How does water yield respond to mountain pine beetle infestation in a semiarid forest?

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Key points:

• Mountain pine beetle (MPB)-caused tree mortality increases water yield in most wet years, and a decrease in water yield mainly happens in dry years; therefore, interannual climate variability is an important driver of water yield response to beetle-caused tree mortality.

• A long-term (multi-decade) aridity index is a reliable indicator of water yield response to MPBs: in a dry year, decreases occur mainly in “water-limited” areas and vegetation mortality levels have only minor effects; in wetter areas, decreases only occur at low mortality levels.

• Generally, in a dry year, low to medium MPB-caused vegetation mortality decreases water yield, and high mortality increases water yield; this response to mortality level is nonlinear and varies by location and year.
Abstract

Mountain pine beetle (MPB) outbreaks in western United States result in widespread tree mortality, transforming forest structure within watersheds. While there is evidence that these changes can alter the timing and quantity of streamflow, there is substantial variation in both the magnitude and direction of responses and the climatic and environmental mechanisms driving this variation are not well understood. Herein, we coupled an eco-hydrologic model (RHESSys) with a beetle effects model and applied it to a semiarid watershed, Trail Creek, in the Bigwood River basin in central Idaho to evaluate how varying degrees of beetle-caused tree mortality influence water yield. Simulation results show that water yield during the first 15 years after beetle outbreak is controlled by interactions among interannual climate variability, the extent of vegetation mortality, and long-term aridity. During wet years, water yield after beetle outbreak increases with greater tree mortality. During dry years, water yield decreases at low to medium mortality but increases at high mortality. The mortality threshold for the direction of change is
location-specific. The change in water yield also varies spatially along aridity gradients during dry years. In relatively wetter areas of the Trail Creek basin, water yield switches from a decrease to an increase when vegetation mortality is greater than 40 percent. In more water-limited areas on the other hand, water yield typically decreases after beetle outbreaks, regardless of mortality level. Results suggest that long-term aridity can be a useful indicator for the direction of water yield changes after disturbance.

1 Introduction

In recent decades, mountain pine beetle (MPB) outbreaks in the Western U.S. and Canada have killed billions of coniferous trees (Bentz et al. 2010). Coniferous forests can provide essential ecosystem services, including water supply for local communities (Anderegg et al. 2013). Therefore, it is essential to understand how ecosystems and watersheds respond to beetle outbreaks and to identify the dominant processes that drive these responses (Bennett et al. 2018). A growing number of studies have qualitatively examined hydrologic responses to beetle outbreaks and disturbance; however these studies have produced conflicting results (Adams et al. 2012; Goeking and Tarboton 2020). While some studies show increases in water yield following beetle outbreak (e.g., Bethlahmy 1974; Potts 1984; Livneh et al. 2015), many others show no change or even decreases (e.g., Guardiola-Claramonte et al. 2011; Biederman et al. 2014; Slinski et al. 2016). To determine which mechanisms control change in water yield following beetle outbreak, more quantitative approaches are needed.

Water yield is often thought to increase after vegetation is killed or removed by disturbances such as fire, thinning, and harvesting (Hubbart 2007; Robles et al. 2014; Chen et al. 2014; Buma and Livneh 2017; Wine et al. 2018). In the Rocky Mountain West, beetle outbreaks have increased water yield through multiple mechanisms. First, defoliation/needle loss can reduce
plant transpiration, canopy evaporation, and canopy snow sublimation losses to the atmosphere (Montesi et al. 2004). Increased canopy openings can also enable snow accumulation and allow more radiation to reach the ground surface, resulting in earlier and larger peak snowmelt events, which can in turn reduce soil moisture and therefore decrease summer evapotranspiration (ET).

Several studies have documented decreases in water yield following disturbances (e.g., mortality, fire, beetle outbreaks; Biederman et al. 2014; Bart et al. 2016; Slinski et al. 2016; Goeking and Tarboton 2020). For example, in the southwestern U.S., beetle outbreaks have decreased streamflow by opening forest canopies and increasing radiation to the understory and at the ground surface, which leads to increases in understory vegetation transpiration (Guardiola-Claramonte et al. 2011), soil evaporation, and therefore increases total ET (Bennett et al. 2018). Tree mortality or removal can reduce streamflow because surviving trees and/or understory vegetation compensates by using more water (Tague et al. 2019).

In a review of 78 studies, Goeking and Tarboton (2020) concluded that the decrease in water yield after tree-mortality mainly happens in semiarid regions. Previous studies also provide rule-of-thumb thresholds above which water yield will increase: at least 20 percent loss of vegetation cover and mean precipitation of 500 mm/year (Adams et al. 2012). However, many watersheds in the western U.S. experience high interannual climate variability (Fyfe et al. 2017), and local environmental gradients (e.g., long-term aridity gradients) may strongly influence vegetation and hydrologic responses to disturbances, including beetle outbreaks, making predictions difficult (Winkler et al. 2014). Given the possibility of either increases or decreases in water yield following beetle outbreaks, modeling approaches are crucial for identifying the specific mechanisms that control these responses.
The overarching goal of this study is to identify mechanisms driving the direction of change in annual water yield after beetle outbreaks in semi-arid regions (note that in the following text, “water yield” refers to means annual water yield). The following specific questions address this goal:

- **Q1:** What is the role of interannual climate variability in water yield response?
- **Q2:** What is the role of mortality level in water yield response?
- **Q3:** How does long-term aridity (defined as temporally averaged potential evapotranspiration relative to precipitation for a period of 38 years) modify these responses, and how do responses vary spatially within a watershed along aridity gradients?

We hypothesize that multiple ecohydrologic processes (e.g., snow accumulation and melt, evaporation, transpiration, drainage, and a range of forest structural and functional responses to beetles) could interactively influence how water yield responds to beetle outbreaks—however, in certain locations one or more processes may dominate. In addition, the dominant ecohydrologic processes may vary over space and time due to interannual climate variability (i.e., precipitation), vegetation mortality, and long-term aridity. In Sect 2, we present a conceptual framework for identifying and depicting dominant hydrological processes through which forests respond to beetle infestation. We use this framework to interpret the modeling results. In Sect 3, we describe our mechanistic modeling approach, i.e., using the Regional Hydro-Ecological Simulation System (RHESSys), which can prescribe a range of vegetation mortality levels, capture the effects of landscape heterogeneity and the role of lateral soil moisture redistribution, and project ecosystem carbon and nitrogen dynamics, including post-disturbance plant recovery.
In Sects 4 and 5, we then present modeling results that explore how multiple mechanisms influence water yield responses.

2 Conceptual framework

2.1 Vegetation response to beetle outbreaks

Mountain pine beetles (MPB) introduce blue stain fungi into the xylem of attacked trees, which reduces water transport in plants and eventually shuts it off (Paine et al. 1997). During outbreaks, MPBs prefer to attack and kill larger host trees that have greater resources (e.g., carbon), while smaller diameter host trees and non-host vegetation (including the understory) remain unaffected (Edburg et al. 2012). After MBP outbreak, trees mainly go through three phases (i.e., red, gray, and old) over time (Hicke et al. 2012). During the red phase, the trees’ needles turn red. During the gray phase, there are no needles in the canopy. During old phase, killed trees have fallen, and understory vegetation and new seedlings experience rapid growth (Hicke et al. 2012; Mikkelson et al. 2013).

2.2 Hydrologic response to beetle outbreaks

Figure 1 describes the main processes that alter evapotranspiration to either decrease or increase water yield, depending on which processes dominate (Adams et al. 2012; Goeking and Tarboton 2020). During the red and gray phases, needles fall to the ground, and there is lower leaf area index (LAI) and a more open canopy (Hicke et al. 2012). This can reduce plant transpiration of infected trees, though remaining trees may compensate to some extent by increasing transpiration in water limited environments (Adams et al. 2012, Tague et al. 2019). A more open canopy intercepts less precipitation, reducing evaporation from the canopy but potentially increasing it from soil and litter layers (Montesi et al. 2004; Sexstone et al. 2018). Meanwhile, an open canopy can increase the proportion of snow falling to the ground and, therefore, increase
snowpack accumulation. With more solar radiation reaching the ground, earlier and larger peak
snowmelt can also occur (Bennett et al. 2018). Generally, earlier snowmelt increases water for
spring streamflow and decreases water for summertime ET (Pomeroy et al. 2012). However,
once snags fall, reductions in longwave radiation can actually lead to later snowmelt (Lundquist
et al. 2013). The open canopy and less competition for resources, such as solar radiation and
nutrients, can also promote understory vegetation growth, which may increase understory
transpiration (Biederman et al. 2014; Tague et al. 2019). Whether water yield increases or
decreases will ultimately depend on the balance of these processes that can alter transpiration and
evaporation in different ways.

Finally, interannual variability in climate (e.g., dry versus wet years) can affect forests’
hydrological responses (Winkler et al. 2014; Goeking and Tarboton 2020). For instance, during
wet years, remaining plants are not water-limited, and reductions in plant transpiration due to
beetle-caused mortality dominate increases in soil evaporation or remaining plant transpiration,
resulting in a higher water yield. In contrast, during dry years, plants are already under water
stress and decreases in plant transpiration caused by tree mortality may be compensated by
increasing soil evaporation and transpiration by remaining trees or understory vegetation, leading
to declines in water yield. Moreover, these responses are also affected by land cover types (e.g.,
young vs old pine, different tree species, etc.), which is not currently well documented (Perry
and Jones 2017; Morillas et al. 2017).

2.3 Review of modeling approaches

Many models, ranging from empirical and lumped to physically-based and fully-distributed,
argue that only physically-based and fully-distributed models can capture how disturbances alter water yield because they represent fine-scale spatial heterogeneity and physical process that vary over space and time. Despite their advantages, process-based models, such as the coupled CLM-ParFlow model (Mikkelson et al. 2013; Penn et al. 2016), the Distributed Hydrology Soil Vegetation Model (Livneh et al. 2015; Sun et al. 2018), and the Variable Infiltration Capacity Model (Bennett et al. 2018) also have some limitations. For example, 1) they may assume constant LAI after disturbances and static vegetation growth (e.g., VIC and DHSVM), 2) they may not include lateral flow to redistribute soil moisture (VIC), and 3) in some cases, the approach to represent the effects of beetle outbreaks may be too simplified (e.g., changing only LAI and conductance without considering two-way beetle-vegetation interactions in post-disturbance biogeochemical and water cycling e.g., as in CLM-ParFlow). Thus, improving current fully distributed process-based models to capture the coupled dynamics between hydrology and vegetation at multiple scales is a critical step for projecting how beetle outbreaks will affect water yield in semiarid systems (Goeking and Tarboton 2020). Here we use RHESSys7.1, which captures these processes.

3 Model, data, and simulation experiment design

3.1 Study area

Our study watershed is Trail Creek, which is located in Blaine County between the Sawtooth National Forest and the Salmon-Challis National Forest (43.44N, 114.19W; Fig. 2). It is a 167-km² sub-catchment in the south part of Big Wood River basin, and is within the wildland-urban interface where residents are vulnerable to the flood and debris flows caused by forest disturbances (Skinner 2013). Trail Creek has frequently experienced beetle outbreaks, notably in 2004 and 2009, when beetles killed 7 and 19 km² of trees, respectively (Berner et al. 2017).
Trail Creek has cold, wet winters and warm, dry summers; mean annual precipitation is approximately 978 mm with 60% snow (Frenzel 1989). The soil is mostly permeable coarse alluvium (Smith 1960). Vegetation is clustered into two major groups along the elevation which ranges from 1760 to 3478 m: sagebrush, riparian species, and grasslands in lower to middle elevation areas and Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta* var. *latifolia*), subalpine fir (*Abies lasiocarpa*), and mixed shrub and herbaceous vegetation in middle-to-higher elevations (Buhidar 2002).

A strong upper to lower vegetation and long-term aridity gradient exists for Trail Creek (Fig. 3). The northern (higher elevation) portion of the basin is mesic and covered principally by evergreen forest; the southern (lower elevation) portion is xeric and covered by shrubs, grasses, and mixed herbaceous species. In total, Trail creek contains 72 sub-basins and two of them (e.g., Fig. 3, sub-basin 412 and 416) are urban areas. If we classify this basin into different zones according to an aridity index, i.e., the ratio of 38-year average annual potential evapotranspiration (PET) to precipitation (P) (Sect 3.4), there is a distinct gradient: the northern and high elevation area is balanced (i.e., PET/P between 0.8 and 2) and evergreen tree coverage is more than 50%; the southern part is water-limited (i.e., PET/P > 2) and evergreen tree coverage is less than 30% (Figs. 2 and 3).

3.2 Model descriptions

3.2.1 Ecohydrologic model

The Regional Hydro-ecologic Simulation System (RHESSys) (Tague and Band 2004) is a mechanistic model designed to simulate the effects of climate and land use change on ecosystem carbon and nitrogen cycling and hydrology. RHESSys fully couples hydrological processes (including streamflow, lateral flow, ET, and soil moisture, etc.), plant growth and vegetation...
dynamics (including photosynthesis, maintenance respiration, and mortality, etc.), and soil biogeochemical cycling (including soil organic matter decomposition, mineralization, nitrification, denitrification, and leaching, etc.). It has been widely tested and applied in several mountainous watersheds in western North America, including many in the Pacific and Inland Northwest (e.g., Tague and Band 2004; Garcia and Tague 2015; Hanan et al. 2017; Hanan et al. 2018; Lin et al. 2019; Son and Tague 2019). RHESSys represents a watershed using a hierarchical set of spatial units, including patches, zones, sub-basins, and the full basin, to simulate various hydrologic and biogeochemical processes occurring in these multiple scales (Tague and Band 2004). The patch is the finest spatial scale at which vertical soil moisture and soil biogeochemistry are simulated. In every patch, there are multiple canopy strata layers to simulate the biogeochemical processes related to plant growth and nutrient uptake. Meteorological forcing inputs (e.g., temperature, precipitation, humidity, wind speed, and solar radiation) are handled at the zone level, and spatially interpolated and downscaled for each patch based on elevation, slope, and aspect. Sub-basins are closed drainage areas entering both sides of a single stream reach (the water budget is closed in sub-basins). The largest spatial unit is the basin, which aggregates the streamflow from sub-basins (Tague and Band 2004; Hanan et al. 2018). In RHESSys, streamflow is the sum of overland flow and baseflow, and we consider streamflow as the water yield of each sub-basin. RHESSys models vertical and lateral hydrologic fluxes, including canopy interception, plant transpiration, canopy evaporation/sublimation, snow accumulation, snowmelt and sublimation, soil evaporation, soil infiltration, and subsurface drainage. Canopy interception is based on the water-holding capacity of vegetation, which is also a function of plant area index (PAI). Both the canopy evaporation and transpiration are modeled using the standard Penman-Monteith equation.
Snow accumulation is calculated from incoming precipitation and is assumed to fall evenly across each zone. Snowmelt is based on a quasi-energy budget approach accounting for radiation input, sensible and latent heat fluxes, and advection. Soil evaporation is constrained by both energy and atmospheric drivers, as well as a maximum exfiltration rate, which is controlled by soil moisture (Tague and Band 2004). Vertical drainage and lateral flow is a function of topography and soil hydraulic conductivity, which decays exponentially with depth (Tague and Band 2004; Hanan et al. 2018).

Vegetation carbon and nitrogen dynamics are calculated separately for each canopy layer within each patch, while soil and litter carbon and nitrogen cycling are simulated at the patch level. Photosynthesis is calculated based on the Farquhar model considering the limitations of nitrogen, light, stomatal conductance (which is influenced by soil water availability), vapor pressure deficit, atmospheric CO₂ concentration, radiation, and air temperature (Farquhar and von Caemmerer 1982; Tague and Band 2004). Maintenance respiration is based on Ryan (1991), which computes respiration as a function of nitrogen concentration and air temperature. Growth respiration is calculated as a fixed ratio of new carbon allocation for each vegetation component (Ryan 1991; Tague and Band 2004). Net photosynthesis is allocated to leaves, stems, and roots at daily steps based on the Dickinson partitioning method, which varies with each plant development stage (Dickinson et al. 1998). LAI is estimated from leaf carbon and specific leaf area for each vegetation type. The soil and litter carbon and nitrogen cycling (heterotrophic respiration, mineralization, nitrification, and denitrification, etc.) are modified from the BIOME_BGC and CENTURY-NGAS models (White and Running 1994; Parton et al. 1996; Tague and Band 2004). A detailed description of RHESSys model algorithms can be found in Tague and Band (2004).
3.2.2 Beetle effects model

Edburg et al. (2012) designed and developed a model of MPB effects on carbon and nitrogen dynamics for integration with the Community Land Model Version 4 (CLM4) (Lawrence et al. 2011, Fig. 4). Here we integrated this beetle effects model into RHESSys (Fig. 4). Beetles attack trees mainly during late summer, and needles will turn from green to red at the beginning of the following summer. We simplify this process with prescribed tree mortality on September 1 to represent a beetle outbreak of the current year. The advantage of this integration is that RHESSys accounts for the lateral connectivity in water and nitrogen fluxes among patches which is not represented in CLM4 (Fan et al. 2019). Differences in our approach compared to other hydrological models of beetle effects (e.g., VIC, CLM-ParFlow, and DHSVM) include dynamic changes in plant carbon and nitrogen cycling caused by beetle attack, plant recovery, and effects on hydrological responses. Previous studies of hydrologic effects of beetle outbreaks have mainly focused on consequences of changes in LAI and stomatal resistance during each phase of beetle outbreak but have missed feedbacks between carbon and nitrogen dynamics, vegetation recovery, and hydrology (Mikkelson et al. 2013; Livneh et al. 2015; Penn et al. 2016; Sun et al. 2018; Bennett et al. 2018).

To better represent the effects of beetle-caused tree mortality, we added a snag pool (standing dead tree stems) and a dead foliage pool (representing the red needle phase) in RHESSys (Fig. 4). All leaf biomass (including carbon and nitrogen) become part of dead foliage pools. After one year (Hicke et al. 2012; Edburg et al. 2011) the dead foliage is transferred to litter pools at an exponential rate with a half-life of two years (Edburg et al. 2012). Similarly, stem carbon and nitrogen are moved to the snag pool immediately after outbreak. After five years (Edburg et al. 2012), carbon and nitrogen in snags begin to move into the coarse woody debris (CWD) pool at
an exponential decay rate with a half-life of ten years (Edburg et al. 2011). After outbreak, the coarse root pools that are killed move to the CWD and fine root pools move to litter pools. To simplify, we assume a uniform mortality level for all evergreen patches across landscape. Due to the limitation of land cover data, we cannot separate pine and fir in these evergreen patches. However, this will not affect the interpretation of our results because we analyze them based on mortality level and evergreen vegetation coverage rather than different species.

In the integrated model, the reduction of leaf carbon and nitrogen after beetle outbreak can directly decrease LAI and canopy height, which consequently affects energy (i.e., longwave radiation and the interception of shortwave radiation) and hydrologic (i.e., transpiration and canopy interception) fluxes. We calculate two types of LAI: Live LAI (i.e., only live leaf is included), and Total LAI (i.e., both live and dead leaves are included). The calculation of plant transpiration is based on Live LAI, while the calculation of other canopy properties, including interception and canopy evaporation, is based on Total LAI. The calculation of canopy height includes the living stem and the snag pool.

3.3 Input data

We used the US Geologic Survey (USGS) National Elevation Dataset (NED) at 10 m resolution to calculate the topographic properties of Trail Creek, including elevation, slope, aspect, basin boundaries, sub-basins, and patches. Using NED, we delineated 16705 100-m resolution patches within 72 sub-basins. We used the National Land Cover Database (NLCD) to identify five vegetation and land cover types, i.e., evergreen, grass/herbaceous, shrub, deciduous, and urban (Homer et al. 2015). We determined soil properties for each patch using the POLARIS database (probabilistic remapping of SSURGO; Chaney et al. 2016). Parameters for soil and vegetation
were based on previous research and literature (White et al. 2000; Law et al. 2003; Ackerly 2004; Berner and Law 2016; Hanan et al. 2016).

Climate inputs for this study, including maximum and minimum temperatures, precipitation, relative humidity, radiation, and wind speed, were acquired from gridMET for years from 1980 to 2018. GridMET provides daily high-resolution (1/24 degree or ~4 km) gridded meteorological data (Abatzoglou 2013). It is a blended climate dataset that combines the temporal attributes of gauge-based precipitation data from NLDAS-2 (Mitchell et al. 2004) with the spatial attributes of gridded climate data from PRISM (Daly et al. 1994).

3.4 Simulation experiments

To quantify how water yield responds to beetle-caused mortality, we designed the following simulation experiment. We prescribed a beetle outbreak in September 1989, the mortality level (%) is applied to all evergreen patches for each sub-basin. After beetle outbreak, red needles stay on the trees for one year before they start to fall (transferred to the litter pool) at an exponential rate with a half-life of two years. The snag pools stay in the standing trees for five years and then start to fall and are added to the CWD pool which decays at an exponential rate with a half-life of ten years.

To address Q1 (i.e., the role of interannual variability), we compared water yield responses during a dry water year, 1994 (i.e., five years after beetle outbreak with precipitation 611 mm), to responses during a wet year, 1995 (i.e., six years after beetle outbreak with precipitation 1394 mm). This enabled us to estimate the role of interannual climate variability in driving changes in water yield following beetle attack. The dry year are selected based on years that have precipitation below the 15th percentile across 38 years of annual precipitation data (from 1979 to 2017) (Searcy 1959, see Fig. S1). During these early period after beetle outbreak (e.g., 1994 and
1995) the forest is experiencing large changes in vegetation canopy cover, plant transpiration, and soil moisture. We chose these two successive years because they have almost similar canopy and vegetation status in terms of fallen dead foliage and residual vegetation regrowth, which makes this comparison reasonable. However, it is possible that antecedent climate conditions may affect the following year’s response. For example, soil moisture can be depleted during a drought year, affecting initial conditions the following year. Moreover, under drought conditions, less reactive nitrogen is taken up by the plants or leaching is reduced, so more nitrogen will be left for the following year. Therefore, the difference in water yield responses between 1994 and 1995 might be affected by not only climate variations but also initial conditions in the hydrology and the biogeochemistry. To consider the time lag effect (antecedent conditions affecting the current year’s response), we also analyzed other dry and wet years.

To address Q2 (i.e., the role of vegetation mortality), we prescribe a range of infestation-caused mortality levels (i.e., from 10% to 60% by a step of 10% in terms of carbon, uniformly applied to all evergreen patches for each sub-basins) and a control run (no mortality) to quantify the response of forests in water yield to vegetation mortality level (for each sub-basin vegetation mortality is evergreen mortality multiplied by evergreen coverage of that basin). The differences in water yield between each mortality level and the control run represent the effects of beetle kill: a positive value means that mortality increased water yield, and vice versa.

We quantified the water budget for each sub-basin to examine which hydrological process contribute to the water yield responses: water yield (Q), precipitation (P), canopy evaporation (E_{canopy}, canopy evaporation and snow sublimation), transpiration (T), ground evaporation (E_{ground, includes bare soil evaporation, pond evaporation, and litter evaporation), snow sublimation (Sublim, ground), soil storage change ($\frac{dS_{soil}}{dt}$), litter storage change
(\(dS_{\text{litter}}/dt\)), snowpack storage change (\(dS_{\text{snowpack}}/dt\)) and canopy storage change (\(dS_{\text{canopy}}/dt\)).

The storage components include soil, litter, and canopy. According to Eq. (1), if the storage increases, water yield decreases.

\[
Q = P - E_{\text{canopy}} - E_{\text{ground}} - \text{Sublim} - T - \frac{d(S_{\text{soil}} + S_{\text{litter}} + S_{\text{canopy}} + S_{\text{snowpack}})}{dt}
\]

(1)

Calculating water balance differences between different mortality scenarios and control scenario results in Eq. (2):

\[
\Delta Q = \Delta E_{\text{canopy}} + \Delta E_{\text{ground}} + \Delta \text{Sublim} + \Delta T + \Delta \left(\frac{d(S_{\text{soil}} + S_{\text{litter}} + S_{\text{canopy}} + S_{\text{snowpack}})}{dt}\right)
\]

(2)

To address Q3 (i.e., the role of long-term aridity), we calculated the long-term aridity index (PET/P, Fig. 3) across the basin and analyzed the relationship between long-term aridity index and hydrologic response. As mentioned earlier, the long-term aridity index is defined as the ratio of mean annual potential ET (PET) to annual precipitation (P), averaged over 38 years (water year 1980-2018) of historical meteorological data. Based on the long-term aridity index, we classified our sub-basins into three types (McVicar et al. 2012, Table 1).
4 Results

4.1 Simulated vegetation response to beetle outbreak at basin-scale

4.1.1 Vegetation response to beetle outbreaks

Figure 5 shows the basin-scale vegetation response after beetle outbreak in 1989. Live LAI dropped immediately after beetle outbreak, then gradually recovered to pre-outbreak levels during following years (Fig. 5a). Total LAI (i.e., including dead foliage) showed a slight increase during the first ten years after beetle outbreak (1990 – 2000), which is due to the retention of dead leaves in the canopy and the simultaneous growth of residual (unaffected) overstory and understory vegetation (Fig. 5b). The dead foliage pool (Fig. 5c) remained in place for one year and then began to fall to ground (converted to litter) exponentially with a half-life of two years, and the snag pool (Fig. 5d) remained in place for five years and then began to fall to ground (converted to CWD) exponentially with a half-life of ten years. These behaviors of the dead foliage and snag pools are similar to Edburg et al. (2012), which demonstrates that the integrated model is simulating expected vegetation dynamics following beetle outbreak.

4.1.2 Time series of hydrologic response to beetle outbreak

Figure 6 shows the changes in simulated water fluxes and soil moisture over the basin after beetle outbreak with various evergreen mortality levels. During the first 15 years after beetle outbreak, scenarios where the evergreen mortality level was larger than zero had higher basin-scale water yield than the control scenario (where the evergreen mortality level was zero). This was especially true during wet years; however, there was no significant increase during dry years (i.e., 1992, 1994, 2001, and 2004; Fig. 6a). The year-to-year soil storage fluxes responded strongly in the first two years after beetle outbreak, then stabilized to the pre-outbreak condition (Fig. 6b). Note that year-to-year soil storage change is not the same as soil water storage. After
beetle outbreak, the soil can hold some portion of water that not being up taken by the plants, but it was confined by the soil water holding capacity. This phenomenon indicates that the soil has some resilience to vegetation change.

Beetle outbreaks reduced transpiration during wet years but did not have significant effects in dry years (Fig. 6c). This is because transpiration in dry years was water-limited and so was much lower than the potential rate (more water is partitioned to evaporation; Biederman et al. 2014). Thus, killing more trees had little effect on stand scale transpiration because remaining trees utilized any water released by the dead trees in dry years. On the other hand, plant transpiration in wet years was close to the potential rate; therefore, decreases in canopy cover reduced transpiration. The simulation results did not show any apparent effect on snowmelt after beetle outbreak.

The evaporation response was opposite in dry and wet years: evaporation increased in dry years, while it decreased in wet years (Fig. 6d). This phenomenon is caused by tradeoffs and interactions among multiple processes, as will be explained in more detail in the next section.

4.2 The role of spatial heterogeneity in water yield response

4.2.1 Spatial patterns of hydrologic response along long-term aridity gradient

4.2.1.1 Evaporation

Beetle outbreak had opposite effects on evaporation between a dry year and a wet year (Fig. 7). In the dry year, most sub-basins experienced higher evaporation for beetle outbreak scenarios than in the control scenario (Fig. 7a). This was the cumulative consequence of decreased canopy evaporation and increased ground (soil, litter, pond) evaporation due to decreases in LAI (caused by mortality). In the dry year, the latter effect (i.e., increased ground evaporation) dominated
over the former effect so that overall consequence was increased evaporation. When the
vegetation mortality level (calculated as the percentage of evergreen patches in a sub-basin
multiplied by the mortality level of evergreen caused by beetles) was higher than 20%, a few sub-
basins in the balanced (more mesic) area showed some decrease, indicating that the effects of
decreasing canopy evaporation exceeded the effects of increasing ground evaporation. In the wet
year, most of the sub-basins located in the balanced area showed decreases in evaporation, and
the decreasing trend showed linear relationship with vegetation mortality level (where canopy
evaporation decreases are dominant, Fig. 7b). However, sub-basins located in much drier regions
(aridity >3.5) had relatively insignificant responses to vegetation mortality levels and some of
them even had slight increases in evaporation (where ground evaporation increases are dominant
due to drier long-term climate and less pine coverage resulted in lower canopy mortality).

4.2.1.2 Transpiration

Beetle outbreak decreased transpiration in both dry and wet years, and with higher mortality
levels the decrease became larger (Fig. 8). However, during the dry year, the water-limited area
showed less change than the balanced area; some sub-basins even showed slight increases. This
increase in the water-limited part of the basin occurred because after beetles kill some overstory
evergreen trees, the living trees and understory plants together can exhibit higher transpiration
rates in dry years (Tsamir et al. 2019). In the wet year, when most canopies reach potential
transpiration rates (less competition for water), beetle outbreaks can reduce transpiration rates by
decreasing Live LAI.

4.2.1.3 Total ET
Figure 9 depicts the spatial pattern of changes in total ET (i.e., evaporation and transpiration) after beetle outbreak. In a dry year, the balanced and water-limited areas showed opposite responses to mortality: the balanced area showed a decrease in ET and the water-limited area showed a slight increase. In the balanced area, larger ET decreases occurred with higher mortality levels. However, increases in ET in water-limited regions were less sensitive to vegetation mortality level, and even for high vegetation mortality levels (>40%), ET still increased (Fig. 9a). During the wet year, most sub-basins experienced decreasing ET after beetle outbreak and the magnitude was larger with higher vegetation mortality. The different responses of ET were driven by different hydrologic responses (transpiration, ground evaporation and canopy evaporation) competing with each other; this competition was influenced by climate conditions, mortality level, and spatial heterogeneity in long-term aridity.

4.2.1.4 Water yield

In the dry year (1994), beetle-caused vegetation mortality affected water yield (Fig. 10), but the responses differed between the balanced and water-limited areas. For the balanced area, most sub-basins showed slight decreases in water yield after beetle outbreak and no significant differences among low vegetation mortality level (<=40%, Fig. 10a). However, with increased mortality levels, more sub-basins showed increases in water yield, particularly with vegetation mortality higher than 40% (Fig. 10a). Moreover, the vegetation mortality threshold that changed the direction of water yield response was altered by long-term aridity, e.g., it was 40% for aridity 2.0 but 20% for aridity 1.0. For the water-limited area, water yield decreased and was independent from mortality level (Fig. 10a). In the wet year (1995), the water yield in most sub-basins increased after beetle outbreak, and the balanced area increased more significantly than the water-limited area. Furthermore, for the balanced area, higher mortality levels caused larger
increases in water yield which responded more linearly (Fig. 10b). In summary, for a wet year,
increases in water yield occurred for most sub-basins, driven by a decrease in ET. However,
during dry years, the water yield and ET responses were spatially heterogeneous, and the
competing changes in evaporation and transpiration changed the direction and magnitude of ET
and thus water yield response. The competing effect among different hydrologic fluxes for a dry
year is explored in more detail in the next section.

4.2.2 Water budgets to understand decreasing water yield in the dry year
We analyzed the fluxes in greater detail in a dry year (1994) to understand the response of
hydrologic fluxes and resulting water yield. Based on Eq. (2), we identified four hydrological
fluxes that can potentially affect water yield: canopy evaporation (canopy evaporation and
canopy snow sublimation), ground evaporation (bare soil evaporation, ground snow sublimation,
litter evaporation, pond evaporation), plant transpiration, and year-to-year storage change (soil,
canopy, litter, snowpack). These three storage terms (canopy, litter, snowpack) were considered
together with soil storage since their contribution was minor in comparison with other fluxes.
Figure 11 summarized different combinations of these four dominate processes during the dry
year (1994) based on their directions (increase or decrease in water yield) after beetle outbreak.
In total, fourteen combinations of changes in these fluxes (referred to as “response types”) were
found. Five of them resulted in an increase in water yield, and the others resulted in a decrease.

Water yield responses caused by the competition of different hydrologic fluxes showed different
patterns across the aridity gradient (Figs. 3&10). For the balanced area (upper part of the basin),
with low evergreen mortality (<=30%), the major response types were D1 and D2, in which the
increase in ground evaporation dominated over the decrease in transpiration and canopy
evaporation (Fig. 11a, b, and c). However, with higher evergreen mortality (>30%), the major
response type became W2, where the increase in ground evaporation did not exceed the decrease in canopy evaporation and transpiration (Fig. 11e, f, and g). This indicates that, in a dry year, when more evergreen stands are killed, the increase in ground evaporation reaches a limit while transpiration and canopy evaporation continue to decrease with decreasing LAI. The increase in ground evaporation was triggered either by decreased Total LAI and open canopy, which allowed more solar radiation penetration to the ground for evaporation (Fig. S5c), or less transpiration from plants, which left more water available to evaporate (Fig. 8a). The decrease in plant transpiration and canopy evaporation was driven by a lower Live LAI and a lower Total LAI, respectively (Fig. S5 a&c and Fig. 8a).

The decrease in water yield in the water-limited area (lower part of the basin) was driven by different hydrologic flux competitions in different mortality levels. When evergreen stand mortality level was low (<=30%), the response types were D5 and D7, in which the increase in ground and canopy evaporation dominated over the decrease of transpiration (Fig. 11a, b, and c). However, with high evergreen stand mortality (>30%), the response types became D1 and D2 (Fig. 11e, f, and g), in which the canopy evaporation changed from an increase to a decrease that was driven by a decrease in Total LAI (Fig. S5c). When mortality was low, the increases in growth from residual plants and understory outstripped the litter fall of dead foliage; thus, Total LAI increased, and vice versa when mortality was high.

5 Discussion

5.1 Role of interannual climate variability

During the first 15 years after beetle attack, various hydrologic processes opposed and/or reinforced one another to either increase or decrease water yield: a decrease in Live LAI can reduce transpiration, while a decrease in Total LAI can enhance ground evaporation but diminish
canopy evaporation (Montesi et al. 2004; Tsamir et al. 2019). Interannual climate variability played an important role in determining which of these competing effects dominate and, therefore, drove the direction of water yield response to beetle outbreak (Winkler et al. 2014; Goeking and Tarboton 2020). Our results show that mainly decreases in water yield occurred in dry years, while increases occurred in wet years. During a wet year, plant ET can reach its potential so that any reductions in actual plant ET will dominate over any increases in ground evaporation, resulting in a net increase in water yield. During a dry year, the relative dominance of these competing effects had greater spatial heterogeneity because the water stress status of the plants varied across the basin (as explained in Sect 4.2.2; Fig. 11).

However, the responses we observed in the dry year (1994) and in the wet year (1995) were also affected by the previous year's climate (mainly precipitation) and its effects on hydrologic and biogeochemical processes, which set the initial conditions for the dry and wet year (e.g., soil moisture, nitrogen availability, etc.). Therefore, we also analyzed other water years during the first ten years after beetle outbreak to examine whether our findings for dry and wet years follow a general pattern and to what extent they are influenced by antecedent conditions. Results indicate that our findings are robust through the study time period. For example, water yield generally decreased during dry years (1992, 1994, and 2001, see Figs. S1 and S2) and always increased during wet years (1993 and from 1995 to 2000, see Fig. S1 and S2).

Adams et al. (2012) provide a threshold of precipitation under which water yield increases after disturbances: at least 500 mm/year (Goeking and Tarboton 2020). The average annual precipitation over this study basin is 600-900 mm in dry years, and higher than 900 mm in wet years. Recent field work observation also find annual climate variability can affect the magnitude of evapotranspiration fluxes that change the water yield direction (Biederman et al. 2014). Our
results corroborate these earlier studies by revealing that there are precipitation thresholds above which tree removal increases water yield (Figs. 10, S1 and S2).

5.2 Role of vegetation mortality

Vegetation mortality is another important factor that influences water yield response. We found that during the wet year, beetle outbreak increased water yield across the basin and the magnitude of these increases grew linearly with the level of vegetation mortality (Fig. 10b). In the dry year, however, the response of water yield to the level of vegetation mortality was more complicated because mortality influenced not only the magnitude of change but also the direction (Fig. 10a). These opposing results (due to mortality level) mainly occurred in the “balanced” northern part of the basin, where the competing effects of mortality (i.e., increases in ground evaporation versus decreases in transpiration) are more balanced (Fig. 11). The level of vegetation mortality played a less significant role in changing water yield in the southern “water-limited” area. Vegetation mortality level determined the magnitudes of Live LAI, Total LAI, transpiration, canopy evaporation, and ground evaporation in such a way that it governed the direction of change in both ET and water yield. Thus, when vegetation mortality level was higher than 40%, its effect of decreasing transpiration became the dominant process and its effect of increasing soil evaporation became minor (Fig. 11 f&g; Guardiola-Claramonte et al. 2011).

Besides the precipitation threshold of at least 500 mm/year, Adams et al. (2012) also estimate that when at least 20% of vegetation cover is removed, water yield can increase. According to previous analysis (Sect 4.1), for a dry year, water yield increases when more than 40% of vegetation is removed (Fig. 10a). Our model simulations indicate similar mortality thresholds exist for driving water yield increases during the dry year, however, we did not find evidence that such a threshold exists during wet years. These differences between dry and wet years
suggest that the effects of mortality on water yield depend on climate variability. Other studies corroborate this finding by demonstrating that the relationship between mortality level and water yield response is complicated and nonlinear (Moore and Wondzell 2005).

5.3 Role of long-term aridity index (PET/P)

Long-term aridity indices can be used to predict where water yield will decrease after disturbance. We found that water yield always increased in a wet year, irrespective of the climatic aridity index (Fig. 10a). For dry years, long-term aridity index became important in driving the direction of water yield responses to beetle outbreak. In areas that are less water-limited (balanced areas), the direction of water-yield responses to beetle outbreak in a dry year was mixed and depended on mortality level. For water-limited areas, in a dry year, water yield showed a more consistent decrease trend, and it was also less affected by mortality level. These results agree with previous studies finding that water yield decreases largely happen in semiarid areas (Guardiola-Claramonte et al. 2011; Biederman et al. 2014).

The decrease in water yield for water-limited area can be driven by increases in canopy evaporation or transpiration, which were different in the hydrologically-balanced area (driven by increase of ground evaporation). There, the increase in canopy evaporation was due to an increase in total LAI which is a combined effect of delayed decay of dead foliage and fast growth of residual and understory plants (Fig. 11d type D5, D7, D8 & D9; Fig. S5). The surviving and understory plants in the water-limited area can also have higher transpiration rates after mortality (Fig. 11d type D6 and Fig. 8). Similarly, in field studies, Tsamir et al. (2019) found an increase in photosynthesis and transpiration after thinning in a semi-arid forest. These findings illustrate that in addition to top-down climate variability, the long-term aridity index
(which also varies with bottom-up drivers such as vegetation and local topography) can be another useful indicator of how water yield will respond to disturbances.

5.4 Uncertainties

While our findings revealed how topoclimatic gradients influenced water yield responses to beetle infestation, some uncertainties remain. For one, we used uniform mortality levels for all patches across the watershed rather than location and vegetation-specific mortality levels. However, in reality beetles usually attack older trees first (Edburg et al. 2011). Thus, incorporating a more mechanistic understanding of beetle attack patterns with our beetle effects model could enable us to simulate more realistic outbreak scenarios moving forward. Another source of uncertainty came from the model treatment of litter pools. In the current implementation, we ignored the effects of litter on ground albedo and snowmelt (Lundquist et al. 2013), which could have an effect on rates of AET and PET and therefore our calculated long-term aridity index. Also, because we focused on water yield responses during the first 15 years after beetle outbreak, we may have missed some of the long-term effects (e.g., after the ecosystem has begun to recover) on forest hydrology. Future research should integrate the short-term and long-term effects and interactions among beetle outbreak, vegetation dynamics, and hydrology. Since Trail Creek is either “balanced” or “water-limited” in terms of aridity, other “energy-limited” regions could also be investigated.

6 Conclusion

We tested a coupled ecohydrologic and beetle effects model in a semi-arid basin in southern Idaho to examine how watershed hydrology responds to beetle outbreak and how interannual climatic variability, vegetation mortality, and long-term aridity influence these responses. Simulation results indicate that each factor can play a discrete role in driving hydrological
processes (e.g., the direction and magnitude of changes in plant transpiration, canopy and soil evaporation, soil and litter moisture, snow sublimation, etc.). These combined effects determine the overall water budget and water yield of the basin. While interannual climate variability is the key factor driving the direction of change in water yield, vegetation mortality levels and long-term aridity modify water yield responses.

In dry years, the water yield of most sub-basins slightly decreased after beetle outbreak when vegetation mortality level was lower than 40%; while during wet years in most sub-basins it increased. Our results show that long-term aridity index is a reliable indicator of the water yield decreases that occur during dry years due to the fact that there is a consistent decrease in water yield in the most water-limited portion of the basin. Generally, the effects of vegetation mortality on water yield during dry years is less uniform and depends on local, long-term aridity conditions. During wet years, on the other hand, mortality typically causes increases in water yield. This illustrates that together interannual climate variability and mortality can have a stronger effect on the direction of water yield response in water-limited regions than interannual climate variability alone. Future studies to predict water yield response to disturbance should consider the interactions of these factors and capture the fluctuations of competing water fluxes and storage change that control overall water budget and water yield.

Using our novel RHESSys-beetle effects modeling framework, we demonstrate that the direction of hydrologic response is a function of multiple factors (e.g., interannual climate variability, vegetation mortality level, and long-term aridity) and that these results do not necessarily conflict with each other but are representative of different conditions. The mechanisms behind these changes compete with each other resulting in a water yield increases or decreases (Fig. 1). Contradictory findings in previous studies may result from differing mortality levels (disturbance
severity), or differences in aridity, and consequently, the emergent drivers that dominate water yield responses differ. Disentangling these drivers is difficult or impossible using a purely empirical approach where it can be challenging or cost-prohibitive to experiment under a broad range of controlled conditions. Distributed process-based models on the other hand, provide a useful tool for examining these dynamics.

Findings from this study can assist water supply stakeholders in risk management in beetle outbreak locations. For example, during wet years, more attention might be focused on “balanced” areas, i.e., wet regions, for flooding and erosion risks after beetle outbreaks since these regions may experience large increase in runoff due to decreases in plant transpiration and increases in soil moisture. During the dry years, attention might need to shift to “water-limited” areas for managing wildfire risk since these regions will experience elevated ET and lower soil and litter moisture. Because multiple factors interact to influence hydrological processes after beetle outbreak, water and forests management must respond to spatial and temporal variations in climate, aridity, and vegetation mortality levels.

**Code and data availability**

The coupled RHESSys model code is available online at: https://github.com/renjianning/RHESSys/tree/historical_fire

The data used in this study are available at: https://osf.io/tsu9z/?view_only=72bfa7b376ad40c59278312f49b03a69

**Author contributions**

JR, JA and JAH conceived of study. JR designed study with support from JA, JAH and EH. JR and EH developed RHESSys code for coupling beetle effect model and parallelizing model runs
with help from JA, JAH, NT, ML, CK, and JTA. JR performed model simulations and developed figures with help from all authors. ML and JTA generated downscaled meteorological data. JR wrote manuscript with input from all authors.

Competing interests

The authors declare that they have no conflict of interest.

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**Table 1. Classification of aridity index.**

| Aridity Index (i.e. PET/P) | Type          |
|---------------------------|---------------|
| > 2                       | Water - limited |
| 0.8 - 2                   | Balanced      |
| < 0.8                     | Energy - limited |
Figure 1. Mechanism of water yield responses to beetle-caused mortality during the red and gray phases (0 – 10 years after beetle outbreak), semicircle boxes represent understory responses and square boxes represent overstory responses.
Figure 2. Land cover, elevation, and tree mortality for Trail Creek. (a) is the land cover map with the main vegetation type, (b) is the elevation gradient, and (c) is the severity of beetle caused tree mortality (during the period 2003-2012 Meddens et al. (2012)). Note that, for our modeling experiments, we prescribe beetle outbreak uniformly across evergreen patches instead of using historical beetle outbreak data.
Figure 3. Trail creek evergreen forest cover percentage for each sub-basin, sub-basin ID, and long-term aridity index. Aridity index is defined as annual mean potential evapotranspiration (PET) / precipitation (P) from 38 years of data (see Sect 3.4), PET/P > 2 is water-limited, PET/P < 0.8 is energy-limited, PET/P between 0.8 and 2 is balanced. Recall that only evergreen forest trees are attacked during beetle outbreaks.
Figure 4. Conceptual framework of the beetle effect model.  
(a) Normal background mortality routine in RHESSys before beetle outbreak.  
(b) Mortality from bark beetles. We add snag (standing dead trees) and dead foliage (needles still on dead trees) pools, shown in the dashed circle. After a beetle outbreak, carbon (C) and Nitrogen (N) move from stems to snag pools (black dashed arrow). After staying in the snag pool for $m$ years, C and N move from snag to coarse wood debris pools (CWD) with an exponential decay rate to represent the snag fall (gray dashed arrow). It is a similar process for leaf C and N, which move from leaf to dead foliage to litter pools (black dotted arrow). Furthermore, C and N in the CWD and fine root pools move to the litter pool immediately after outbreak (solid black and gray arrows). Figure modified from Edburg et al. (2012).
Figure 5. Basin-scale vegetation responses after beetle outbreak for different evergreen mortality level. (a) Annual live leaf area index (Live LAI), (b) Annual total LAI (LAI calculated including dead foliage pool), (c) Daily dead foliage pool, and (d) Daily snag pool after outbreak. The green background color is the period before beetle outbreak, and the red background color is after the beetle outbreak.
Figure 6. Basin-scale annual sum of hydrologic fluxes responses after beetle outbreak (1989) for different evergreen mortality levels. (a) Annual water yield calculated as annual sum of basin streamflow, and (b) annual soil water storage change calculated as water year soil water storage at the end of water year minus soil water storage at the beginning of water year. (c) Transpiration is the annual sum of transpiration for both overstory and understory. (d) Evaporation is calculated as the annual sum of canopy evaporation, ground evaporation, and snow sublimation.
Figure 7. Relationship among long-term aridity, vegetation mortality level, and differences in evaporation for a dry year (1994, a) and wet year (1995, b). Differences are calculated as the normalized differences (%) of evaporation between each evergreen mortality scenario and the control run for no beetle outbreak. Vegetation mortality for each sub-basin is calculated as the percentage of evergreen patches multiplied by the mortality level of evergreen caused by beetles. Long-term aridity is defined as temporally averaged (38 years) potential evapotranspiration relative to precipitation.
Figure 8. Relationship among long-term aridity, vegetation mortality, and differences in transpiration for a dry year (1994, a) and wet year (1995, b).
Figure 9. Relationship among long-term aridity, vegetation mortality level and differences in ET for a dry year (1994, a) and a wet year (1995, b).
Figure 10. Relationship among long-term aridity, vegetation mortality level and Differences in water yield for a dry year (1994, a) and wet year (1995, b).
Figure 11. Water yield response types after beetle outbreak for different evergreen mortality scenarios compared with control scenario. D1 to D9 are water yield decrease types and W1 to W5 are water yield increase types. In panel D and H, the left side of each type are increasing fluxes that cause water yield decreases and the right side are decreasing fluxes that cause water yield increase. If the left side is larger than the right side, water yield increases, and vice versa. (Note: this mortality is evergreen mortality, which is different from vegetation mortality.)