

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

3 Jianning Ren<sup>1,3</sup>, Jennifer Adam<sup>1</sup>, Jeffrey A. Hicke<sup>2</sup>, Erin Hanan<sup>3</sup>, Naomi Tague<sup>4</sup>, Mingliang Liu<sup>1</sup>,  
4 Crystal Kolden<sup>5</sup>, John T. Abatzoglou<sup>5</sup>

5

6 <sup>1</sup> Department of Civil & Environmental Engineering, Washington State University, 99163,  
7 Pullman, USA

8 <sup>2</sup> Department of Geography, University of Idaho, 83844, Moscow, USA

9 <sup>3</sup> Department of Natural Resources and Environmental Sciences, University of Nevada, 89501,  
10 Reno, USA

11 <sup>4</sup> Bren School of Environmental Science & Management, University of California, 93106, Santa  
12 Barbara, USA

13 <sup>5</sup> Management of Complex Systems, University of California, 95344, Merced, USA

14

15 *Correspondence: Jennifer Adam (jcadam@wsu.edu)*

16

17

18

19

20 **Key points:**

21 • Mountain pine beetle (MPB)-caused tree mortality increases water yield in most  
22 wet years, and decreases in water yield mainly happen in dry years; therefore, interannual  
23 climate variability is an important driver of water yield response to beetle-caused tree  
24 mortality.

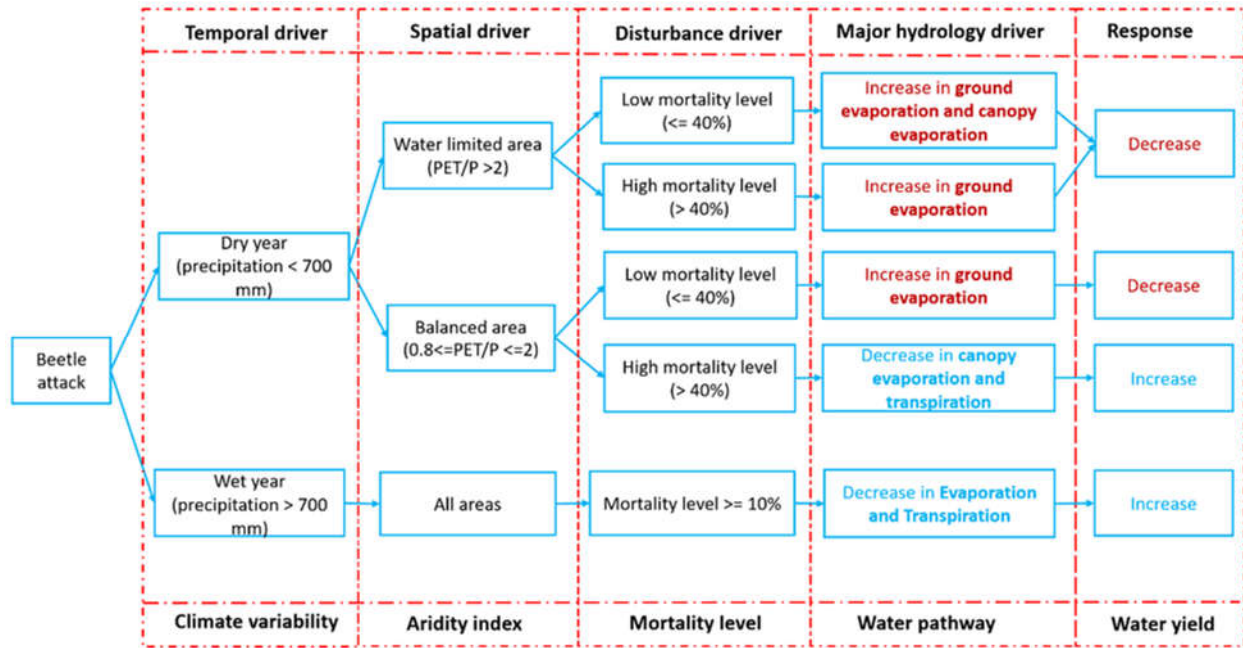
25 • A long-term (multi-decade) aridity index is a reliable indicator of water yield  
26 response to MPBs: in a dry year, decreases in water yield occur mainly in water-limited  
27 areas and the level of vegetation mortality only has minor effects; in wetter areas,  
28 decreases in water yield only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

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

32

33

34 **Graphical abstract**



35

36 **Abstract**

37 Mountain pine beetle (MPB) outbreaks in the western United States result in widespread tree  
 38 mortality, transforming forest structure within watersheds. While there is evidence that these  
 39 changes can alter the timing and quantity of streamflow, there is substantial variation in both the  
 40 magnitude and direction of hydrologic responses, and the climatic and environmental  
 41 mechanisms driving this variation are not well understood. Herein, we coupled an eco-  
 42 hydrologic model (RHESSys) with a beetle effects model and applied it to a semiarid watershed,  
 43 Trail Creek, in the Bigwood River basin in central Idaho, USA, to examine how varying degrees  
 44 of beetle-caused tree mortality influence water yield. Simulation results show that water yield  
 45 during the first 15 years after beetle outbreak is controlled by interactions among interannual  
 46 climate variability, the extent of vegetation mortality, and long-term aridity. During wet years,  
 47 water yield after beetle outbreak increased with greater tree mortality; this was driven by  
 48 mortality-caused decreases in evapotranspiration. During dry years, water yield decreased at low

49 to medium mortality but increased at high mortality. The mortality threshold for the direction of  
50 change was location-specific. The change in water yield also varied spatially along aridity  
51 gradients during dry years. In relatively wetter areas of the Trail Creek basin, post-outbreak  
52 water yield decreased at low mortality (driven by an increase in ground evaporation) and  
53 increased when vegetation mortality was greater than 40 percent (driven by a decrease in canopy  
54 evaporation and transpiration). In contrast, in more water-limited areas, water yield typically  
55 decreased after beetle outbreaks, regardless of mortality level (although the driving mechanisms  
56 varied). Our findings highlight the complexity and variability of hydrologic responses and  
57 suggest that long-term (i.e., multi-decadal mean) aridity can be a useful indicator for the  
58 direction of water yield changes after disturbance.

## 59 **1 Introduction**

60 In recent decades, mountain pine beetle (MPB) outbreaks in the Western U.S. and Canada have  
61 killed billions of coniferous trees (Bentz et al. 2010). Coniferous forests can provide essential  
62 ecosystem services, including water supply for local communities (Anderegg et al. 2013).  
63 Therefore, it is essential to understand how ecosystems and watersheds respond to beetle  
64 outbreaks and to identify the dominant processes that drive these responses (Bennett et al. 2018).  
65 A growing number of studies have qualitatively examined hydrologic responses to beetle  
66 outbreaks and disturbance; however, these studies have produced conflicting results (Adams et  
67 al. 2012; Goeking and Tarboton 2020). While some studies show increases in water yield  
68 following beetle outbreak (e.g., Bethlahmy 1974; Potts 1984; Livneh et al. 2015), many others  
69 show no change or even decreases (e.g., Guardiola-Claramonte et al. 2011; Biederman et al.  
70 2014; Slinski et al. 2016). To determine which mechanisms control change in water yield  
71 following beetle outbreak, more quantitative approaches are needed.

72 Water yield is often thought to increase after vegetation is killed or removed by  
73 disturbances such as fire, thinning, and harvesting (Hubbart 2007; Robles et al. 2014; Chen et al.  
74 2014; Buma and Livneh 2017; Wine et al. 2018). In the Rocky Mountain West, beetle outbreaks  
75 have increased water yield through multiple mechanisms. First, defoliation/needle loss can  
76 reduce plant transpiration, canopy evaporation, and canopy snow sublimation losses to the  
77 atmosphere (Montesi et al. 2004). Snow sublimation is an important process in snow-dominated  
78 forest systems. Beetle-caused decreases in total sublimation can increase water yield, especially  
79 since canopy sublimation is more sensitive to disturbances than ground snow sublimation (Frank  
80 et al. 2019). Increased canopy openings can also enable snow accumulation and allow more  
81 radiation to reach the ground surface, resulting in earlier and larger peak snowmelt events, which  
82 can in turn reduce soil moisture and therefore decrease summer evapotranspiration (ET).

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

91 In a review of 78 studies, Goeking and Tarboton (2020) concluded that the decrease in  
92 water yield after tree-mortality mainly happens in semiarid regions. Previous studies also provide  
93 rule-of-thumb thresholds above which water yield will increase: at least 20 percent loss of  
94 vegetation cover and mean precipitation of 500 mm/year (Adams et al. 2012). However, many

95 watersheds in the western U.S. experience high interannual climate variability (Fyfe et al. 2017),  
96 and local environmental gradients (e.g., long-term aridity gradients) may strongly influence  
97 vegetation and hydrologic responses to disturbances such as beetle outbreaks, making such rules-  
98 of-thumb difficult to apply in practice (Winkler et al. 2014). Given the possibility of either  
99 increases or decreases in water yield following beetle outbreaks, modeling approaches are crucial  
100 for identifying the specific mechanisms that control these responses.

101 Our overarching goal was to identify mechanisms driving the direction of change in annual  
102 water yield after beetle outbreaks in semi-arid regions (note that in the following text, “water  
103 yield” refers to mean annual water yield). To accomplish this goal, we asked the following  
104 questions:

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

110 We hypothesized that multiple ecohydrologic processes (e.g., snow accumulation and melt,  
111 evaporation, transpiration, drainage, and a range of forest structural and functional responses to  
112 beetles) could interactively influence how water yield responds to beetle outbreaks—however, in  
113 certain locations one or more processes may dominate. In addition, the dominant ecohydrologic  
114 processes may vary over space and time due to interannual climate variability (i.e.,  
115 precipitation), vegetation mortality, and long-term aridity. In Section 2, we present a conceptual  
116 framework for identifying and depicting dominant hydrological processes through which forests  
117 respond to beetle infestation. We used this framework to interpret the modeling results. In

118 Section 3, we describe our mechanistic modeling approach, i.e., using the Regional Hydro-  
119 Ecological Simulation System (RHESSys), which can prescribe a range of vegetation mortality  
120 levels, capture the effects of landscape heterogeneity and the role of lateral soil moisture  
121 redistribution, and project ecosystem carbon and nitrogen dynamics, including post-disturbance  
122 plant recovery. In Sections 4 and 5, we then present modeling results that explore how multiple  
123 mechanisms influence water yield responses. This study can help inform management in beetle-  
124 affected watersheds by providing a tool for identifying locations that should be prioritized for  
125 mitigating flooding and erosion risk under different climate conditions.

## 126 **2 Conceptual framework**

### 127 2.1 Vegetation response to beetle outbreaks

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

### 137 2.2 Hydrologic response to beetle outbreaks

138 Figure 1 describes the main processes that alter evapotranspiration to either decrease or increase  
139 water yield, depending on which processes dominate (Adams et al. 2012; Goeking and Tarboton  
140 2020). During the red and gray phases, needles fall to the ground, and there is lower leaf area

141 index (LAI) and a more open canopy (Hicke et al. 2012). During these phases, changes in  
142 canopy cover can interact with hydroclimatic conditions across a watershed to alter transpiration  
143 and evaporation in a variety of ways.

144 Canopy mortality can reduce transpiration rates in infected trees, though in water-limited  
145 environments, remaining trees may compensate to some extent by increasing transpiration  
146 (Adams et al. 2012, Tague et al. 2019). More open canopies (i.e., following tree mortality)  
147 intercept less precipitation than closed canopies, reducing canopy evaporation but potentially  
148 increasing it from soil and litter layers (Montesi et al. 2004; Sexstone et al. 2018). Meanwhile,  
149 open canopies can also increase the proportion of snow falling to the ground and, therefore,  
150 increase snowpack accumulation. With more solar radiation reaching the ground, earlier and  
151 larger peak snowmelt can also occur (Bennett et al. 2018). Generally, earlier snowmelt increases  
152 water for spring streamflow and decreases water for summertime ET (Pomeroy et al. 2012).  
153 However, once snags fall, reductions in longwave radiation can actually lead to later snowmelt  
154 (Lundquist et al. 2013). An open canopy, combined with less competition for resources, such as  
155 solar radiation and nutrients, can also promote understory vegetation growth, which may increase  
156 understory transpiration (Biederman et al. 2014; Tague et al. 2019). In some riparian corridors,  
157 the regreening of surviving vegetation and the compensatory response of remaining tissues could  
158 diminish the reduction in ET caused by foliage fall, leading to no significant water yield response  
159 to beetle-caused mortality (Snyder et al. 2012; Nagler et al. 2018). Therefore, whether water  
160 yield increases or decreases following beetle outbreak ultimately depends on how these  
161 processes interact.



162 Interannual variability in climate (e.g., dry versus wet years) can affect how hydrologic  
163 processes interact in forested watersheds (Winkler et al. 2014; Goeking and Tarboton 2020). For  
164 instance, during wet years, remaining plants are not water-limited, and reductions in plant  
165 transpiration due to beetle-caused mortality dominate over increases in soil evaporation or  
166 remaining plant transpiration, resulting in a higher water yield. In contrast, during dry years,  
167 plants are already under water stress and decreases in plant transpiration caused by tree mortality  
168 may be compensated by increasing soil evaporation and transpiration by remaining trees or  
169 understory vegetation, leading to declines in water yield. Moreover, these responses are also  
170 affected by land cover types (e.g., young versus old trees, different tree species, etc.), which is  
171 not currently well documented (Perry and Jones 2017; Morillas et al. 2017).

### 172 2.3 Review of modeling approaches

173 Many models, ranging from empirical and lumped to physically-based and fully-distributed,  
174 have been used to study hydrologic responses to disturbances. Goeking and Tarboton (2020)  
175 argue that only physically-based and fully-distributed models can capture how disturbances alter  
176 water yield because they represent fine-scale spatial heterogeneity and physical process that vary  
177 over space and time. Despite their advantages, many process-based models, such as the coupled  
178 CLM-ParFlow model (Mikkelsen et al. 2013; Penn et al. 2016), the Distributed Hydrology Soil  
179 Vegetation Model (Livneh et al. 2015; Sun et al. 2018), and the Variable Infiltration Capacity  
180 Model (Bennett et al. 2018) also have some limitations. For example, 1) they may assume  
181 constant LAI after disturbances and static vegetation growth (e.g., VIC and DHSVM), 2) they  
182 may not include lateral flow to redistribute soil moisture (VIC), and 3) in some cases, the  
183 approach to represent the effects of beetle outbreaks may be too simplified (e.g., changing only  
184 LAI and conductance without considering two-way beetle-vegetation interactions in post-

185 disturbance biogeochemical and water cycling e.g., as in CLM-ParFlow). Thus, improving  
186 current fully distributed process-based models to capture the coupled dynamics between  
187 hydrology and vegetation at multiple scales is a critical step for projecting how beetle outbreaks  
188 will affect water yield in semiarid systems (Goeking and Tarboton 2020). Here we use RHESys  
189 – Beetle model, which captures these processes.

### 190 **3 Model, data, and simulation experiment design**

#### 191 3.1 Study area

192 Our study focused on the Trail Creek watershed, which is located in Blaine County between the  
193 Sawtooth National Forest and the Salmon-Challis National Forest (43.44N, 114.19W; Fig. 2). It  
194 is a 167-km<sup>2</sup> sub-catchment in the south part of Big Wood River basin and is within the  
195 wildland-urban interface where residents are vulnerable to the flood and debris flows caused by  
196 forest disturbances (Skinner 2013). Trail Creek has frequently experienced beetle outbreaks,  
197 notably in 2004 and 2009, when beetles killed 7 and 19 km<sup>2</sup> of trees, respectively (Berner et al.  
198 2017).

199 Trail Creek has cold, wet winters and warm, dry summers; mean annual precipitation is  
200 approximately 978 mm, 60% of which falls as snow (Frenzel 1989). The soil is mostly  
201 permeable coarse alluvium (Smith 1960). Elevations range from 1760 to 3478 m. Along this  
202 elevation gradient, there are also strong vegetation and aridity gradients (Fig. 3). The northern  
203 (higher elevation) portion of the basin is mesic and covered principally by evergreen forest,  
204 containing Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta* var. *latifolia*),  
205 subalpine fir (*Abies lasiocarpa*), and mixed shrub and herbaceous vegetation. The southern  
206 (lower elevation) portion is xeric and covered by shrubs, grasses, and mixed herbaceous species,  
207 including sagebrush, riparian species, and grasslands (Buhidar 2002).

208 In total, Trail creek contains 72 sub-basins and two of them (e.g., Fig. 3, sub-basin 412 and  
209 416) are urban areas. When we classified this basin into different zones according to an aridity  
210 index, i.e., the ratio of 38-year average annual potential evapotranspiration (PET) to precipitation  
211 (P) (Section 3.4), two distinct hydrologic-vegetation cover types emerged: the northern and high  
212 elevation area is balanced (i.e., PET/P between 0.8 and 2) and evergreen tree coverage is more  
213 than 50%; the southern part is water-limited (i.e., PET/P > 2) and evergreen tree coverage is less  
214 than 30% (Figs. 2 and 3).

## 215 3.2 Model descriptions

### 216 3.2.1 Ecohydrologic model

217 The Regional Hydro-ecologic Simulation System (RHESys; Tague and Band 2004) is a  
218 mechanistic model designed to simulate the effects of climate and land use change on ecosystem  
219 carbon and nitrogen cycling and hydrology. RHESys fully couples hydrological processes  
220 (including streamflow, lateral flow, ET, and soil moisture, etc.), plant growth and vegetation  
221 dynamics (including photosynthesis, maintenance respiration, and mortality, etc.), and soil  
222 biogeochemical cycling (including soil organic matter decomposition, mineralization,  
223 nitrification, denitrification, and leaching, etc.). It has been widely tested and applied in several  
224 mountainous watersheds in western North America, including many in the Pacific and Inland  
225 Northwest (e.g., Tague and Band 2004; Garcia and Tague 2015; Hanan et al. 2017; 2018; 2021;  
226 Lin et al. 2019; Son and Tague 2019).

227 RHESys represents a watershed using a hierarchical set of spatial units, including patches,  
228 zones, sub-basins, and the full basin, to simulate various hydrologic and biogeochemical  
229 processes occurring at these scales (Tague and Band 2004). The patch is the finest spatial scale at  
230 which vertical soil moisture and soil biogeochemistry are simulated. In every patch, there are

231 multiple canopy strata layers to simulate the biogeochemical processes related to plant growth  
232 and nutrient uptake. Meteorological forcing inputs (e.g., temperature, precipitation, humidity,  
233 wind speed, and solar radiation) are handled at the zone level, and spatially interpolated and  
234 downscaled for each patch based on elevation, slope, and aspect. Sub-basins are closed drainage  
235 areas entering both sides of a single stream reach (the water budget is closed in sub-basins). The  
236 largest spatial unit is the basin, which aggregates the streamflow from sub-basins (Tague and  
237 Band 2004; Hanan et al. 2018). In RHESSys, streamflow is the sum of overland flow and  
238 baseflow, and we consider streamflow as the *water yield* of each sub-basin.

239 RHESSys models vertical and lateral hydrologic fluxes, including canopy interception,  
240 plant transpiration, canopy evaporation/sublimation, snow accumulation, snowmelt and  
241 sublimation, soil evaporation, soil infiltration, and subsurface drainage. Canopy interception is  
242 based on the water-holding capacity of vegetation, which is also a function of plant area index  
243 (PAI). Both the canopy evaporation and transpiration are modeled using the standard Penman-  
244 Monteith equation (Monteith 1965). Snow accumulation is calculated from incoming  
245 precipitation and is assumed to fall evenly across each zone. Snowmelt is based on a quasi-  
246 energy budget approach accounting for radiation input, sensible and latent heat fluxes, and  
247 advection. Soil evaporation is constrained by both energy and atmospheric drivers, as well as a  
248 maximum exfiltration rate, which is controlled by soil moisture (Tague and Band 2004). Vertical  
249 drainage and lateral flow are a function of topography and soil hydraulic conductivity, which  
250 decays exponentially with depth (Tague and Band 2004; Hanan et al. 2018). Supplementary  
251 material section S1 contains a more detailed synopsis of the soil hydrologic model.

252 Vegetation carbon and nitrogen dynamics are calculated separately for each canopy layer  
253 within each patch, while soil and litter carbon and nitrogen cycling are simulated at the patch

254 level. Photosynthesis is calculated based on the Farquhar model, which considers the limitations  
255 of nitrogen, light, stomatal conductance (influenced by soil water availability), vapor pressure  
256 deficit, atmospheric CO<sub>2</sub> concentration, radiation, and air temperature (Farquhar and von  
257 Caemmerer 1982; Tague and Band 2004). Maintenance respiration is based on Ryan (1991),  
258 which computes respiration as a function of nitrogen concentration and air temperature. Growth  
259 respiration is calculated as a fixed ratio of new carbon allocation for each vegetation component  
260 (Ryan 1991; Tague and Band 2004). Net photosynthesis is allocated to leaves, stems, and roots at  
261 daily steps based on the Dickinson partitioning method, which varies with each plant  
262 development stage (Dickinson et al. 1998). LAI is estimated from leaf carbon and specific leaf  
263 area for each vegetation type. The soil and litter carbon and nitrogen cycling (heterotrophic  
264 respiration, mineralization, nitrification, and denitrification, etc.) are modified from the  
265 BIOME\_BGC and CENTURY-NGAS models (White and Running 1994; Parton et al. 1996;  
266 Tague and Band 2004). A detailed description of RHESSys model algorithms can be found in  
267 Tague and Band (2004).

### 268 3.2.2 Beetle effects model

269 Edburg et al. (2012) designed and developed a model of MPB effects on carbon and nitrogen  
270 dynamics for integration with the Community Land Model Version 4 (CLM4) (Lawrence et al.  
271 2011, Fig. 4). Here we integrated this beetle effects model into RHESSys (Fig. 4). Beetles attack  
272 trees mainly during late summer, and needles will turn from green to red at the beginning of the  
273 following summer. We simplify this process with prescribed tree mortality on September 1 to  
274 represent beetle outbreak for a given year. The advantage of this integration is that RHESSys  
275 accounts for the lateral connectivity in water and nitrogen fluxes among patches which is not  
276 represented in CLM4 (Fan et al. 2019). Our approach differs from other hydrological models of

277 beetle effects (e.g., VIC, CLM-ParFlow, and DHSVM) because it includes dynamic changes in  
278 plant carbon and nitrogen cycling caused by beetle attack, plant recovery, and their effects on  
279 hydrological responses. Previous studies of hydrologic effects of beetle outbreaks have mainly  
280 focused on consequences of changes in LAI and stomatal resistance during each phase of  
281 mortality but have missed feedbacks between carbon and nitrogen dynamics, vegetation  
282 recovery, and hydrology (Mikkelsen et al. 2013; Livneh et al. 2015; Penn et al. 2016; Sun et al.  
283 2018; Bennett et al. 2018).

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

297 In the integrated model, the reduction of leaf carbon and nitrogen after beetle outbreak can  
298 directly decrease LAI and canopy height, which consequently affects energy (i.e., longwave  
299 radiation and the interception of shortwave radiation) and hydrologic (i.e., transpiration and

300 canopy interception) fluxes. The model calculates two types of LAI: *Live LAI* (i.e., only live leaf  
301 is included), and *Total LAI* (i.e., both live and dead leaves are included). Plant transpiration is a  
302 function of *Live LAI*, while other canopy properties, including interception and canopy  
303 evaporation, is a function of *Total LAI*. The calculation of canopy height includes living stems  
304 and the snag pool.

### 305 3.3 Input data

306 We used the US Geologic Survey (USGS) National Elevation Dataset (NED) at 10 m resolution  
307 to calculate the topographic properties of Trail Creek, including elevation, slope, aspect, basin  
308 boundaries, sub-basins, and patches. Using NED, we delineated 16705 100-m resolution patches  
309 within 72 sub-basins. We used the National Land Cover Database (NLCD) to identify five  
310 vegetation and land cover types, i.e., evergreen, grass/herbaceous, shrub, deciduous, and urban  
311 (Homer et al. 2015). We determined soil properties for each patch using the POLARIS database  
312 (probabilistic remapping of SSURGO; Chaney et al. 2016). Parameters for soil and vegetation  
313 were based on previous research and literature (White et al. 2000; Law et al. 2003; Ackerly  
314 2004; Berner and Law 2016; Hanan et al. 2016; 2021).

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

321 3.4 Simulation experiments

322 To quantify how water yield responds to beetle-caused mortality, we prescribed a beetle outbreak  
323 in September 1989, where the mortality level (%) was applied to all evergreen patches for each  
324 sub-basin. After beetle outbreak, red needles remained on the trees for one year before they  
325 started to fall (transferred to the litter pool) at an exponential rate with a half-life of two years.  
326 The snag pools remained as standing trees for five years and then began to fall and were added to  
327 the CWD pool which decays at an exponential rate with a half-life of ten years.

328 To address Q1 (i.e., the role of interannual variability), we compared water yield responses  
329 during a dry water year, 1994 (i.e., five years after beetle outbreak with an annual precipitation  
330 of 611 mm), to responses during a wet year, 1995 (i.e., six years after beetle outbreak with an  
331 annual precipitation of 1394 mm). This enabled us to estimate the role of interannual climate  
332 variability in driving changes in water yield following beetle attack. The dry year was selected  
333 from years that had precipitation below the 15<sup>th</sup> percentile of annual precipitation data (1980 to  
334 2018; Searcy 1959; see Fig. S1). During the early period after beetle outbreak (e.g., 1994 and  
335 1995) the forest experienced large changes in vegetation canopy cover, plant transpiration, and  
336 soil moisture. We chose these two successive years because their canopy and vegetation status  
337 were similar in terms of fallen dead foliage and residual vegetation regrowth, which makes this  
338 comparison reasonable. However, it is possible that antecedent climate conditions may affect the  
339 following year's response. For example, soil moisture can be depleted during a drought year,  
340 affecting initial conditions the following year. Moreover, under drought conditions, less reactive  
341 nitrogen is taken up by the plants or leaching is reduced, so more nitrogen will be left for the  
342 following year. Therefore, the difference in water yield responses between 1994 and 1995 might  
343 be affected by not only by climate variations but also initial hydrologic and biogeochemical



344 conditions. To consider the time lag effect (antecedent conditions affecting the current year's  
345 response), we also analyzed other dry and wet years.

346 To address Q2 (i.e., the role of vegetation mortality), we prescribed a range of beetle-  
347 caused mortality levels (i.e., from 10% to 60% by a step of 10% in terms of a reduction in  
348 carbon, uniformly applied to all evergreen patches for each sub-basin) and a control run (no  
349 mortality). This enabled us to quantify how forest water yield responded to the level of  
350 vegetation mortality (for each sub-basin **vegetation mortality** is **evergreen mortality** multiplied  
351 by evergreen coverage of that basin). The differences in water yield between each mortality level  
352 and the control run represent the effects of beetle kill: a positive value means that mortality  
353 increased water yield, and vice versa.

354 We quantified the water budget for each sub-basin to examine which hydrological  
355 processes contribute to the water yield responses: water yield (Q), precipitation (P), canopy  
356 evaporation ( $E_{canopy}$ , canopy evaporation and snow sublimation), transpiration (T), ground  
357 evaporation ( $E_{ground}$ , includes bare soil evaporation, pond evaporation, and litter evaporation),  
358 snow sublimation (Sublim, ground), soil storage change ( $dS_{soil}/dt$ ), litter storage change  
359 ( $dS_{litter}/dt$ ), snowpack storage change ( $dS_{snowpack}/dt$ ) and canopy storage change  
360 ( $dS_{canopy}/dt$ ). We summarized these rate variables at an annual time step.

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

$$363 \quad Q = P - E_{canopy} - E_{ground} - Sublim - T - \frac{d(S_{soil} + S_{litter} + S_{canopy} + S_{snowpack})}{dt} \quad (1)$$

364 **Q:** Water yield (mm/year)

365 **P**: Precipitation (mm/year)  
366 **E<sub>canopy</sub>**: Canopy evaporation (including canopy snow sublimation, mm/year)  
367 **E<sub>ground</sub>**: Ground evaporation includes bare soil evaporation, pond evaporation, and litter  
368 evaporation (mm/year)

369 **T**: Transpiration (mm/year)

370 **Sublim**: Ground snow sublimation (mm/year)

371  $dS_{soil}/dt$ : Change in soil water storage calculated at yearly interval (mm/year)

372  $dS_{litter}/dt$ : Change in litter water storage calculated at yearly interval (mm/year)

373  $dS_{canopy}/dt$ : Change in canopy water storage calculated at yearly interval (mm/year)

374  $dS_{snowpack}/dt$ : change in snowpack water storage calculated at yearly interval (mm/year)

375 Calculating water balance differences between different mortality scenarios and control  
376 scenario results in Eq. (2) (Note that precipitation is a model input and is unaffected by mortality  
377 and so  $\Delta P = 0$ ).

378 
$$\Delta Q = \Delta E_{canopy} + \Delta E_{ground} + \Delta Sublim + \Delta T + \Delta \left( \frac{d(S_{soil} + S_{litter} + S_{canopy} + S_{snowpack})}{dt} \right) \quad (2)$$

379 To address Q3 (i.e., the role of long-term aridity), we calculated a long-term aridity index  
380 (PET/P, Fig. 3) across the basin and analyzed the relationship between long-term aridity index  
381 and hydrologic response. As mentioned earlier, the long-term aridity index is defined as the ratio  
382 of mean annual potential ET (PET) to annual precipitation (P), averaged over 38 years (water  
383 year 1980-2018) of historical meteorological data. Based on the long-term aridity index, we

384 classified our sub-basins into three types (i.e., water-limited, balanced, energy-limited; McVicar  
385 et al. 2012; Table 1).

## 386 **4 Results**

### 387 4.1 Simulated vegetation response to beetle outbreak at basin-scale

#### 388 4.1.1 Vegetation response to beetle outbreaks

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

#### 400 4.1.2 Time series of hydrologic response to beetle outbreak

401 Figure 6 shows the changes in simulated water fluxes and soil moisture over the basin after  
402 beetle outbreak with various evergreen mortality levels. During the first 15 years after beetle  
403 outbreak, scenarios where the evergreen mortality level was larger than zero had higher basin-  
404 scale water yield than the control scenario (where the evergreen mortality level was zero). This  
405 was especially true during wet years; however, there was no significant increase during dry years  
406 (i.e., 1992, 1994, 2001, and 2004; Fig. 6a). The year-to-year soil storage fluxes responded

407 strongly in the first two years after beetle outbreak, then stabilized to the pre-outbreak condition  
408 (Fig. 6b). Note that year-to-year soil storage change is not the same as soil water storage. After  
409 beetle outbreak, the soil held some portion of the water that was not taken up by plants, but this  
410 was constrained by the soil water holding capacity. This phenomenon indicates that the soil has  
411 some resilience to vegetation change.

412 Beetle outbreaks reduced transpiration during wet years but did not have significant effects  
413 in dry years (Fig. 6c). This occurred because transpiration in dry years was water-limited and  
414 was therefore much lower than the potential rate (more water was partitioned to evaporation;  
415 similar to Biederman et al. 2014). Thus, killing more trees had little effect on stand scale  
416 transpiration because remaining trees used any water released by the dead trees in dry years. On  
417 the other hand, plant transpiration in wet years was close to the potential rate; therefore,  
418 decreases in canopy cover reduced transpiration. There was no apparent effect of beetle outbreak  
419 on snowmelt.

420 Snow sublimation played an essential role in driving the evaporation responses we  
421 observed. In the Trail Creek watershed, snow sublimation accounted for around 50% of total  
422 evaporation (not shown in the figure), and around 60% came from the canopy. Canopy  
423 sublimation accounted for an even larger proportion of total sublimation during high snow years  
424 (Fig. S7 d and Fig. S1). These results are similar to other western US forests where 50 to 60% of  
425 total sublimation has been found to come from canopy sublimation, which is more sensitive to  
426 beetle kill than ground snow sublimation (Molotch et al. 2007; Frank et al. 2019). We also found  
427 that during the first three years after beetle outbreak, when dead foliage was still on the canopy,  
428 canopy sublimation increases by approximately 6% due to an increase in *Total LAI* as new  
429 needles grew and dead foliage remained on the canopy. This increased canopy snow interception

430 and subsequent sublimation (Fig. 5). However, when the dead foliage fell to the ground and  
431 snags began to fall, the canopy sublimation decreased by approximately 10% for the most severe  
432 mortality scenario (60% evergreen mortality) compared to the no-outbreak scenario. This  
433 occurred because canopy *Total LAI* decreased and there was less canopy interception (Fig. 5).  
434 Ground snow sublimation was less sensitive to beetle-kill (Fig. S7b). In the first three years after  
435 beetle-kill (at 60% mortality), ground snow sublimation increased by approximately 7.5% due to  
436 an increase of aerodynamic conductance caused by higher understory canopy height. However,  
437 from 1993 to 2002, there was no obvious changes in ground snow sublimation after beetle  
438 outbreak. When all dead foliage and more than 50% of snags fell to the ground, ground snow  
439 sublimation decreased because snowmelt increased as the canopy opened (Fig. 5 and Fig. S7b).  
440 In general, for the 60% mortality scenario, the ground snow sublimation first increased by  
441 approximately 5% when dead foliage is still on the trees, then decreased by approximately 6%  
442 when the canopy is open.

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

## 446 4.2 The role of spatial heterogeneity in water yield response

### 447 4.2.1 Spatial patterns of hydrologic response along long-term aridity gradient

#### 448 4.2.1.1 Evaporation

449 Beetle outbreak had opposite effects on evaporation between a dry year and a wet year  
450 (Fig. 7). In the dry year, most sub-basins experienced higher evaporation for beetle outbreak  
451 scenarios than in the control scenario (Fig. 7a). This was the cumulative consequence of

452 decreased canopy evaporation and increased ground (soil, litter, pond) evaporation due to  
453 decreases in LAI (caused by mortality). In the dry year, the latter effect (i.e., increased ground  
454 evaporation) dominated over the former, leading to an overall increase in evaporation. When the  
455 vegetation mortality level (calculated as *the percentage of evergreen patches in a sub-basin*  
456 *multiplied by the mortality level of evergreen caused by beetles*) was higher than 20%, a few sub-  
457 basins in the balanced (more mesic) area experienced a decrease in evaporation, indicating that  
458 the effects of decreasing canopy evaporation outstripped the effects of increasing ground  
459 evaporation. In the wet year, most of the sub-basins located in the balanced area (where canopy  
460 evaporation decreases dominated) experienced decreases in evaporation. This decrease  
461 responded linearly to the level of vegetation mortality (Fig. 7b). However, sub-basins located in  
462 much drier regions (aridity >3.5) had relatively minimal responses to the level of vegetation  
463 mortality levels and some of them even had slight increases in evaporation (where ground  
464 evaporation increases are dominant due to drier long-term climate and lower canopy mortality  
465 resulted from less evergreen coverage).

#### 466 4.2.1.2 Transpiration

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

#### 475 4.2.1.3 Total ET

476 In a dry year, the balanced and water-limited areas had opposite responses to mortality: the  
477 balanced area experienced a decrease in ET and the water-limited area experienced a slight  
478 increase (Fig. 9). In the balanced area, larger ET decreases occurred with higher mortality levels.  
479 However, increases in ET in water-limited regions were less sensitive to vegetation mortality  
480 level, even when mortality was high (>40%), ET still increased (Fig. 9a). During the wet year,  
481 most sub-basins experienced decreasing ET after beetle outbreak and the magnitude was larger  
482 with higher vegetation mortality. The different responses of ET were driven by different  
483 hydrologic responses (transpiration, ground evaporation, and canopy evaporation) competing  
484 with each other; this competition was influenced by climate conditions, mortality level, and  
485 spatial heterogeneity in long-term aridity.

#### 486 4.2.1.4 Water yield

487 In the dry year (1994), beetle-caused vegetation mortality affected water yield (Fig. 10), but the  
488 responses differed between the balanced and water-limited areas. For the **balanced area**, most  
489 sub-basins showed slight decreases in water yield after beetle outbreak and no significant  
490 differences among low vegetation mortality level ( $\leq 40\%$ , Fig. 10a). However, with increased  
491 mortality, more sub-basins showed increases in water yield, particularly with vegetation  
492 mortality higher than 40% (Fig. 10a). Moreover, the vegetation mortality threshold that changed  
493 the direction of water yield response was altered by long-term aridity, e.g., it was 40% for aridity  
494 2.0 but 20% for aridity 1.0. For **the water-limited area**, water yield decreased and was  
495 independent from mortality level (Fig. 10a). In the wet year (1995), the water yield in most sub-  
496 basins increased after beetle outbreak, and the balanced area increased more significantly than  
497 the water-limited area. Furthermore, in the balanced area, higher mortality levels caused larger

498 increases in water yield which responded more linearly (Fig. 10b). In summary, for a wet year,  
499 increases in water yield occurred for most sub-basins, driven by a decrease in ET. However,  
500 during dry years, the water yield and ET responses were spatially heterogeneous, and the  
501 competing changes in evaporation and transpiration changed the direction and magnitude of ET  
502 and thus water yield response. The competing effect among different hydrologic fluxes for a dry  
503 year is explored in more detail in the next section.

#### 504 4.2.2 Water budgets to understand decreasing water yield in the dry year

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

516 Water yield responses caused by the competition of different hydrologic fluxes showed  
517 different patterns across the aridity gradient (Figs. 3&10). For the balanced area (upper part of  
518 the basin), with low evergreen mortality ( $\leq 30\%$ ), the major response types were D1 and D2, in  
519 which the increase in ground evaporation dominated over the decrease in transpiration and  
520 canopy evaporation (Fig. 11a, b, and c). However, with higher evergreen mortality ( $>30\%$ ), the



521 major response type became W2, where the increase in ground evaporation did not exceed the  
522 decrease in canopy evaporation and transpiration (Fig. 11e, f, and g). This indicates that, in a dry  
523 year, when more evergreen stands are killed, the increase in ground evaporation reaches a limit  
524 while transpiration and canopy evaporation continue to decrease with decreasing LAI. The  
525 increase in ground evaporation was triggered either by decreased *Total LAI* and open canopy,  
526 which allowed more solar radiation penetration to the ground for evaporation (Fig. S5c), or less  
527 transpiration from plants, which left more water available to evaporate (Fig. 8a). The decrease in  
528 plant transpiration and canopy evaporation was driven by a lower *Live LAI* and a lower *Total*  
529 *LAI*, respectively (Fig. S5 a&c and Fig. 8a).

530 The decrease in water yield in the water-limited area (i.e., the lower part of the basin) was  
531 driven by differences in how competing hydrologic responses interacted under different levels of  
532 mortality levels. When evergreen stand mortality level was low ( $\leq 30\%$ ), the response types  
533 were D5 and D7, in which the increase in ground and canopy evaporation dominated over the  
534 decrease of transpiration (Fig. 11a, b, and c). However, with high evergreen stand mortality  
535 ( $>30\%$ ), the response types became D1 and D2 (Fig. 11e, f, and g), in which the canopy  
536 evaporation changed from an increase to a decrease that was driven by a decrease in *Total LAI*  
537 (Fig. S5c). When mortality was low, the increases in growth from residual plants and understory  
538 outstripped the litter fall of dead foliage; thus, *Total LAI* increased, and vice versa when  
539 mortality was high.

## 540 **5 Discussion**

### 541 5.1 Role of interannual climate variability

542 During the first 15 years after beetle attack, various hydrologic processes opposed and/or  
543 reinforced one another to either increase or decrease water yield: a decrease in *Live LAI* can

544 reduce transpiration, while a decrease in *Total LAI* can enhance ground evaporation but diminish  
545 canopy evaporation (Montesi et al. 2004; Tsamir et al. 2019). Interannual climate variability  
546 plays an important role in determining which of these competing effects dominate and, therefore,  
547 drove the direction of water yield response to beetle outbreak (Winkler et al. 2014; Goeking and  
548 Tarboton 2020). Our results show that mainly decreases in water yield occurred in dry years,  
549 while in wet years water yield increases. During a wet year, we found that plant ET reached its  
550 potential so that reductions in actual plant ET dominated over increases in ground evaporation,  
551 resulting in a net increase in water yield. During a dry year, the relative dominance of these  
552 competing effects had greater spatial heterogeneity because the water stress status of the plants  
553 varied across the basin (as explained in Sect 4.2.2; Fig. 11).

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

563       Adams et al. (2012) provide a threshold of precipitation under which water yield increases  
564 after disturbances: at least 500 mm/year. The average annual precipitation over this study basin  
565 was 600-900 mm in dry years, and higher than 900 mm in wet years. Recent field observations  
566 also suggest that annual climate variability can affect the magnitude of evapotranspiration fluxes

567 that have potential to change the water yield direction (Biederman et al. 2014). Our results  
568 corroborate these earlier studies by revealing that there are precipitation thresholds above which  
569 tree removal increases water yield (Figs. 10, S1 and S2).

## 570 5.2 Role of vegetation mortality

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

585 Besides the precipitation threshold of at least 500 mm/year, Adams et al. (2012) also  
586 estimate that when at least 20% of vegetation cover is removed, water yield can increase.  
587 According to previous analysis (Sect 4.1), for a dry year, water yield increases when more than  
588 40% of vegetation is removed (Fig. 10a). Our model simulations indicate similar mortality  
589 thresholds exist for driving water yield increases during the dry year, however, we did not find

590 evidence that such a threshold exists during wet years. These differences between dry and wet  
591 years suggest that the effects of mortality on water yield depend on climate variability. Similarly,  
592 other studies demonstrate that the relationship between mortality level and water yield response  
593 is complicated and nonlinear (Moore and Wondzell 2005).

### 594 5.3 Role of long-term aridity index (PET/P)

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

604 The decrease in water yield for water-limited area can be driven by increases in canopy  
605 evaporation or transpiration, which were different in the hydrologically-balanced area (driven by  
606 increase of ground evaporation). There, the increase in canopy evaporation was due to an  
607 increase in *Total LAI* which is a combined effect of delayed decay of dead foliage and fast  
608 growth of residual and understory plants (Fig. 11d type D5, D7, D8 & D9; Fig. S5). The  
609 surviving and understory plants in the water-limited also had higher transpiration rates after  
610 mortality (Fig. 11d type D6 and Fig. 8). Similarly, in field studies, Tsamir et al. (2019) found an  
611 increase in photosynthesis and transpiration after thinning in a semi-arid forest. These findings  
612 illustrate that in addition to top-down climate variability, the long-term aridity index (which also

613 varies with bottom-up drivers such as vegetation and local topography) can be another useful  
614 indicator of how water yield will respond to disturbances.

615 In addition to evaporation and transpiration, snow sublimation can also influence the  
616 direction of hydrologic responses. Similar to other process-based snow models, we found that  
617 once dead foliage fell to the ground, canopy sublimation decreased (e.g., Sexstone et al. 2018;  
618 Koeniger et al. 2008), which in turn increased water yield relative to the period when dead  
619 needles remained on the trees (Fig. 5 and Fig. S7). In water-limited regions, the decrease in  
620 canopy sublimation was much smaller than in the balanced regions because there were smaller  
621 changes in *Total LAI* (Fig. S5 c and d). However, immediately after beetle outbreak (e.g., 1990 –  
622 19992), we found that canopy sublimation increased in both regions due to an increase in *Total*  
623 *LAI* (Fig. S7). This finding is supported by observational studies showing that canopy  
624 sublimation can increase with increasing leaf area (Koeniger et al. 2008).

625 We also found that ground/snowpack sublimation decreased when all dead foliage fell to  
626 the ground because snowmelt increased with the opening of the canopy. However, this finding  
627 differs from other studies that suggest snowpack sublimation can increase with a more open  
628 canopy (Biederman et al. 2014; Harpold et al. 2014). The latter can occur because open canopies  
629 may allow more snow to reach ground, which can increase sublimation. However, in our study,  
630 faster snowmelt appeared to dominate over increases in ground sublimation. These contrasts  
631 between our research and previous studies illustrate a sophisticated balance between canopy-  
632 atmosphere-environmental processes that must be accounted for when studying the sublimation  
633 response to disturbances (Edburg et al. 2012; Frank et al. 2019). Although RHESys is a  
634 powerful tool for representing these complex interactions, some process representations warrant  
635 further analysis. For example, RHESys currently ignores the effects of litter on ground albedo

636 and snowmelt (Lundquist et al. 2013), which could affect Actual ET and PET rates, and therefore  
637 the long-term aridity index.

#### 638 5.4 Uncertainties and recommendations for future research

639 We found the long-term (38-year) aridity index for our study region was a key driver  
640 influencing hydrologic responses to beetle outbreaks. While this trend is likely to continue in the  
641 future as climate change intensifies aridity in the western US (Livneh and Badger 2020), the  
642 classification of water-limited/balanced region based on 38-year aridity index may change. Thus,  
643 projecting how responses will change under future aridity scenarios requires further modeling  
644 research. We used historical 38-years (1980-2018) data to calculate the aridity index (PET/P).  
645 This method can be extended to project future responses to beetle outbreaks by using future  
646 climate data from generalized circulation models (GCMs) to drive the process-based,  
647 ecohydrologic-beetle effects model. Another consideration, however, is that as aridity continues  
648 to increase, vegetation may shift from evergreen to more drought-tolerant shrub or grass species.  
649 This would in turn alter beetle outbreak patterns and the corresponding water yield responses  
650 (Abatzoglou and Kolden 2013; Bart et al. 2016). However, this process is not well understood  
651 and is not currently represented in our modeling framework. A key uncertainty in predicting  
652 future beetle effects is how vegetation will respond to climate change.

653 Another key uncertainty is how beetle attacks will change in the future. We used uniform  
654 mortality levels for all patches across the watershed and focused our analyses on potential beetle  
655 effects. However, in reality beetles usually attack older trees first (Edburg et al. 2011). Thus,  
656 incorporating a more mechanistic understanding of beetle attack patterns with our beetle effects  
657 model could enable us to simulate more realistic outbreak scenarios moving forward. We also  
658 focused on water yield responses during the first 15 years after beetle outbreak in a watershed

659 that contained balanced or water-limited sub-basins. Future research should analyze long-term  
660 effects (e.g., after the ecosystem begins to recover) on forest hydrology and also investigate  
661 wetter, energy-limited regions.

## 662 **6 Conclusion**

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

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

682 factors and capture the fluctuations of competing water fluxes and storage change that control  
683 overall water budget and water yield.

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

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

704



705 **Code and data availability**

706 The coupled RHESSys model code is available online at:

707 <https://github.com/renjianning/RHESSys/releases/tag/7.1.1>

708 The data used in this study are available at:

709 [https://osf.io/tsu9z/?view\\_only=72bfa7b376ad40c59278312f49b03a69](https://osf.io/tsu9z/?view_only=72bfa7b376ad40c59278312f49b03a69)

710 **Author contributions**

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

716 **Competing interests**

717 The authors declare that they have no conflict of interest.

718 **Acknowledgments**

719 This project is supported by National Science Foundation of United States under award numbers  
720 DMS-1520873 and DEB-1916658.

721

- 723 Abatzoglou, John T. 2013. “Development of Gridded Surface Meteorological Data for  
724 Ecological Applications and Modelling.” *International Journal of Climatology* 33 (1):  
725 121–31. <https://doi.org/10.1002/joc.3413>.
- 726 Abatzoglou, John T., and Crystal A. Kolden. 2011. “Climate Change in Western US Deserts:  
727 Potential for Increased Wildfire and Invasive Annual Grasses.” *Rangeland Ecology &  
728 Management* 64 (5): 471–78. <https://doi.org/10.2111/REM-D-09-00151.1>
- 729 Ackerly, David D. 2004. “Adaptation, Niche Conservatism, and Convergence: Comparative  
730 Studies of Leaf Evolution in the California Chaparral.” *The American Naturalist* 163 (5):  
731 654–71. <https://doi.org/10.1086/383062>.
- 732 Adams, Henry D., Charles H. Luce, David D. Breshears, Craig D. Allen, Markus Weiler, V.  
733 Cody Hale, Alistair M. S. Smith, and Travis E. Huxman. 2012. “Ecohydrological  
734 Consequences of Drought- and Infestation- Triggered Tree Die-off: Insights and  
735 Hypotheses.” *Ecohydrology* 5 (2): 145–59. <https://doi.org/10.1002/eco.233>.
- 736 Anderegg, William R. L., Jeffrey M. Kane, and Leander D. L. Anderegg. 2013. “Consequences  
737 of Widespread Tree Mortality Triggered by Drought and Temperature Stress.” *Nature  
738 Climate Change* 3 (1): 30–36. <https://doi.org/10.1038/nclimate1635>.
- 739 Baret, F., A. Olioso, J. L. Luciani, J. F. Hanocq, and J. C. Monterrot. 1989. “Estimation à partir  
740 de mesures de réflectance spectrale du rayonnement photosynthétiquement actif absorbé  
741 par une culture de blé.” *Agronomie* 9 (9): 885–95. <https://doi.org/10.1051/agro:19890906>.
- 742 Bart, Ryan R., Christina L. Tague, and Max A. Moritz. 2016. “Effect of Tree-to-Shrub Type  
743 Conversion in Lower Montane Forests of the Sierra Nevada (USA) on Streamflow.”  
744 Edited by Julia A. Jones. *PLOS ONE* 11 (8): e0161805.  
745 <https://doi.org/10.1371/journal.pone.0161805>.
- 746 Bennett, Katrina E., Theodore J. Bohn, Kurt Solander, Nathan G. McDowell, Chonggang Xu,  
747 Enrique Vivoni, and Richard S. Middleton. 2018. “Climate-Driven Disturbances in the  
748 San Juan River Sub-Basin of the Colorado River.” *Hydrology and Earth System Sciences*  
749 22 (1): 709–25. <https://doi.org/10.5194/hess-22-709-2018>.
- 750 Bentz, Barbara J., Jacques Régnière, Christopher J Fettig, E. Matthew Hansen, Jane L. Hayes,  
751 Jeffrey A. Hicke, Rick G. Kelsey, Jose F. Negrón, and Steven J. Seybold. 2010. “Climate  
752 Change and Bark Beetles of the Western United States and Canada: Direct and Indirect  
753 Effects.” *BioScience* 60 (8): 602–13. <https://doi.org/10.1525/bio.2010.60.8.6>.
- 754 BERNER, L. T., B. E. LAW, A. J. MEDDENS, and J. A. HICKE. 2017. “Tree Mortality from  
755 Fires and Bark Beetles at 1-Km Resolution, Western USA, 2003-2012.” Collection. Tree  
756 Mortality from Fires and Bark Beetles at 1-Km Resolution, Western USA, 2003-2012.  
757 2017. <https://doi.org/10.3334/ornl daac/1512>.
- 758 Berner, Logan T., and Beverly E. Law. 2016. “Plant Traits, Productivity, Biomass and Soil  
759 Properties from Forest Sites in the Pacific Northwest, 1999–2014.” *Scientific Data* 3 (1):  
760 1–14. <https://doi.org/10.1038/sdata.2016.2>.
- 761 Bethlahmy, Nedavia. 1974. “More Streamflow after a Bark Beetle Epidemic.” *Journal of  
762 Hydrology* 23 (3): 185–89. [https://doi.org/10.1016/0022-1694\(74\)90001-8](https://doi.org/10.1016/0022-1694(74)90001-8).
- 763 Biederman, J. A., A. A. Harpold, D. J. Gochis, B. E. Ewers, D. E. Reed, S. A. Papuga, and P. D.  
764 Brooks. 2014. “Increased Evaporation Following Widespread Tree Mortality Limits  
765 Streamflow Response.” *Water Resources Research* 50 (7): 5395–5409.  
766 <https://doi.org/10.1002/2013WR014994>.

767 Biederman, J. A., A. A. Harpold, D. J. Gochis, B. E. Ewers, D. E. Reed, S. A. Papuga, and P. D.  
768 Brooks. 2014. "Increased Evaporation Following Widespread Tree Mortality Limits  
769 Streamflow Response." *Water Resources Research* 50 (7): 5395–5409.  
770 <https://doi.org/10.1002/2013WR014994>.

771 Buhidar, Balthasar. 2002. "The Big Wood River Watershed Management Plan."  
772 [https://www.deq.idaho.gov/media/450316-  
773 \\_water\\_data\\_reports\\_surface\\_water\\_tmdls\\_big\\_wood\\_river\\_big\\_wood\\_entire.pdf](https://www.deq.idaho.gov/media/450316-_water_data_reports_surface_water_tmdls_big_wood_river_big_wood_entire.pdf).

774 Buma, Brian, and Ben Livneh. 2017. "Key Landscape and Biotic Indicators of Watersheds  
775 Sensitivity to Forest Disturbance Identified Using Remote Sensing and Historical  
776 Hydrography Data." *Environmental Research Letters* 12 (7): 074028.  
777 <https://doi.org/10.1088/1748-9326/aa7091>.

778 Chaney, Nathaniel W., Eric F. Wood, Alexander B. McBratney, Jonathan W. Hempel, Travis W.  
779 Nauman, Colby W. Brungard, and Nathan P. Odgers. 2016. "POLARIS: A 30-Meter  
780 Probabilistic Soil Series Map of the Contiguous United States." *Geoderma* 274 (July):  
781 54–67. <https://doi.org/10.1016/j.geoderma.2016.03.025>.

782 Chen, Fei, Guo Zhang, Michael Barlage, Ying Zhang, Jeffrey A. Hicke, Arjan Meddens,  
783 Guangsheng Zhou, William J. Massman, and John Frank. 2014. "An Observational and  
784 Modeling Study of Impacts of Bark Beetle–Caused Tree Mortality on Surface Energy and  
785 Hydrological Cycles." *Journal of Hydrometeorology* 16 (2): 744–61.  
786 <https://doi.org/10.1175/JHM-D-14-0059.1>.

787 Daly, Christopher, Ronald P. Neilson, and Donald L. Phillips. 1994. "A Statistical-Topographic  
788 Model for Mapping Climatological Precipitation over Mountainous Terrain." *Journal of*  
789 *Applied Meteorology* 33 (2): 140–58. [https://doi.org/10.1175/1520-  
790 0450\(1994\)033<0140:ASTMFM>2.0.CO;2](https://doi.org/10.1175/1520-0450(1994)033<0140:ASTMFM>2.0.CO;2).

791 Dickinson, Robert E., Muhammad Shaikh, Ross Bryant, and Lisa Graumlich. 1998. "Interactive  
792 Canopies for a Climate Model." *Journal of Climate* 11 (11): 2823–36.  
793 [https://doi.org/10.1175/1520-0442\(1998\)011<2823:ICFACM>2.0.CO;2](https://doi.org/10.1175/1520-0442(1998)011<2823:ICFACM>2.0.CO;2).

794 Edburg, Steven L., Jeffrey A. Hicke, Paul D. Brooks, Elise G. Pendall, Brent E. Ewers, Urszula  
795 Norton, David Gochis, Ethan D. Gutmann, and Arjan JH Meddens. 2012. "Cascading  
796 Impacts of Bark Beetle-Caused Tree Mortality on Coupled Biogeophysical and  
797 Biogeochemical Processes." *Frontiers in Ecology and the Environment* 10 (8): 416–24.  
798 <https://doi.org/10.1890/110173>.

799 Edburg, Steven L., Jeffrey A. Hicke, David M. Lawrence, and Peter E. Thornton. 2011.  
800 "Simulating Coupled Carbon and Nitrogen Dynamics Following Mountain Pine Beetle  
801 Outbreaks in the Western United States." *Journal of Geophysical Research:*  
802 *Biogeosciences* 116 (G4): G04033. <https://doi.org/10.1029/2011JG001786>.

803 Fan, Y., M. Clark, D. M. Lawrence, S. Swenson, L. E. Band, S. L. Brantley, P. D. Brooks, et al.  
804 2019. "Hillslope Hydrology in Global Change Research and Earth System Modeling."  
805 *Water Resources Research* 0 (0). <https://doi.org/10.1029/2018WR023903>.

806 Farquhar, G. D., and S. von Caemmerer. 1982. "Modelling of Photosynthetic Response to  
807 Environmental Conditions." In *Physiological Plant Ecology II: Water Relations and*  
808 *Carbon Assimilation*, edited by O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler,  
809 549–87. Encyclopedia of Plant Physiology. Berlin, Heidelberg: Springer.  
810 [https://doi.org/10.1007/978-3-642-68150-9\\_17](https://doi.org/10.1007/978-3-642-68150-9_17).

811 Frank, John M., William J. Massman, Brent E. Ewers, and David G. Williams. 2019. “Bayesian  
812 Analyses of 17 Winters of Water Vapor Fluxes Show Bark Beetles Reduce Sublimation.”  
813 *Water Resources Research* 55 (2): 1598–1623. <https://doi.org/10.1029/2018WR023054>.

814 Frenzel, Steven A. 1989. “Water Resources of the Upper Big Wood River Basin, Idaho.” US  
815 GEological Survey. <https://idwr.idaho.gov/files/legal/CMR50/CMR50-1989-Water-Resources-of-the-Upper-Big-Wood-River-Basin-Idaho.pdf>.

817 Fyfe, John C., Chris Derksen, Lawrence Mudryk, Gregory M. Flato, Benjamin D. Santer, Neil C.  
818 Swart, Noah P. Molotch, et al. 2017. “Large Near-Term Projected Snowpack Loss over  
819 the Western United States.” *Nature Communications* 8 (1): 14996.  
820 <https://doi.org/10.1038/ncomms14996>.

821 Garcia, E. S., and C. L. Tague. 2015. “Subsurface Storage Capacity Influences Climate–  
822 Evapotranspiration Interactions in Three Western United States Catchments.” *Hydrology  
823 and Earth System Sciences* 19 (12): 4845–58. <https://doi.org/10.5194/hess-19-4845-2015>.

824 Goeking, Sara A., and David G. Tarboton. 2020. “Forests and Water Yield: A Synthesis of  
825 Disturbance Effects on Streamflow and Snowpack in Western Coniferous Forests.”  
826 *Journal of Forestry* 118 (2): 172–92. <https://doi.org/10.1093/jofore/fvz069>.

827 Guardiola-Claramonte, M., Peter A. Troch, David D. Breshears, Travis E. Huxman, Matthew B.  
828 Switanek, Matej Durcik, and Neil S. Cobb. 2011. “Decreased Streamflow in Semi-Arid  
829 Basins Following Drought-Induced Tree Die-off: A Counter-Intuitive and Indirect  
830 Climate Impact on Hydrology.” *Journal of Hydrology* 406 (3): 225–33.  
831 <https://doi.org/10.1016/j.jhydrol.2011.06.017>.

832 Hanan, Erin J., Carla M. D’Antonio, Dar A. Roberts, and Joshua P. Schimel. 2016. “Factors  
833 Regulating Nitrogen Retention During the Early Stages of Recovery from Fire in Coastal  
834 Chaparral Ecosystems.” *Ecosystems* 19 (5): 910–26. <https://doi.org/10.1007/s10021-016-9975-0>.

836 Hanan, Erin J., Christina Tague, Janet Choate, Mingliang Liu, Crystal Kolden, and Jennifer  
837 Adam. 2018. “Accounting for Disturbance History in Models: Using Remote Sensing to  
838 Constrain Carbon and Nitrogen Pool Spin-Up.” *Ecological Applications: A Publication  
839 of the Ecological Society of America* 28 (5): 1197–1214.  
840 <https://doi.org/10.1002/eap.1718>.

841 Hanan, Erin J., Christina (Naomi) Tague, and Joshua P. Schimel. 2017. “Nitrogen Cycling and  
842 Export in California Chaparral: The Role of Climate in Shaping Ecosystem Responses to  
843 Fire.” *Ecological Monographs* 87 (1): 76–90. <https://doi.org/10.1002/ecm.1234>.

844 Hanan, Erin J., Jianning Ren, Christina L. Tague, Crystal A. Kolden, John T. Abatzoglou, Ryan  
845 R. Bart, Maureen C. Kennedy, Mingliang Liu, and Jennifer C. Adam. 2021. “How  
846 Climate Change and Fire Exclusion Drive Wildfire Regimes at Actionable Scales.”  
847 *Environmental Research Letters* 16 (2): 024051. <https://doi.org/10.1088/1748-9326/abd78e>.

849 Harpold, Adrian A., Joel A. Biederman, Katherine Condon, Manuel Merino, Yoganand  
850 Korgaonkar, Tongchao Nan, Lindsey L. Sloat, Morgan Ross, and Paul D. Brooks. 2014.  
851 “Changes in Snow Accumulation and Ablation Following the Las Conchas Forest Fire,  
852 New Mexico, USA: CHANGES IN SNOW FOLLOWING FIRE.” *Ecohydrology* 7 (2):  
853 440–52. <https://doi.org/10.1002/eco.1363>.

854 Hicke, Jeffrey A., Morris C. Johnson, Jane L. Hayes, and Haiganoush K. Preisler. 2012. “Effects  
855 of Bark Beetle-Caused Tree Mortality on Wildfire.” *Forest Ecology and Management*  
856 271 (May): 81–90. <https://doi.org/10.1016/j.foreco.2012.02.005>.

857 Homer, Collin G., Jon Dewitz, Limin Yang, Suming Jin, Patrick Danielson, George Z. Xian,  
858 John Coulston, Nathaniel Herold, James Wickham, and Kevin Megown. 2015.  
859 “Completion of the 2011 National Land Cover Database for the Conterminous United  
860 States – Representing a Decade of Land Cover Change Information.” *Photogrammetric*  
861 *Engineering and Remote Sensing* 81: 345354.

862 Hubbart, Jason A. 2007. “Timber Harvest Impacts on Water Yield in the Continental/Maritime  
863 Hydroclimatic Region of the United States,” 12.

864 Koeniger, Paul, Jason Hubbart, Timothy Link, and John Marshall. 2008. “Isotopic Variation of  
865 Snowcover and Streamflow in Response to Changes in Canopy Structure in a Snow-  
866 Dominated Mountain Catchment.” *Hydrological Processes* 22 (February): 557–66.

867 Law, B. E., O. J. Sun, J. Campbell, S. Van Tuyl, and P. E. Thornton. 2003. “Changes in Carbon  
868 Storage and Fluxes in a Chronosequence of Ponderosa Pine.” *Global Change Biology* 9  
869 (4): 510–24. <https://doi.org/10.1046/j.1365-2486.2003.00624.x>.

870 Lawrence, David M., Keith W. Oleson, Mark G. Flanner, Peter E. Thornton, Sean C. Swenson,  
871 Peter J. Lawrence, Xubin Zeng, et al. 2011. “Parameterization Improvements and  
872 Functional and Structural Advances in Version 4 of the Community Land Model.”  
873 *Journal of Advances in Modeling Earth Systems* 3 (1).  
874 <https://doi.org/10.1029/2011MS00045>.

875 Lin, Laurence, Lawrence E. Band, James M. Vose, Taehee Hwang, Chelcy Ford Miniati, and  
876 Paul V. Bolstad. 2019. “Ecosystem Processes at the Watershed Scale: Influence of  
877 Flowpath Patterns of Canopy Ecophysiology on Emergent Catchment Water and Carbon  
878 Cycling.” *Ecohydrology* 0 (0): e2093. <https://doi.org/10.1002/eco.2093>.

879 Livneh, Ben, and Andrew M. Badger. 2020. “Drought Less Predictable under Declining Future  
880 Snowpack.” *Nature Climate Change* 10 (5): 452–58. [https://doi.org/10.1038/s41558-020-](https://doi.org/10.1038/s41558-020-0754-8)  
881 [0754-8](https://doi.org/10.1038/s41558-020-0754-8).

882 Livneh, Ben, Jeffrey S. Deems, Brian Buma, Joseph J. Barsugli, Dominik Schneider, Noah P.  
883 Molotch, K. Wolter, and Carol A. Wessman. 2015. “Catchment Response to Bark Beetle  
884 Outbreak and Dust-on-Snow in the Colorado Rocky Mountains.” *Journal of Hydrology*  
885 523 (April): 196–210. <https://doi.org/10.1016/j.jhydrol.2015.01.039>.

886 Lundquist, Jessica D., Susan E. Dickerson-Lange, James A. Lutz, and Nicoleta C. Cristea. 2013.  
887 “Lower Forest Density Enhances Snow Retention in Regions with Warmer Winters: A  
888 Global Framework Developed from Plot-Scale Observations and Modeling.” *Water*  
889 *Resources Research* 49 (10): 6356–70. <https://doi.org/10.1002/wrcr.20504>.

890 Lundquist, Jessica D., Paul J. Neiman, Brooks Martner, Allen B. White, Daniel J. Gottas, and F.  
891 Martin Ralph. 2008. “Rain versus Snow in the Sierra Nevada, California: Comparing  
892 Doppler Profiling Radar and Surface Observations of Melting Level.” *Journal of*  
893 *Hydrometeorology* 9 (2): 194–211. <https://doi.org/10.1175/2007JHM853.1>.

894 McVicar, Tim R., Michael L. Roderick, Randall J. Donohue, Ling Tao Li, Thomas G. Van Niel,  
895 Axel Thomas, Jürgen Grieser, et al. 2012. “Global Review and Synthesis of Trends in  
896 Observed Terrestrial Near-Surface Wind Speeds: Implications for Evaporation.” *Journal*  
897 *of Hydrology* 416–417 (January): 182–205. <https://doi.org/10.1016/j.jhydrol.2011.10.024>.

898 Meddens, Arjan, Jeffrey A. Hicke, and Charles A. Ferguson. 2012. “Spatiotemporal Patterns of  
899 Observed Bark Beetle-Caused Tree Mortality in British Columbia and the Western  
900 United States.” *Ecological Applications: A Publication of the Ecological Society of*  
901 *America* 22 (October): 1876–91. <https://doi.org/10.2307/41723101>.

902 Mikkelsen, K. M., R. M. Maxwell, I. Ferguson, J. D. Stednick, J. E. McCray, and J. O. Sharp.  
903 2013. "Mountain Pine Beetle Infestation Impacts: Modeling Water and Energy Budgets  
904 at the Hill-Slope Scale." *Ecohydrology* 6 (1): 64–72. <https://doi.org/10.1002/eco.278>.

905 Mitchell, Kenneth E., Dag Lohmann, Paul R. Houser, Eric F. Wood, John C. Schaake, Alan  
906 Robock, Brian A. Cosgrove, et al. 2004. "The Multi-Institution North American Land  
907 Data Assimilation System (NLDAS): Utilizing Multiple GCIP Products and Partners in a  
908 Continental Distributed Hydrological Modeling System." In .  
909 <https://doi.org/10.1029/2003JD003823>.

910 Molotch, Noah P., Peter D. Blanken, Mark W. Williams, Andrew A. Turnipseed, Russell K.  
911 Monson, and Steven A. Margulis. 2007. "Estimating Sublimation of Intercepted and Sub-  
912 Canopy Snow Using Eddy Covariance Systems." *Hydrological Processes* 21 (12): 1567–  
913 75. <https://doi.org/10.1002/hyp.6719>.

914 Monteith, J. L. 1965. "Evaporation and Environment." *Symposia of the Society for Experimental*  
915 *Biology* 19: 205–34.

916 Montesi, James, Kelly Elder, R. A. Schmidt, and Robert E. Davis. 2004. "Sublimation of  
917 Intercepted Snow within a Subalpine Forest Canopy at Two Elevations." *Journal of*  
918 *Hydrometeorology* 5 (5): 763–73. [https://doi.org/10.1175/1525-  
919 7541\(2004\)005<0763:SOISWA>2.0.CO;2](https://doi.org/10.1175/1525-7541(2004)005<0763:SOISWA>2.0.CO;2).

920 Moore, R Dan, and S M Wondzell. 2005. "PHYSICAL HYDROLOGY AND THE EFFECTS  
921 OF FOREST HARVESTING IN THE PACIFIC NORTHWEST: A REVIEW," 22.

922 Morillas, L., R. E. Pangle, G. E. Maurer, W. T. Pockman, N. McDowell, C.-W. Huang, D. J.  
923 Krofcheck, et al. 2017. "Tree Mortality Decreases Water Availability and Ecosystem  
924 Resilience to Drought in Piñon-Juniper Woodlands in the Southwestern U.S." *Journal of*  
925 *Geophysical Research: Biogeosciences* 122 (12): 3343–61.  
926 <https://doi.org/10.1002/2017JG004095>.

927 Mu, Qiaozhen, Faith Ann Heinsch, Maosheng Zhao, and Steven W. Running. 2007.  
928 "Development of a Global Evapotranspiration Algorithm Based on MODIS and Global  
929 Meteorology Data." *Remote Sensing of Environment* 111 (4): 519–36.  
930 <https://doi.org/10.1016/j.rse.2007.04.015>.

931 Mu, Qiaozhen, Maosheng Zhao, and Steven W. Running. 2011. "Improvements to a MODIS  
932 Global Terrestrial Evapotranspiration Algorithm." *Remote Sensing of Environment* 115  
933 (8): 1781–1800. <https://doi.org/10.1016/j.rse.2011.02.019>.

934 Nash, J. E., and J. V. Sutcliffe. 1970. "River Flow Forecasting through Conceptual Models Part I  
935 — A Discussion of Principles." *Journal of Hydrology* 10 (3): 282–90.  
936 [https://doi.org/10.1016/0022-1694\(70\)90255-6](https://doi.org/10.1016/0022-1694(70)90255-6).

937 NRCS. n.d. "SNOTEL." [https://www.wcc.nrcs.usda.gov/about/mon\\_automate.html](https://www.wcc.nrcs.usda.gov/about/mon_automate.html).

938 Nagler, Pamela L., Uyen Nguyen, Heather L. Bateman, Christopher J. Jarchow, Edward P.  
939 Glenn, William J. Waugh, and Charles van Riper. 2018. "Northern Tamarisk Beetle  
940 (*Diorhabda Carinulata*) and Tamarisk (*Tamarix* Spp.) Interactions in the Colorado River  
941 Basin." *Restoration Ecology* 26 (2): 348–59. <https://doi.org/10.1111/rec.12575>.

942 Paine, T. D., K. F. Raffa, and T. C. Harrington. 1997. "Interactions Among Scolytid Bark  
943 Beetles, Their Associated Fungi, and Live Host Conifers." *Annual Review of Entomology*  
944 42 (1): 179–206. <https://doi.org/10.1146/annurev.ento.42.1.179>.

945 Parton, W. J., A. R. Mosier, D. S. Ojima, D. W. Valentine, D. S. Schimel, K. Weier, and A. E.  
946 Kulmala. 1996. "Generalized Model for N<sub>2</sub> and N<sub>2</sub>O Production from Nitrification and

947 Denitrification.” *Global Biogeochemical Cycles* 10 (3): 401–12.  
948 <https://doi.org/10.1029/96GB01455>.

949 Penn, Colin A., Lindsay A. Bearup, Reed M. Maxwell, and David W. Clow. 2016. “Numerical  
950 Experiments to Explain Multiscale Hydrological Responses to Mountain Pine Beetle Tree  
951 Mortality in a Headwater Watershed.” *Water Resources Research* 52 (4): 3143–61.  
952 <https://doi.org/10.1002/2015WR018300>.

953 Perry, Timothy D., and Julia A. Jones. 2017. “Summer Streamflow Deficits from Regenerating  
954 Douglas-Fir Forest in the Pacific Northwest, USA: Summer Streamflow Deficits from  
955 Regenerating Douglas-Fir Forest.” *Ecohydrology* 10 (2): e1790.  
956 <https://doi.org/10.1002/eco.1790>.

957 Pomeroy, John, Xing Fang, and Chad Ellis. 2012. “Sensitivity of Snowmelt Hydrology in  
958 Marmot Creek, Alberta, to Forest Cover Disturbance: SENSITIVITY OF SNOWMELT  
959 HYDROLOGY TO FOREST DISTURBANCE.” *Hydrological Processes* 26 (12): 1891–  
960 1904. <https://doi.org/10.1002/hyp.9248>.

961 Potts, Donald F. 1984. “Hydrologic Impacts of a Large-Scale Mountain Pine Beetle  
962 (*Dendroctonus Ponderosae* Hopkins) Epidemic1.” *JAWRA Journal of the American  
963 Water Resources Association* 20 (3): 373–77. [https://doi.org/10.1111/j.1752-  
964 1688.1984.tb04719.x](https://doi.org/10.1111/j.1752-1688.1984.tb04719.x).

965 Robles, Marcos D., Robert M. Marshall, Frances O’Donnell, Edward B. Smith, Jeanmarie A.  
966 Haney, and David F. Gori. 2014. “Effects of Climate Variability and Accelerated Forest  
967 Thinning on Watershed-Scale Runoff in Southwestern USA Ponderosa Pine Forests.”  
968 *PLOS ONE* 9 (10): e111092. <https://doi.org/10.1371/journal.pone.0111092>.

969 Ryan, Michael G. 1991. “Effects of Climate Change on Plant Respiration.” *Ecological  
970 Applications* 1 (2): 157–67. <https://doi.org/10.2307/1941808>.

971 Searcy, James Kincheon. 1959. “Flow-Duration Curves.” Report 1542A. Water Supply Paper.  
972 USGS Publications Warehouse. <https://doi.org/10.3133/wsp1542A>.

973 Sexstone, Graham A., David W. Clow, Steven R. Fassnacht, Glen E. Liston, Christopher A.  
974 Hiemstra, John F. Knowles, and Colin A. Penn. 2018. “Snow Sublimation in Mountain  
975 Environments and Its Sensitivity to Forest Disturbance and Climate Warming.” *Water  
976 Resources Research* 54 (2): 1191–1211. <https://doi.org/10.1002/2017WR021172>.

977 Skinner, Kenneth D. 2013. “Post-Fire Debris-Flow Hazard Assessment of the Area Burned by  
978 the 2013 Beaver Creek Fire near Hailey, Central Idaho.” USGS Numbered Series 2013–  
979 1273. Open-File Report. Reston, VA: U.S. Geological Survey.  
980 <http://pubs.er.usgs.gov/publication/ofr20131273>.

981 Sliniski, Kimberly M., Terri S. Hogue, Aaron T. Porter, and John E. McCray. 2016. “Recent Bark  
982 Beetle Outbreaks Have Little Impact on Streamflow in the Western United States.”  
983 *Environmental Research Letters* 11 (7): 074010. [https://doi.org/10.1088/1748-  
984 9326/11/7/074010](https://doi.org/10.1088/1748-9326/11/7/074010).

985 Smith, Frederick W., D. Arthur Sampson, and James N. Long. 1991. “Comparison of Leaf Area  
986 Index Estimates from Tree Allometrics and Measured Light Interception.” *Forest Science*  
987 37 (6): 1682–88. <https://doi.org/10.1093/forestscience/37.6.1682>.

988 Smith, Rex Onis. 1960. “Geohydrologic Evaluation of Streamflow Records in the Big Wood  
989 River Basin, Idaho.” USGS Numbered Series 1479. Water Supply Paper. U.S. Govt.  
990 Print. Off., <http://pubs.er.usgs.gov/publication/wsp1479>.

- 991 Son, Kyongho, and Christina Tague. 2019. "Hydrologic Responses to Climate Warming for a  
992 Snow-Dominated Watershed and a Transient Snow Watershed in the California Sierra."  
993 *Ecohydrology* 12 (1): e2053. <https://doi.org/10.1002/eco.2053>.
- 994 Sun, Ning, Mark Wigmosta, Tian Zhou, Jessica Lundquist, Susan Dickerson-Lange, and  
995 Nicoleta Cristea. 2018. "Evaluating the Functionality and Streamflow Impacts of  
996 Explicitly Modelling Forest–Snow Interactions and Canopy Gaps in a Distributed  
997 Hydrologic Model." *Hydrological Processes* 32 (13): 2128–40.  
998 <https://doi.org/10.1002/hyp.13150>.
- 999 Snyder, Keirith A., Russell L. Scott, and Kenneth McGwire. 2012. "Multiple Year Effects of a  
1000 Biological Control Agent (*Diorhabda Carinulata*) on Tamarix (Saltcedar) Ecosystem  
1001 Exchanges of Carbon Dioxide and Water." *Agricultural and Forest Meteorology* 164  
1002 (October): 161–69. <https://doi.org/10.1016/j.agrformet.2012.03.004>.
- 1003 Tague, C. L., and L. E. Band. 2004. "RHESys: Regional Hydro-Ecologic Simulation System—  
1004 An Object-Oriented Approach to Spatially Distributed Modeling of Carbon, Water, and  
1005 Nutrient Cycling." *Earth Interactions* 8 (19): 1–42. [https://doi.org/10.1175/1087-  
1006 3562\(2004\)8<1:RRHSSO>2.0.CO;2](https://doi.org/10.1175/1087-3562(2004)8<1:RRHSSO>2.0.CO;2).
- 1007 Tague, Christina L., Max Moritz, and Erin Hanan. 2019. "The Changing Water Cycle: The Eco-  
1008 Hydrologic Impacts of Forest Density Reduction in Mediterranean (Seasonally Dry)  
1009 Regions." *Wiley Interdisciplinary Reviews: Water* 0 (0): e1350.  
1010 <https://doi.org/10.1002/wat2.1350>.
- 1011 Tsamir, Mor, Sagi Gottlieb, Yakir Preisler, Eyal Rotenberg, Fyodor Tatarinov, Dan Yakir,  
1012 Christina Tague, and Tamir Klein. 2019. "Stand Density Effects on Carbon and Water  
1013 Fluxes in a Semi-Arid Forest, from Leaf to Stand-Scale." *Forest Ecology and  
1014 Management* 453 (December): 117573. <https://doi.org/10.1016/j.foreco.2019.117573>.
- 1015 White, Joseph D., and Steven W. Running. 1994. "Testing Scale Dependent Assumptions in  
1016 Regional Ecosystem Simulations." *Journal of Vegetation Science* 5 (5): 687–702.  
1017 <https://doi.org/10.2307/3235883>.
- 1018 White, Michael A., Peter E. Thornton, Steven W. Running, and Ramakrishna R. Nemani. 2000.  
1019 "Parameterization and Sensitivity Analysis of the BIOME–BGC Terrestrial Ecosystem  
1020 Model: Net Primary Production Controls." *Earth Interactions* 4 (3): 1–85.  
1021 [https://doi.org/10.1175/1087-3562\(2000\)004<0003:PASAOT>2.0.CO;2](https://doi.org/10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2).
- 1022 Wine, Michael L, Daniel Cadol, and Oleg Makhnin. 2018. "In Ecoregions across Western USA  
1023 Streamflow Increases during Post-Wildfire Recovery." *Environmental Research Letters*  
1024 13 (1): 014010. <https://doi.org/10.1088/1748-9326/aa9c5a>.
- 1025 Winkler, Rita, Sarah Boon, Barbara Zimonick, and Dave Spittlehouse. 2014. "Snow  
1026 Accumulation and Ablation Response to Changes in Forest Structure and Snow Surface  
1027 Albedo after Attack by Mountain Pine Beetle." *Hydrological Processes* 28 (2): 197–209.  
1028 <https://doi.org/10.1002/hyp.9574>.
- 1029 Zhang, Ke, John S. Kimball, Qiaozhen Mu, Lucas A. Jones, Scott J. Goetz, and Steven W.  
1030 Running. 2009. "Satellite Based Analysis of Northern ET Trends and Associated  
1031 Changes in the Regional Water Balance from 1983 to 2005." *Journal of Hydrology* 379  
1032 (1): 92–110. <https://doi.org/10.1016/j.jhydrol.2009.09.047>.
- 1033 Zhao, Maosheng, Steven W. Running, and Ramakrishna R. Nemani. 2006. "Sensitivity of  
1034 Moderate Resolution Imaging Spectroradiometer (MODIS) Terrestrial Primary  
1035 Production to the Accuracy of Meteorological Reanalyses." *Journal of Geophysical  
1036 Research: Biogeosciences* 111 (G1). <https://doi.org/10.1029/2004JG000004>.



1037

1038 *Table 1. Classification of aridity index.*

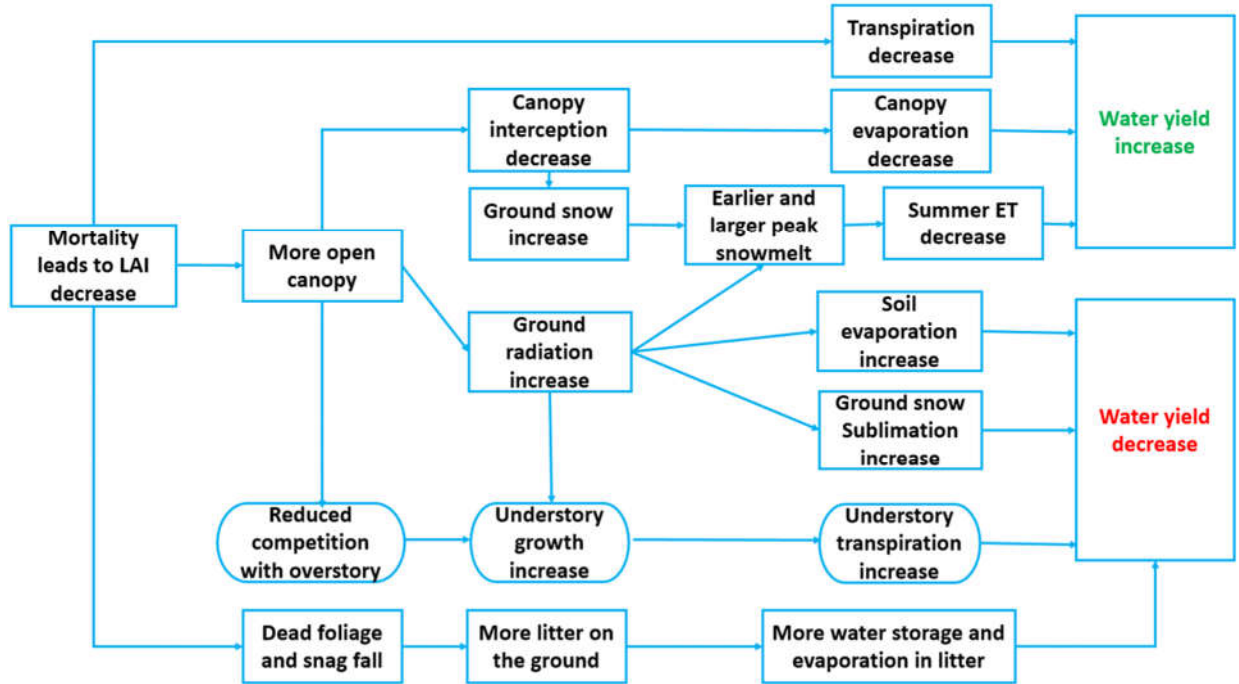
1039

Aridity Index (i.e. PET/P)	Type
> 2	Water - limited
0.8 - 2	Balanced
< 0.8	Energy - limited

1040

1041

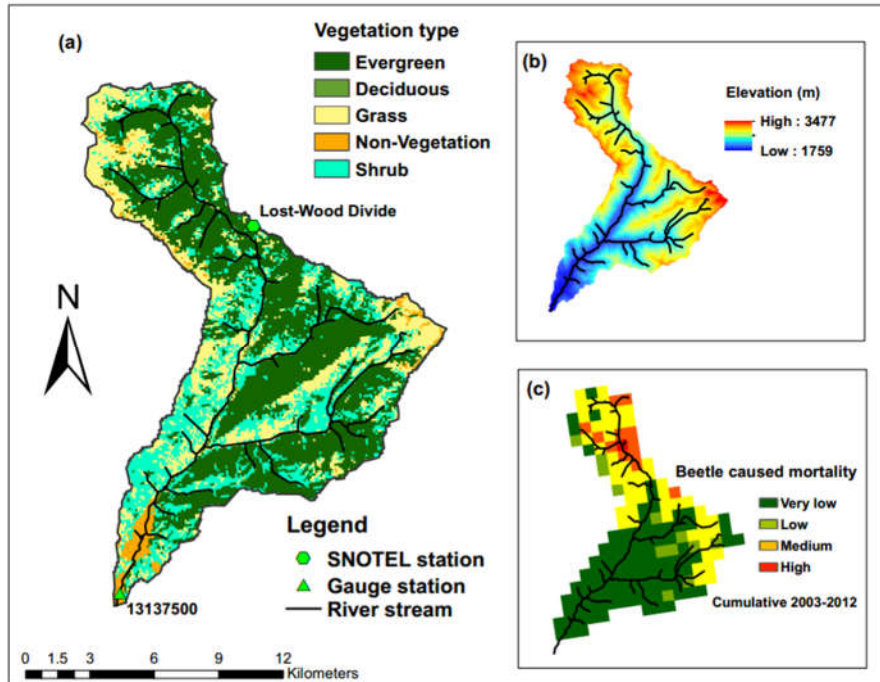
1042



1043

1044 *Figure 1. Mechanism of water yield responses to beetle-caused mortality during the red and*  
 1045 *gray phases (0 – 10 years after beetle outbreak), semicircle boxes represent understory*  
 1046 *responses and square boxes represent overstory responses.*

1047

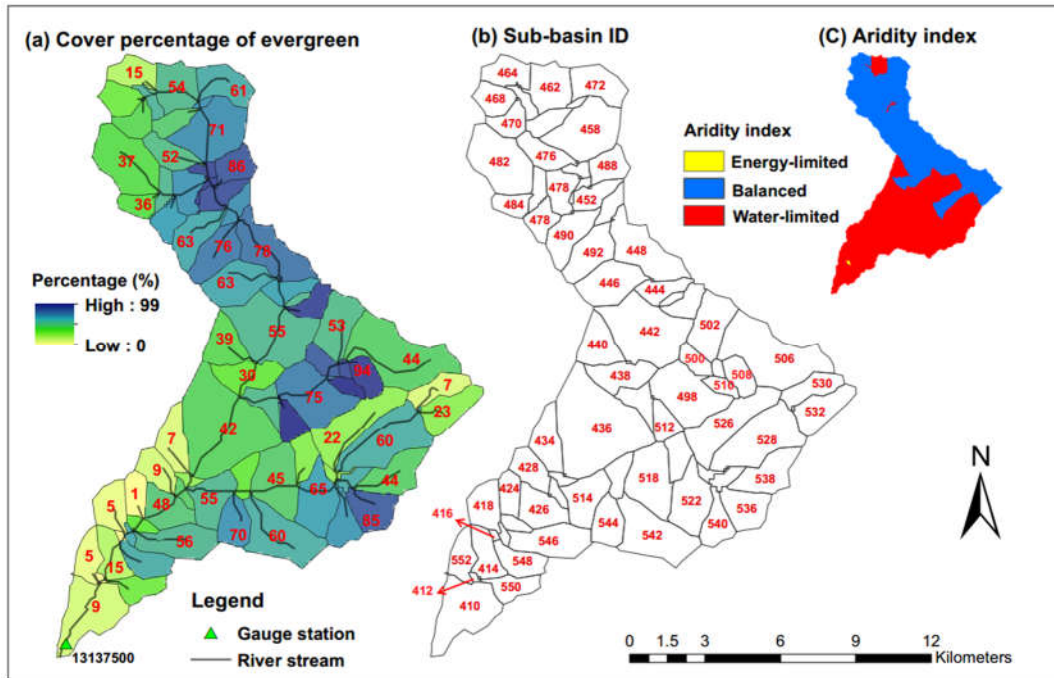


1048

1049 *Figure 2. Land cover, elevation, and tree mortality for Trail Creek. (a) is the land cover map*  
 1050 *with the main vegetation type, (b) is the elevation gradient, and (c) is the severity of beetle*  
 1051 *caused tree mortality (during the period 2003-2012 Meddens et al. (2012)). Note that, for our*  
 1052 *modeling experiments, we prescribe beetle outbreak uniformly across evergreen patches instead*  
 1053 *of using historical beetle outbreak data.*

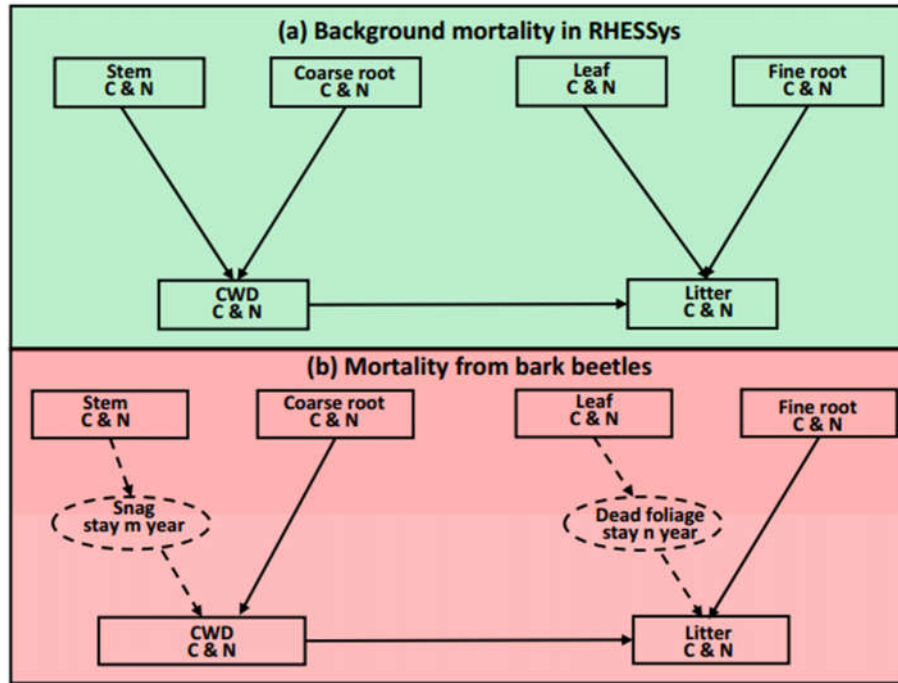
1054

1055



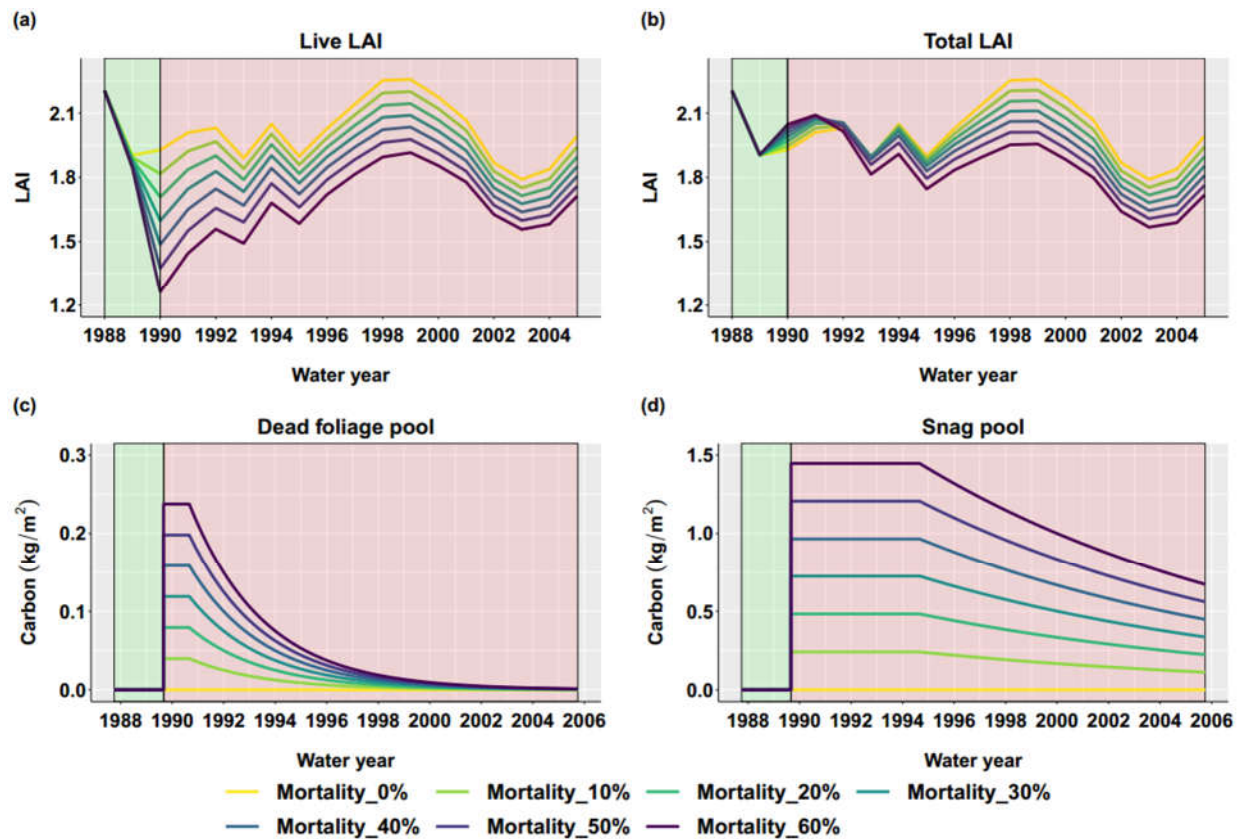
1056

1057 *Figure 3. Trail creek evergreen forest cover percentage for each sub-basin, sub-basin ID, and*  
 1058 *long-term aridity index. Aridity index is defined as annual mean potential evapotranspiration*  
 1059 *(PET) / precipitation (P) from 38 years of data (see Sect 3.4),  $PET/P > 2$  is water-limited,  $PET/P$*   
 1060  *$< 0.8$  is energy-limited,  $PET/P$  between 0.8 and 2 is balanced. Recall that only evergreen forest*  
 1061 *trees are attacked during beetle outbreaks.*  
 1062



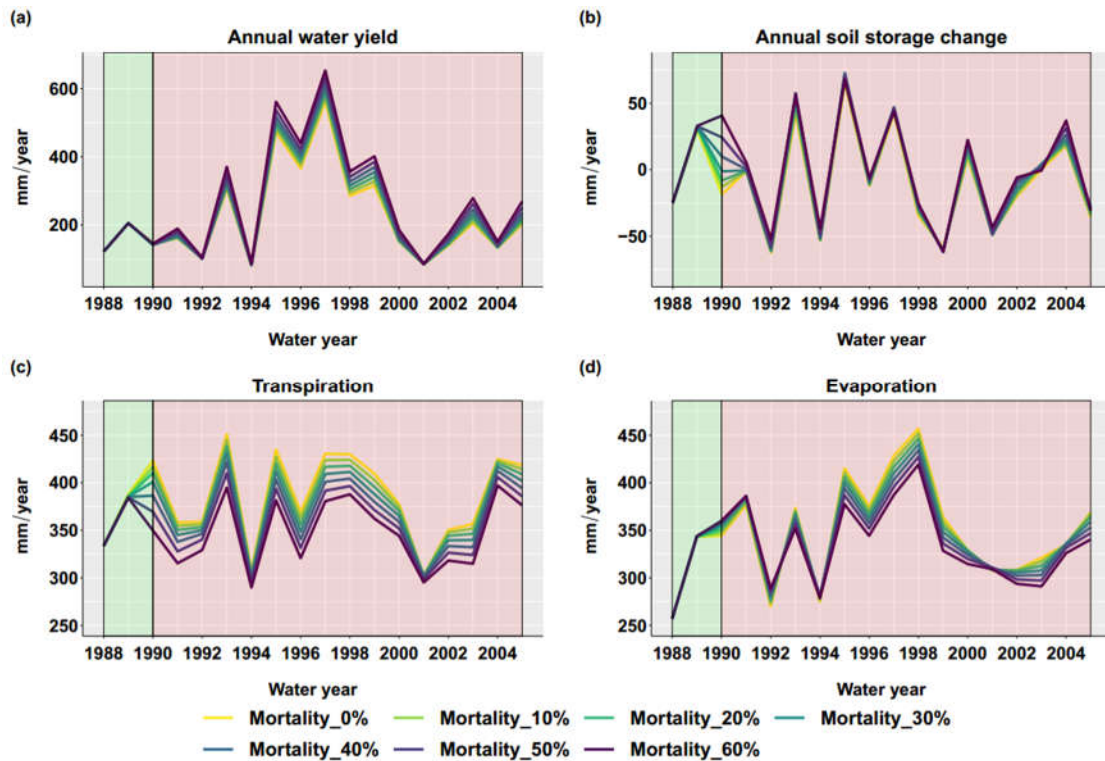
1063

1064 *Figure 4. Conceptual framework of the beetle effect model. (a) Normal background mortality*  
 1065 *routine in RHESSys before beetle outbreak. (b) Mortality from bark beetles. We add snag*  
 1066 *(standing dead trees) and dead foliage (needles still on dead trees) pools, shown in the dashed*  
 1067 *circle. After a beetle outbreak, carbon (C) and Nitrogen (N) move from stems to snag pools*  
 1068 *(black dashed arrow). After staying in the snag pool for m years, C and N move from snag to*  
 1069 *coarse wood debris pools (CWD) with an exponential decay rate to represent the snag fall (gray*  
 1070 *dashed arrow). It is a similar process for leaf C and N, which move from leaf to dead foliage to*  
 1071 *litter pools (black dotted arrow). Furthermore, C and N in the CWD and fine root pools move to*  
 1072 *the litter pool immediately after outbreak (solid black and gray arrows). Figure modified from*  
 1073 *Edburg et al. (2012).*  
 1074



1075

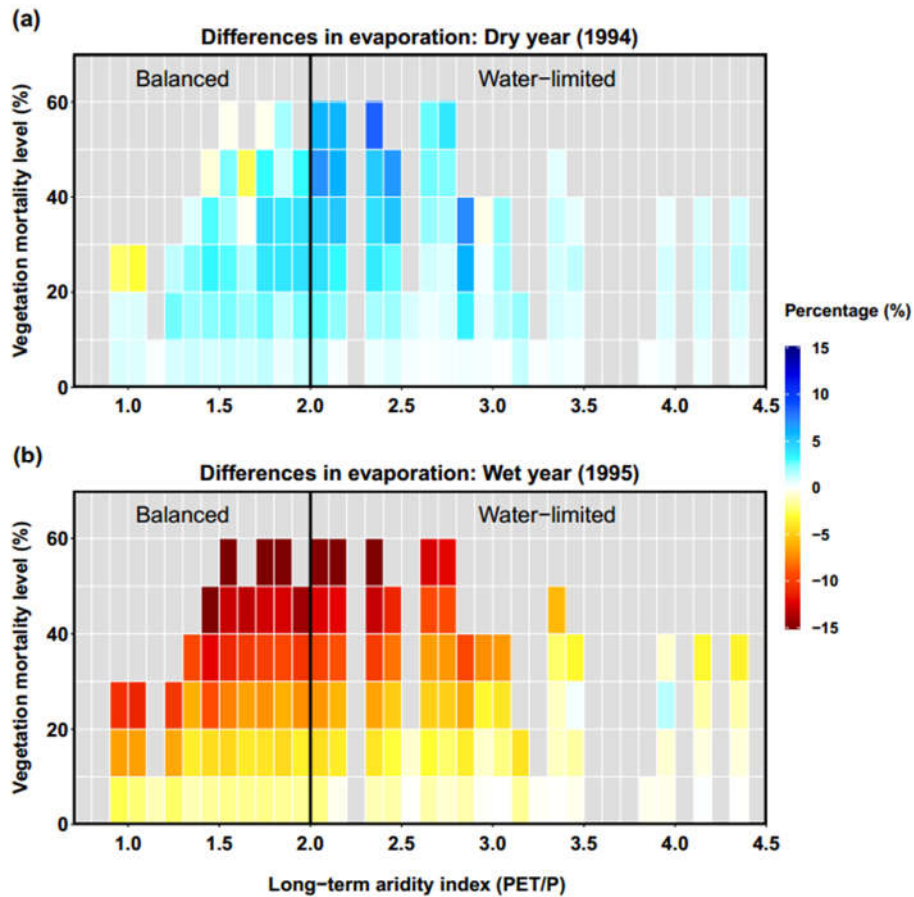
1076 *Figure 5. Basin-scale vegetation responses after beetle outbreak for different evergreen*  
 1077 *mortality level. (a) Annual live leaf area index (Live LAI), (b) Annual Total LAI (LAI calculated*  
 1078 *including dead foliage pool), (c) Daily dead foliage pool, and (d) Daily snag pool after outbreak.*  
 1079 *The green background color is the period before beetle outbreak, and the red background color*  
 1080 *is after the beetle outbreak.*  
 1081



1082

1083 *Figure 6. Basin-scale annual sum of hydrologic fluxes responses after beetle outbreak (1989) for*  
 1084 *different evergreen mortality levels. (a) Annual water yield calculated as annual sum of basin*  
 1085 *streamflow, and (b) annual soil water storage change calculated as water year soil water*  
 1086 *storage at the end of water year minus soil water storage at the beginning of water year. (c)*  
 1087 *Transpiration is the annual sum of transpiration for both overstory and understory. (d)*  
 1088 *Evaporation is calculated as the annual sum of canopy evaporation, ground evaporation, and*  
 1089 *snow sublimation.*  
 1090

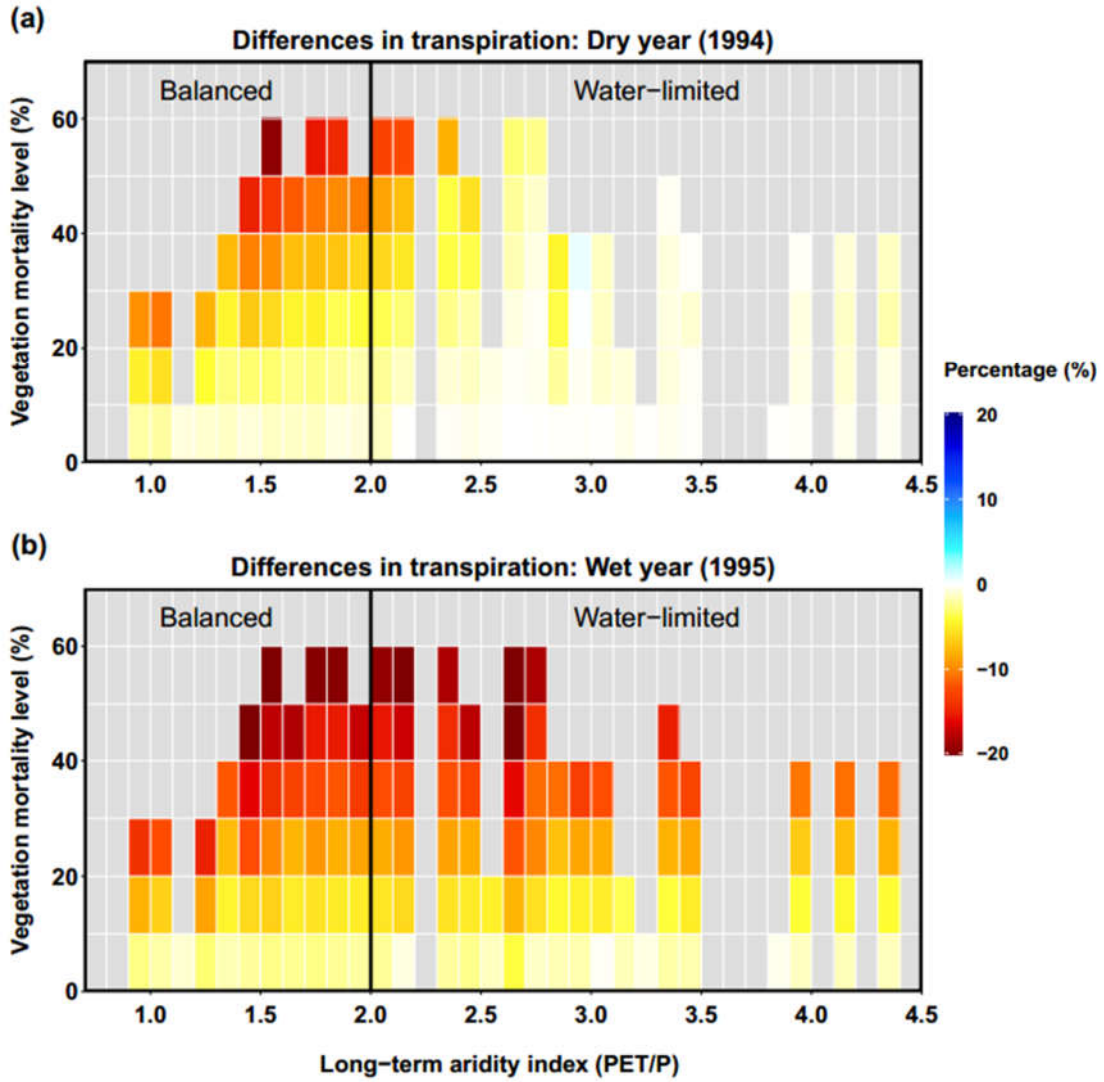




1091

1092 *Figure 7. Relationship among long-term aridity, vegetation mortality level, and differences in*  
 1093 *evaporation for a dry year (1994, a) and wet year (1995, b). Differences are calculated as the*  
 1094 *normalized differences (%) of evaporation between each evergreen mortality scenario and the*  
 1095 *control run for no beetle outbreak. Vegetation mortality for each sub-basin is calculated as the*  
 1096 *percentage of evergreen patches multiplied by the mortality level of evergreen caused by beetles.*  
 1097 *Long-term aridity is defined as temporally averaged (38 years) potential evapotranspiration*  
 1098 *relative to precipitation.*  
 1099

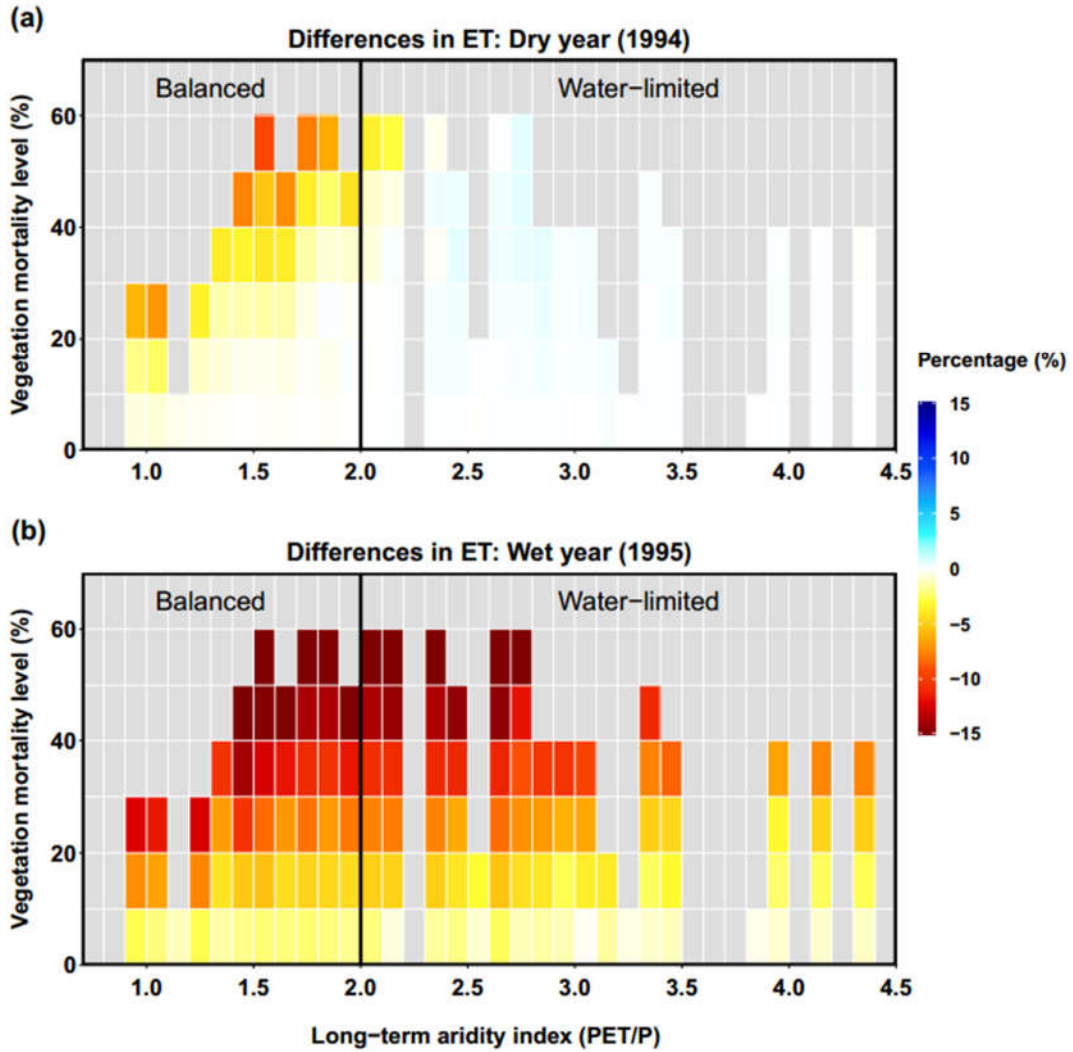




1100

1101 *Figure 8. Relationship among long-term aridity, vegetation mortality, and differences in*  
 1102 *transpiration for a dry year (1994, a) and wet year (1995, b).*

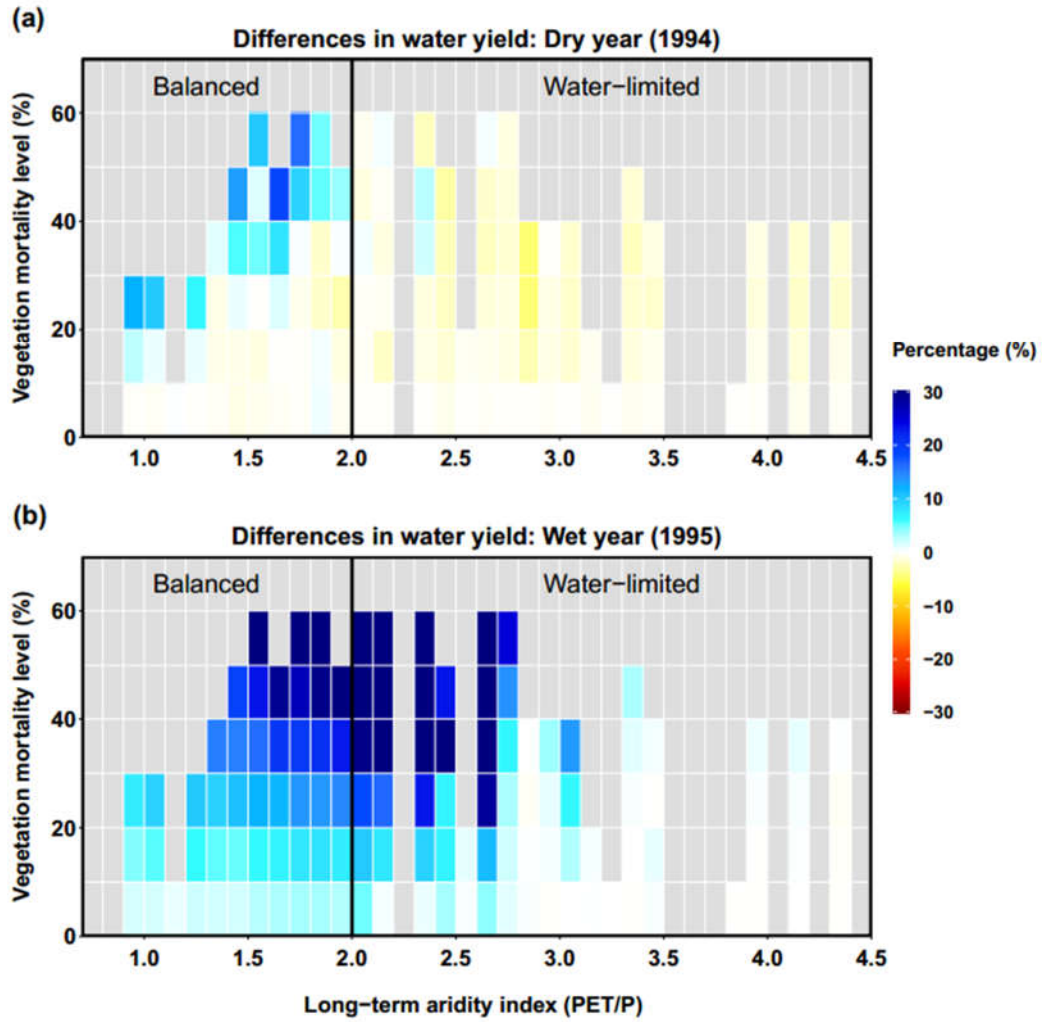
1103



1104

1105 *Figure 9. Relationship among long-term aridity, vegetation mortality level and differences in ET*  
 1106 *for a dry year (1994, a) and a wet year (1995, b).*

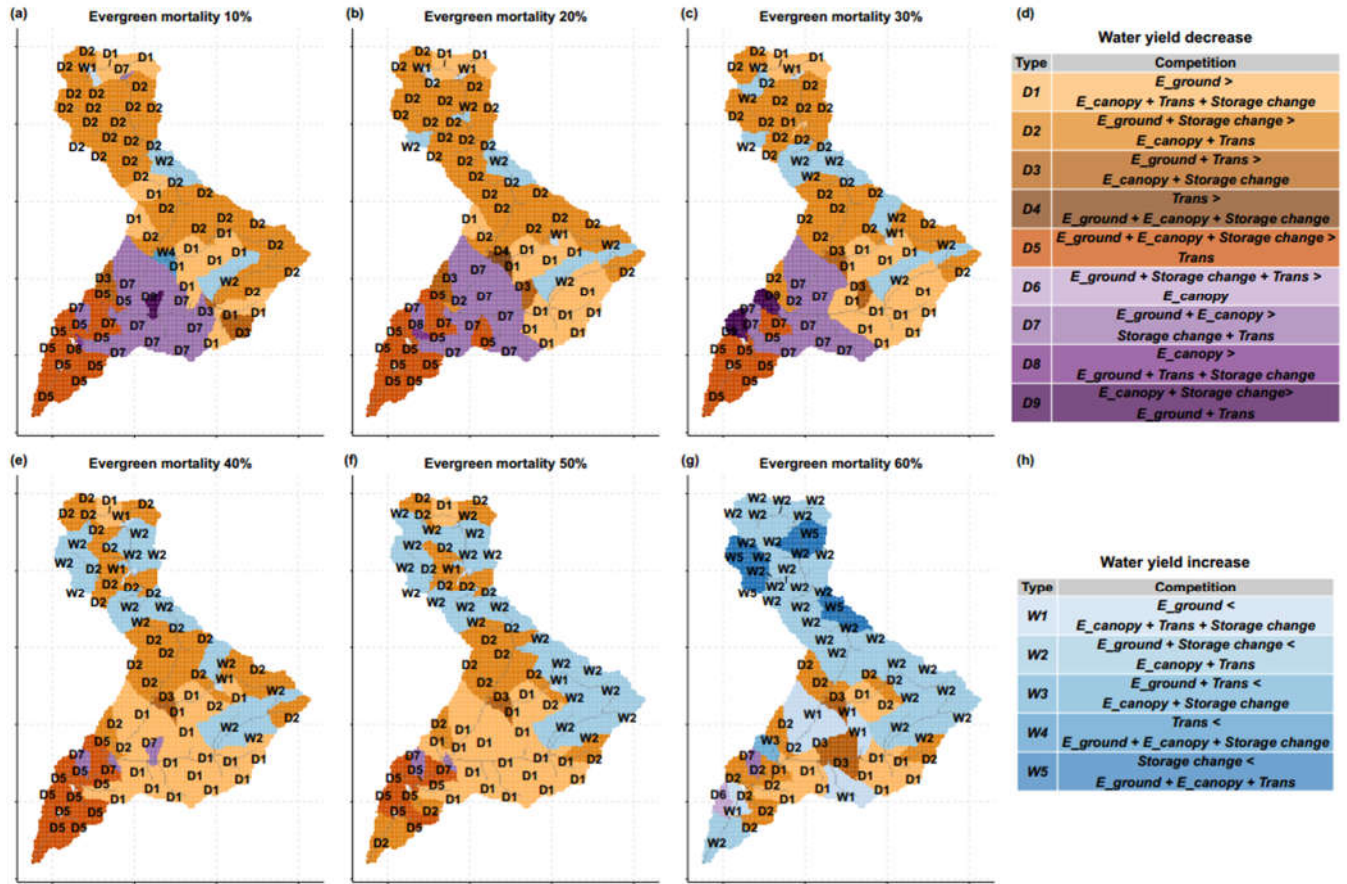
1107



1108

1109 *Figure 10. Relationship among long-term aridity, vegetation mortality level and Differences in*  
 1110 *water yield for a dry year (1994, a) and wet year (1995, b).*

1111



1112

1113 *Figure 11. Water yield response types after beetle outbreak for different evergreen mortality*  
 1114 *scenarios compared with control scenario. D1 to D9 are water yield decrease types and W1 to*  
 1115 *W5 are water yield increase types. In panel D and H, the left side of each type are increasing*  
 1116 *fluxes that cause water yield decreases and the right side are decreasing fluxes that cause water*  
 1117 *yield increase. If the left side is larger than the right side, water yield increases, and vice versa.*  
 1118 *(Note: this mortality is evergreen mortality, which is different from vegetation mortality.)*

1119