q, with increases ranging from 14.5% (in RG) to 47.2% (in CC) when averaged between methods. Increases in mean annual measured water yields, that do not account for climatic variability, provide a useful reality check that more water was leaving the system despite greater atmospheric water demand and no change in precipitation. This assessment is consistent with the inference that warmer, more arid conditions produced smaller, non-significant positive (and sometimes negative) Q changes in un-impacted control basins.

The largest absolute increases in predicted Q occurred in basins with the greatest mean annual Q (VA and CN). Conversely, larger relative changes in predicted Q occurred in the most arid, lowest elevation, and lowest discharge basins (CC and TO). Basins CC and TO having the greatest relative increases in predicted Q despite having the smallest fraction of beetle impacted area seems counter-intuitive. However, CC and TO encompass less alpine terrain near and above treeline than the other study basins (table 1), potentially increasing the relative importance of subalpine forest elevations in generating streamflow. In Colorado, elevations near and immediately above treeline generally have higher precipitation, lower vapor losses (Sexstone et al., 2018), and provide higher relative contributions to streamflow (Knowles et al., 2015) and groundwater recharge (Carroll et al., 2019) than subalpine forests. CC and TO may therefore lack a large alpine snowmelt subsidy, which could dilute the apparent effects of beetle kill in higher elevation basins with more alpine terrain. It is possible that a greater relative importance of subalpine forests in generating streamflow in CC and TO may allow the smaller beetle impacted area in those basins to have a greater effect on streamflow than a larger area in a basin like RG, which has higher forest mortality but more area above treeline (table 1).

The ongoing spruce beetle outbreak in our study basins follows a more thoroughly studied MPB outbreak that occurred in north-central Colorado, less than 300 km away. We modelled our methods of empirical analyses after those used by Biederman et al. (2015) in their study of streamflow impacts following MPB outbreak. Both studies used a control deviation (CD) analysis (Biederman et al. used a cumulative double mass analysis, where we used a non-cumulative approach to simplify autocorrelation removal), as well as time trend analysis (TT) and changes in runoff ratio (Q/P). Using multiple methods of analysis improves our confidence in our results because each makes different assumptions that have different strengths and pitfalls. CD uses a paired basin approach that avoids biases introduced by the challenges of measuring mountain precipitation and temperature, while TT and Q/P approaches better address spatial heterogeneity in hydrologic forcings by more directly accounting for interbasin variation in precipitation and/or temperatures. TT analysis captures the effects of temperature missed by Q/P but may suffer from model overfitting in years and basins that are less temperature dependent. This potential for overfitting, combined with the coarse spatial resolution (5km) of nClimGrid and its dramatic suggested warming trends, may explain the larger flow increases predicted by TT analysis using nClimGrid data. Despite similar methodology, our findings contrast with those of Biederman et al. (2015), which showed that streamflow in basins impacted by MPB in central Colorado were mostly unchanged or lower than before the MPB outbreak. Our findings do however agree with those of Love (1955) and Bethlahmy (1974), which both found increased streamflows in northern Colorado after a spruce beetle outbreak using an analysis of covariance very similar to that used in our CD analysis.

The snowmelt-dominated changes in streamflow lead us to hypothesize that higher predicted Q occurs because beetle kill alters processes occurring during snow accumulation and/or snowmelt. Increased predicted Q following beetle kill appears to be disproportionately driven by flows during the snowmelt period. Water year Q/P increased by 28% in impacted basins, while snowmelt Q/P (ie, snowmelt discharge divided by winter precipitation) increased by 44%, and this trend held in every beetle-impacted basin with significant increases in predicted Q (Figure

3). Additionally, the magnitude of annual peak flows, which are snowmelt driven, increased in all beetle impacted basins except CN, while baseflow driven low flows suggest limited or inconsistent changes in groundwater recharge (figure 7). We cannot be certain whether these altered processes are related to snow accumulation, melt, or runoff of melt water, but the importance of snow processes is supported by studies suggesting that for the same amount of precipitation, SWE is often higher in beetle impacted spruce forests than unimpacted forests (Frank et al., 2019; Sexstone et al., 2018). Alternately, increased snowpack sublimation resulting from reduced canopy shading can limit SWE increases, and Biederman et al. (2014a) suggests these compensating processes resulted in little to no net changes in SWE following a MPB outbreak in northern Colorado. However, in spruce forests Frank et al. (2019) and Sexstone et al. (2018) both show decreased sublimation from canopy intercepted snow, because the thinner needleless canopies of beetle impacted spruce forests intercept a smaller fraction of falling snow. Interception losses dominates sublimation losses from snowpacks in northern Colorado, even with areas above tree line having greater snowfall that forests (Sexstone et al., 2018). With less snowfall sublimated from the canopy, more snow accumulation results in higher peak SWE (Boon, 2007; Pugh & Small, 2012). A deeper snowpack will melt later and faster than a shallower snowpack (Trujillio & Molotch, 2014) and there is some evidence that faster snowmelt leads to more efficient streamflow generation (Barnhart et al., 2020). Moreover, reductions in canopy shading will increase the relative importance of snowpack albedo, which will tend to be reduced, and melt rates increased, by recent litterfall from dead trees (Winkler et al., 2010) and increased exposure of dust covered snow (Painter et al., 2012). While field studies in other spruce beetle outbreaks support changes in SWE and snowmelt driving the higher post-beetle streamflow observed in this study (Frank et al., 2019), we lack the evidence to rule out a scenario where increases in streamflow are driven by reductions in snowmelt or growing season vapor losses.

Decreased transpiration rates in beetle impacted forests may contribute to the higher runoff efficiency observed in our study basins. The largest changes in Q/P occurred during snowmelt, when much of the subalpine forests remains snow-covered, but transpiration rates in subalpine mixed conifer forests may begin to ramp up as early as April and peak in June in the Southern Rocky Mountains (Barnard et al., 2018). Given that average peak flows in our study catchments occur in early June, it is possible that, after beetle kill, a lack of forest transpiration during the snowmelt period allows more snowmelt to reach the stream than if the trees were alive. The model-based findings of Knowles and Molotch (2019) support this possibility, indicating higher soil moisture and clear decreases of ET and T/ET in forests due to beetle kill, particularly during the growing season, which they defined as May through September. However, similar to snowpack process, increased subcanopy ET from soil evaporation and subcanopy vegetation may compensate for lost canopy transpiration (Brown et al., 2014; Biederman et al., 2014b), so basin-scale decreases in ET cannot be assumed to drive increased Q (Goeking & Tarboton, 2020). Outside the snowmelt season, we observed few significant changes to Q/P or low flows, so if changes in forest ET are large enough to increase runoff efficiency, they do not appear to have significant impacts on flows during the late growing season, which could be consistent with storage-limited systems that fill their deeper stores each year (Dralle et al., 2020). We acknowledge that late summer ET changes may still have indirect or delayed effects on streamflow by altering soil moisture and subsurface flow (prior to the following snowmelt season), which is important for connecting subsurface water stores along forested hillslopes to streamflow (Harmon et al., 2020).

As the fraction of Western forests affected by bark beetles grows, understanding how and why their impacts vary across basins will become increasingly important for streamflow forecasting, management planning, and prioritization of conservation resources. While our findings highlight the probable importance of cold season processes (October - July), directly answering process-related questions was beyond the scope of our study. Nonetheless, quantifying process drivers of beetle kill impacts remain critical to predicting streamflow effects. Increased runoff efficiency due to beetle kill may buffer streamflow from declines caused by warming temperatures, higher summer vapor pressure deficits, reduced land surface albedo, and other climate changes (Udall & Overpeck, 2017; McCabe et al., 2020; Woodhouse et al., 2016; Milly & Dunne, 2020). If such buffering effects exist, they will likely decrease over time as food source reduction slows beetle activity (Hart et al., 2015) and vegetation regrows. However, remote sensing evidence suggest multi-decadal increases in land surface albedo in the southern Rocky Mountains, particularly in MPB impacted locations (Vanderhoof et al., 2014), that are consistent with more efficient streamflow generation (Milly & Dunne, 2020). Vegetation regrowth may result in runoff efficiency below pre-outbreak levels if the regrowing vegetation has higher water demands than pervious forests (Vanderhoof & Williams, 2015). Higher peak flows in newly beetle-impacted areas may pose flood risks (Bewley et al., 2010) that merit further study. One of the key management challenges posed by our work is to understand why our findings strongly contrast from those of Biederman et al (2015) working in a MPB impacted system in a nearby part of Colorado. Specifically, we need to better understand how beetle kill affects snow processes and basin-scale ET, and how those processes interact with other hydrologic factors, including snow albedo reductions from dust and litter (Livneh et al., 2015), or with other disturbances like wildfires (Penn et al., 2020) or avalanches (Teich et al., 2019).

5 Conclusions

Using empirical analysis of 27 years of streamflow and precipitation data, we found that runoff efficiency and predicted streamflow increased in five out of six beetle-impacted basins in Southwest Colorado, despite more arid conditions. Increases of 15-45% of annual streamflow volumes are striking for water resource management if they are propagated to reservoir inflows. However, the beetle kill-induced changes may be buffering a period of lower precipitation and higher atmospheric water demand that could make streamflow resources at risk of future changes if beetle kill impacts lessen over time. Spruce beetle kill impacted basins had streamflow changes occurring during the snowmelt season, such as higher peak flows, increases in snowmelt Q/P that exceeded those of annual Q/P, and inconsistent or unchanged low flows. Our findings indicate a need for further investigation into the specific processes responsible for the increased runoff efficiencies observed and why spruce beetle and MPB systems result in divergent streamflow responses. Additionally, there remains a need to address outstanding questions of how forest regrowth, and other forest disturbances like fire, will alter the persistence of increased streamflow during a future with higher vapor pressure deficit and temperature stress on tress, anthropogenic dust deposition onto the snowpack, and changing precipitation and snow accumulation patterns. Because beetle kill disturbance affects key Western US water supply, accurate basin-scale predictions of streamflow response to forest dieoff and its regrowth will only become more valuable in the future.

Acknowledgements and Data

All dataset used in this study are publicly available for download. Stream discharge data for the sites listed is available from https://waterdata.usgs.gov/nwis. Climate data for listed SNOTEL sites in available from https://www.wcc.nrcs.usda.gov/snow/. Climate data from the nClimGrid datasets can be accessed at https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.ncdc:C00332. Insect effected forest polygons can be downloaded from https://www.fs.fed.us/foresthealth/applied-sciences/mapping-reporting/detection-surveys.shtml. Vegetation cover data are available from https://www.landfire.gov/datatool.php. We wish to acknowledge and thank the individuals and organizations that created and/or collected these data and made them publicly available. This work was funded by NSF EAR #2012310.

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