

1 **Variable streamflow response to forest disturbance in the western US: A large-sample**
2 **hydrology approach**

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11 **Key Points:**

- 12 • Large-sample analyses found that while streamflow often increased following forest
13 disturbance, it decreased in some watersheds.
- 14 • The direction of streamflow response to forest disturbance (increase vs. decrease) is
15 dependent on aridity.
- 16 • Forest disturbance is more likely to occur in arid locations, which is also where
17 disturbance tends to result in decreased streamflow.
18

19 **Abstract**

20 Forest cover and streamflow are generally expected to vary inversely because reduced forest
21 cover typically leads to less transpiration and interception. However, recent studies in the
22 western US have found no change or even decreased streamflow following forest disturbance
23 due to drought and insect epidemics. We investigated streamflow response to forest cover change
24 using hydrologic, climatic, and forest data for 159 watersheds in the western US from the
25 CAMELS dataset for the period 2000-2019. Forest change and disturbance were quantified in
26 terms of net tree growth (total growth volume minus mortality volume) and mean annual
27 mortality rates, respectively, from the US Forest Service's Forest Inventory and Analysis
28 database. Annual streamflow was analyzed using multiple methods: Mann-Kendall trend
29 analysis, time trend analysis to quantify change not attributable to annual precipitation and
30 temperature, and multiple regression to quantify contributions of climate, mortality, and aridity.
31 Many watersheds exhibited decreased annual streamflow even as forest cover decreased. Time
32 trend analysis identified decreased streamflow not attributable to precipitation and temperature
33 changes in many disturbed watersheds, yet streamflow change was not consistently related to
34 disturbance, suggesting drivers other than disturbance, precipitation, and temperature. Multiple
35 regression analysis indicated that although change in streamflow is significantly related to tree
36 mortality, the direction of this effect depends on aridity. Specifically, forest disturbances in wet,
37 energy-limited watersheds (i.e., where annual potential evapotranspiration is less than annual
38 precipitation) tended to increase streamflow, while post-disturbance streamflow more frequently
39 decreased in dry water-limited watersheds (where the potential evapotranspiration to
40 precipitation ratio exceeds 2.35).

41

42 **Plain Language Summary**

43 Forest disturbance is typically expected to lead to increased runoff, and therefore more water
44 available for aquatic ecosystems and people, because loss of forest vegetation results in less
45 water being taken up and transpired by plants. We examined streamflow and forest change in
46 159 watersheds in the western U.S. to test this expectation. We found that not all disturbed
47 watersheds experienced increased streamflow. Very dry watersheds were more likely to produce
48 less runoff following forest disturbance and were also more likely to experience forest
49 disturbance.

50 **1. Introduction**

51

52 Based on decades of research, forest cover and streamflow are generally expected to vary
53 inversely (Andréassian, 2004; Bosch and Hewlett, 1982; Hibbert, 1967; Troendle, 1983). Such
54 research is based on a combination of paired watershed experiments (e.g., Brown et al., 2005;
55 Moore et al., 2020), post-hoc analysis of streamflow data in unpaired watersheds where
56 streamflow can be modeled as a function of climatic observations (e.g., Biederman et al., 2015;
57 Zhao et al., 2010), and simulation modeling that encompasses various levels of complexity (e.g.,
58 Bennett et al., 2018; Buma and Livneh, 2015; Sun et al., 2018). The mechanism behind the
59 inverse relationship between forest cover and streamflow includes a combination of reduced
60 evaporation of canopy-intercepted precipitation, and reduced canopy transpiration following
61 forest cover loss (Adams et al., 2012; Hibbert, 1967; Pugh and Gordon, 2012). Conversely, forest
62 recovery or afforestation are assumed to increase total transpiration and evaporative losses of
63 canopy-intercepted precipitation, thus leading to decreased runoff (Andréassian, 2004; Hibbert,
64 1967).

65 Contrary to the hypothesis of an inverse relationship between forest cover and
66 streamflow, observed streamflow changes following recent forest disturbances have been
67 variable in magnitude and direction (Boisramé et al., 2017; Goeking and Tarboton, 2020; Ren et
68 al., 2021; Slinski et al., 2016). Over the past two decades, widespread but low- to moderate-
69 severity forest disturbance has occurred as a result of drought stress, insect epidemics, and
70 disease epidemics, as well as altered wildfire regimes (Adams et al., 2012; Williams et al., 2013),
71 thus providing opportunities to identify circumstances leading to decreased post-disturbance
72 streamflow. Most exceptions to the inverse relationship between forest cover and streamflow
73 occurred as post-disturbance decreases in streamflow, typically at low latitudes and south-facing
74 aspects with high aridity, high incoming solar radiation, and/or where tree canopies were
75 replaced by rapid growth of dense grasses or shrubs (Bennett et al., 2018; Goeking and Tarboton,
76 2020; Guardiola-Claramonte et al., 2011; Morillas et al., 2017; Ren et al., 2021). Even in studies
77 that found conforming streamflow increases following disturbance, the magnitude of streamflow
78 increases was modulated by aridity (Saksa et al., 2019). Although such findings are anomalous in
79 the larger context of decades of forest hydrology research, they highlight alternative hypotheses
80 to the inverse relationship between forest cover and streamflow. One such alternative hypothesis

81 is that although streamflow typically increases following forest disturbance, post-disturbance
82 conditions that lead to increased evaporation (i.e., increased energy at snowpack or soil surface)
83 or increased transpiration (i.e., replacement of sparse trees with dense shrubs) lead to a reduced
84 streamflow response.

85 While numerous studies of runoff response to forest change have focused on site-specific
86 treatments (e.g., harvest, planting) or severe disturbance (e.g., stand-replacing wildfire) in one or
87 two small watersheds, fewer studies have examined lower severity disturbances across broader
88 geographic areas or across more gradual timescales than episodic timber harvesting or wildfire
89 (Andréassian, 2004; Hallema et al., 2017; Wine et al., 2018). Response to less severe forest
90 disturbances may fundamentally differ from severe, stand-replacing disturbances due to their
91 different effects on energy balances affecting snowpack and soil moisture as well as different
92 transpiration rates for pre-disturbance versus post-disturbance vegetation (Adams et al., 2012;
93 Pugh and Gordon, 2012; Reed et al., 2018). Recent tree die-off across western North America
94 has provided the opportunity to examine streamflow responses to disturbance that is less severe
95 but more widespread than the forest changes considered in most previous forest hydrology
96 studies (Adams et al., 2012; Hallema et al., 2017). Studies based on both observations
97 (Biederman et al., 2015, 2014; Guardiola-Claramonte et al., 2011) and simulations (Bennett et
98 al., 2018; Ren et al., 2021) have found unexpected post-disturbance decreases in streamflow.
99 Streamflow response to disturbance at broader scales may not reflect hypotheses developed from
100 study of small watersheds that are commonly the focus of paired watershed experiments
101 (Andréassian, 2004), which underscores the value of broad-scale evaluation of hypotheses that
102 were developed at fine scales.

103 A challenge in testing such hypotheses is the need to balance breadth with depth, i.e.,
104 gathering fine-scale observations from individual watersheds versus coarser observations from
105 many watersheds (Gupta et al., 2014). Large-sample hydrology can complement fine-scale
106 studies of individual small watersheds by identifying broad-scale patterns in streamflow response
107 to forest disturbance. Fine-scale studies have produced useful information about the response of
108 streamflow (e.g., Biederman et al., 2015; Guardiola-Claramonte et al., 2011), snowpack (e.g.,
109 Broxton et al., 2016; Moeser et al., 2020), and individual ecohydrological processes to forest
110 change (e.g., Biederman et al., 2014; Reed et al., 2018). In contrast, large-sample hydrology can
111 evaluate hypotheses across many watersheds to identify circumstances that conform to or deviate

112 from hypothesized relationships (Addor et al., 2019; Gupta et al., 2014; Newman et al., 2015).
113 Another challenge is accounting for the effects of climate variability in streamflow assessments,
114 such that the effects of vegetation change on streamflow are not confounded with climate effects.
115 To address this challenge, quantitative models of streamflow response to vegetation change often
116 include precipitation and temperature as explanatory variables (Zhao et al., 2010).

117 In this study, we used a large sample of catchments to test hypotheses about the direction
118 of runoff response following forest disturbance in semi-arid catchments. Observations consisted
119 of streamflow, vegetation, and climate data, which allowed us to account for streamflow changes
120 related to variability in precipitation and temperature and thus disentangle climate from
121 vegetation effects. Based on previous studies finding exceptions to the inverse relationship
122 between forest cover and streamflow, we developed two alternative hypotheses. First, post-
123 disturbance runoff in catchments conforms with the commonly held paradigm that runoff
124 increases with tree mortality or reductions in net growth. Second, an alternative hypothesis is that
125 in watersheds with higher aridity and incoming solar radiation, runoff is more likely to decrease
126 or not change than in watersheds with lower aridity and solar radiation. A corollary of this
127 hypothesis is that a threshold of aridity index exists above which disturbance results in a
128 decrease in runoff. Our results find this threshold to be an aridity index of 2.35.

129

130 **2. Data and Methods**

131

132 We combined data from the CAMELS large-sample hydrology dataset (CAMELS; Addor
133 et al., 2017) and the US Forest Service’s Forest Inventory and Analysis (FIA) forest monitoring
134 dataset (Bechtold and Patterson, 2005) to answer four questions (Table 1). The ability of each
135 question’s analytical framework to disentangle climatic from forest disturbance effects on
136 streamflow successively increases from the first to the fourth question. For analyses that do not
137 explicitly permit such disentangling, we interpret the results in the context of factors that were
138 not included in the analysis.

139

140 **Table 1. The four questions addressed in this study, the analytical framework used to**
 141 **address each question, and the variables included in the analysis. Q=streamflow;**
 142 **P=precipitation; PET=potential evapotranspiration; T=temperature.**

Question	Analytical framework	Variables analyzed
1) To what extent and where is there a consistent trend in annual Q, Q/P, P, PET, and T, regardless of forest change effects?	Mann-Kendall trend tests (univariate)	Annual Q, Q/P, P, PET, and T
2) To what extent and where do trends in runoff ratio and forest density demonstrate an inverse relationship?	Trend in Q/P vs. net tree growth	Trend (Kendall's Tau) in annual Q/P; net tree growth
3) To what extent has streamflow changed in watersheds with substantial forest disturbance?	Time trend analysis (comparison of observed vs. predicted Q)	Annual Q, P, and T; disturbance (disturbed/not disturbed)
4) How well does the severity of forest disturbance, and the interaction of disturbance severity with aridity, predict change in streamflow?	Multiple regression	Annual Q, P, T; tree mortality; aridity (PET/P)

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144

145 **2.1 Data sources**

146 *2.1.1 Streamflow and climate data*

147

148 Watersheds were selected from the CAMELS dataset, which was compiled for
 149 watersheds that have little or no known land-use change and whose streamflow is relatively
 150 unimpacted by storage or diversions (Addor et al., 2017). However, watersheds in the CAMELS
 151 dataset have been subject to disturbance from wildfire and other causes of tree mortality that
 152 have been quantified by FIA. From the entire CAMELS dataset, we first constrained our analysis
 153 to watersheds in the western US for which we could obtain estimates of forest characteristics
 154 from the FIA dataset. Then we removed watersheds where runoff ratio was calculated as larger
 155 than 1.0 (runoff greater than precipitation) in any one year, which indicates an impossible water
 156 budget and where data is presumed to be in error. Precipitation and streamflow data within the
 157 CAMELS dataset were derived from Daymet climate data and USGS streamflow gages,
 158 respectively (Addor et al., 2017), and these separate data sources do not impose constraints of
 159 water budget closure. While we recognize that some catchments may have runoff ratios greater
 160 than 1.0, e.g., in volcanic or karst landscapes, and that runoff ratios near but less than 1.0 may be
 161 similarly implausible, we had no means of quantifying realistically vs. unrealistically high runoff
 162 ratios. These constraints yielded 159 watersheds, out of 211 candidate watersheds as 52 (25%)
 163 had runoff ratio greater than 1.0. The fact that 25% of watersheds had runoff ratios greater than

164 1.0 is indicative of the uncertainty and difficulty in compiling quality controlled data over large
 165 samples, even for curated datasets such as CAMELS. The watersheds selected had a wide range
 166 of physical and land cover characteristics (Table 2), runoff ratios, and humidity indices (Fig. 1),
 167 giving the study a broad degree of generality. Given the criteria for inclusion in the CAMELS
 168 dataset (Addor et al., 2017), we assumed that stream gauges for each watershed quantify actual
 169 runoff, and that withdrawals, transfers, and changes in storage are negligible.

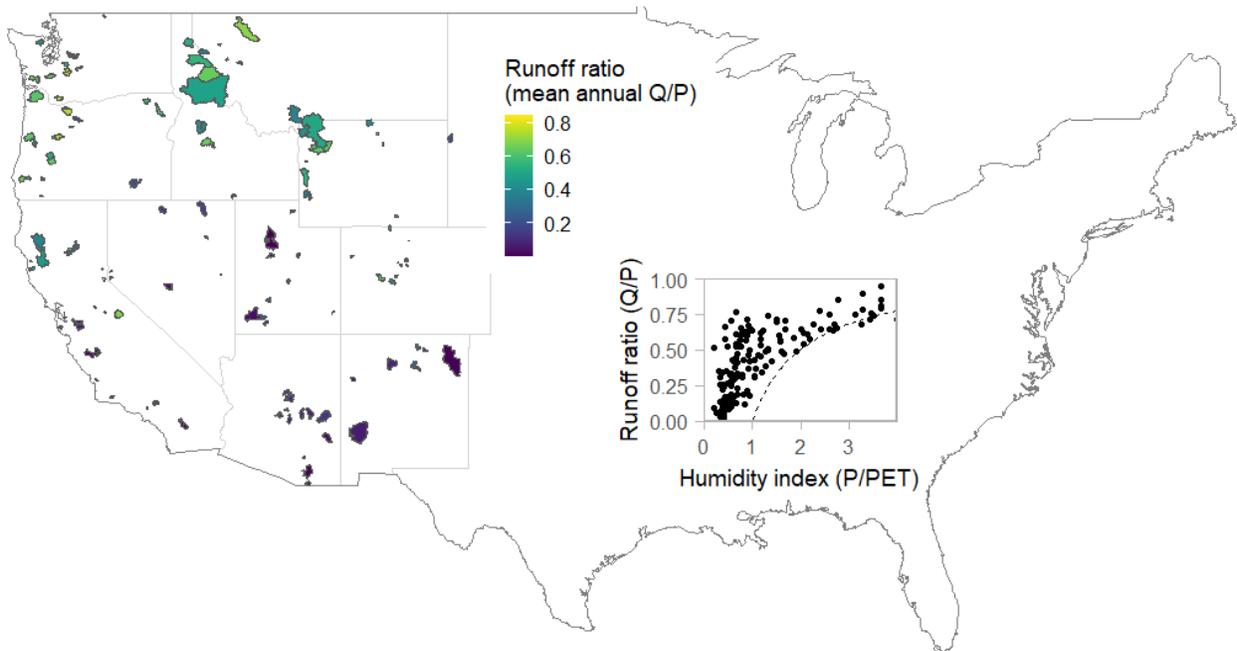
170

171 **Table 2. Characteristics of 159 watersheds used in this study. Values are summarized from**
 172 **CAMELS attributes (Addor et al., 2017).**

	Area (km ²)	Mean slope (m/km)	Mean elevation (m)	Runoff ratio	P (mm/yr)	PET (mm/yr)	Fraction forested
Median	238	92.8	1,613	0.419	822	1,084	0.76
Mean	649	92.0	1,650	0.409	1,062	1,088	0.64
Standard deviation	1,454	35.3	882	0.241	674	206	0.34

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176

177 **Fig. 1. Watersheds from the CAMELS database used in our analyses (n=159). Inset plot**
 178 **shows watersheds in nondimensional space based on long-term CAMELS attributes; the**
 179 **dashed curve represents energy limitation on streamflow, expressed as $Q=P-PET$ framed in**
 180 **terms of the dimensionless axes as $Q/P=1-1/(P/PET)$, where Q =annual streamflow,**
 181 **P =annual precipitation, and PET =annual potential evapotranspiration.**

182 The CAMELS dataset includes daily time series of climatic variables and streamflow as
183 well as time-averaged catchment characteristics. We used temporally averaged variables
184 representing basin characteristics such as mean incoming solar radiation (SRAD), and aridity,
185 defined as the ratio of mean annual potential evapotranspiration (PET) to mean annual
186 precipitation, all from the CAMELS dataset (Addor et al., 2017). We summed CAMELS daily
187 streamflow and precipitation values to get total annual water year streamflow and precipitation.
188 Annual mean temperature was calculated by first averaging CAMELS minimum and maximum
189 daily temperature to get daily mean temperature and then averaging the daily mean temperature.
190 Additionally, we estimated annual PET by first using the Hamon method (Hamon, 1963; Lu et
191 al., 2005) to estimate daily PET based on precipitation, temperature, and day length from the
192 CAMELS dataset, and then aggregating daily values to annual PET.

193 Because the CAMELS dataset extends only through water year 2014, while available
194 forest data extend through 2019, we used USGS streamflow data and Daymet gridded climate
195 data for water years 2015-2019 to extend the record of our analysis through water year 2019.
196 USGS streamflow data were obtained through the R package *DataRetrieval* (Hirsch and De
197 Cicco, 2015). Daymet gridded precipitation, minimum temperature, and maximum temperature
198 values were downloaded using the R package *daymetr* (Hufkens et al., 2018) and extracted as
199 area-weighted averages within each CAMELS catchment boundary, following the methods used
200 to construct the CAMELS time series (Newman et al., 2015). That extraction process yielded
201 time series analogous to the time series within the CAMELS dataset. We then aggregated daily
202 values to annual values in the same manner as described above for the CAMELS time series. We
203 cross checked our extended dataset by ensuring that we could replicate water year 2014 in the
204 CAMELS data, finding that the only differences were due to numerical rounding.

205

206 2.1.2 *Forest and disturbance data*

207

208 Data on forest conditions and disturbances were obtained from the US Forest Service's
209 Forest Inventory and Analysis (FIA) program. The FIA program established plot locations using
210 probabilistic sampling to obtain a representative sample with mean spacing of 5 km across all
211 forest types and owner groups (Bechtold and Patterson, 2005). In the western US, 10% of plots
212 are measured each year and each plot is therefore measured once every ten years. Each year's

213 subsample of plots is spatially distributed such that the sample of forest conditions is both
214 spatially and temporally balanced. This sampling design was developed to produce unbiased
215 estimates of forest attributes that represent discrete areas such as watersheds (Bechtold and
216 Patterson, 2005).

217 Data collected from FIA plots include detailed tree measurements that permit calculation
218 of plot-level volume of both live and dead trees, volume of net tree growth, volume of trees that
219 recently died (i.e., “mortality trees”), and many other variables (USDA, 2010). Each plot is
220 associated with an expansion factor that facilitates estimation of forest characteristics and their
221 associated sampling errors for discrete areas, based on data from multiple plots over the same
222 sampling period (Bechtold and Patterson, 2005; Burrill et al., 2018). FIA estimates are updated
223 annually based on a 10-year moving window such that the estimate in any one year is based on
224 data collected during the previous 10 years (e.g., an estimate with a nominal date of 2019 is
225 based on data collected during 2010-2019). FIA implemented this nationally consistent,
226 probabilistic sample in 2000, although the onset of data collection varied among states, with
227 Wyoming being the last state to fully implement this design in 2011.

228 We characterized forest disturbance using FIA’s estimates of net tree growth and tree
229 mortality and their associated standard errors, for the period 2010-2019, from the publicly
230 accessible EVALIDator tool (USDA, 2020). Each estimate was constrained to a watershed
231 represented by an 8-digit Hydrologic Unit Code (HUC8) that contains a CAMELS catchment.
232 Although ideally we would have produced FIA estimates at the scale of CAMELS watersheds,
233 these smaller watersheds contained small sample sizes of FIA plots and thus were associated
234 with high uncertainty at the CAMELS scale. The forested portions of most HUC8 catchments
235 exist at relatively high elevations that tend to be less impacted by water transfers and human
236 activities (i.e., nonforest land uses), which is also where CAMELS watersheds occur (Addor et
237 al., 2017). To test whether forest conditions in CAMELS versus HUC8 watersheds were similar,
238 we computed the percentage of area at each scale that experienced forest change between 2001
239 and 2019 as determined from the National Land Cover Database change product (Homer et al.,
240 2020). We found that the distributions of forest change at the two scales were not significantly
241 different based on $p=0.51$ from the Kolmogorov-Smirnov test for equal distributions. This result
242 supports the use of FIA data at the HUC8 scale as representative of CAMELS watersheds.

243 Mean annual net growth and mortality rates are expressed as volume per year (Burrill et
244 al., 2018) rather than numbers of trees because under normal conditions with no disturbance,
245 small trees typically die at higher rates than larger or older trees due to self-thinning that occurs
246 naturally as forest stands develop over time (Yoda et al., 1963). Net growth is defined as
247 volumetric growth of all live trees minus the total volume of trees that died in the previous ten
248 years (i.e., mortality volume). Values of net growth greater than zero indicate that tree growth
249 has outpaced mortality, while negative net growth is indicative of mortality that occurred faster
250 than growth of live trees. To assess the severity of forest disturbance, we estimated each
251 watershed's mean annual mortality rate and standardized that rate by the total of live volume
252 plus mortality volume. Note that watersheds with high mean annual mortality can also have
253 positive net growth if post-disturbance recovery and live tree growth occurs more rapidly than
254 mortality. A strength of using net growth and mortality estimates is that it permits assessment of
255 quantitative relationships between forest conditions and hydrologic variables, as opposed to
256 being limited by categorical mapping of disturbance or rules-of-thumb such as having >20% of
257 area affected (Goeking and Tarboton, 2020).

258

259 **2.2 Methods**

260

261 We used multiple analytical methods to address our objectives. First, we used trend
262 analysis to identify monotonic trends in individual water budget components and drivers.
263 Second, we qualitatively related trends in runoff ratio to forest change across gradients of
264 latitude and aridity. Third, we used time trend analysis (Zhao et al., 2010) to quantify the
265 magnitude of streamflow change that cannot be attributed to precipitation and temperature
266 drivers, and then correlated the magnitude of unattributed streamflow change with forest
267 disturbance, latitude, solar radiation, and aridity. Fourth, we evaluated the relative importance of
268 several factors – including temperature, precipitation, and the interaction of forest disturbance
269 and aridity – for predicting change in streamflow across decades using a multiple regression
270 model.

271

272 2.2.1 *Trends in water budget components and drivers*

273

274 Our first question was whether runoff ratio has changed over time, i.e., whether there is
275 any monotonic trend, regardless of climate or forest disturbance effects. We answered this
276 question using the nonparametric Mann-Kendall trend test, which determines whether the central
277 tendency of a variable changes solely as a function of time (Helsel et al., 2020). We tested for
278 trends in annual runoff ratio (Q/P) as well as water budget components and drivers, including
279 annual streamflow (Q), annual total precipitation (P), annual mean temperature (T), and annual
280 potential evapotranspiration (PET). Each variable was tested independently of vegetation effects.
281 Each test evaluated two time periods: first, the period 2000-2019, which was the basis for our
282 subsequent analyses of streamflow response to forest disturbance, and second, 1980-2019, for
283 the purpose of determining whether any other long-term trends exist that extend prior to the
284 period covered in our analysis.

285 Watersheds with significant trends in Q, P, Q/P, T, and PET were identified based on
286 two-sided p-values associated with Kendall's tau (Helsel et al., 2020) evaluated with the
287 *MannKendall* function in the *Kendall* package (McLeod, 2011) for R statistical analysis software
288 (R Core Team, 2020). Two-sided p-values <0.1, which correspond to one-side p-values <0.05,
289 were considered statistically significant.

290

291 2.2.2 *Runoff ratio and forest density change*

292

293 Our second question was whether there is general support for the hypothesis that forest
294 cover is inversely related to annual runoff, across a large sample of watersheds spanning a range
295 of aridity, incoming solar radiation, and latitude. Under this hypothesis, we expected that most
296 watersheds that experienced forest cover loss (i.e., disturbance) exhibited increases in runoff
297 ratio, and that watersheds that experienced forest cover gain (i.e., increased tree density in the
298 absence of disturbance) exhibited decreases in runoff ratio. An alternative hypothesis, based on
299 recent observations of decreased streamflow following forest disturbance as summarized by
300 Goeking and Tarboton (2020), is that post-disturbance runoff sometimes decreases in more arid,
301 low-latitude watersheds with higher incoming solar radiation.

302 To characterize watersheds as disturbed versus undisturbed and as having increased
303 versus decreased runoff ratio, we determined whether net growth and trend in runoff ratio (Q/P)
304 were each positive or negative for each watershed. Watersheds were characterized as having
305 increased versus decreased runoff ratio on the basis of Kendall's tau, which allows dimensionless
306 comparison of trends in runoff ratio across watersheds whose runoff ratios may vary widely
307 (Helsel et al., 2020), again using R package *Kendall* (McLeod, 2011).

308 Net tree growth estimates for 2010-2019 encompass a temporal averaging period
309 beginning in 2000 for plots measured in 2010, and in 2009 for plots measured in 2019, because
310 growth is calculated from individual tree growth representing the 10 years prior to plot
311 measurement (USDA, 2010). Therefore, we conducted trend analysis for the period 2000-2019,
312 which encompasses the averaging period for FIA plot measurements.

313 We categorized watersheds into two groups: those that met the expectation that the
314 change in runoff ratio is inversely related to forest cover change (conforming watersheds), and
315 those that did not meet this expectation (nonconforming watersheds). Conforming watersheds
316 included watersheds where tree volume increased (i.e., positive tree growth) and Q/P decreased,
317 as well as those where tree volume decreased (i.e., negative tree growth) and Q/P increased.
318 Similarly, nonconforming watersheds consisted of those where both tree volume and Q/P
319 increased and where both tree volume and Q/P decreased. This categorization resulted in four
320 combinations of change in tree volume and trend in Q/P.

321 We assessed differences in aridity, solar radiation, and latitude among the four categories
322 of conforming and nonconforming watersheds. Aridity was compared among watersheds in the
323 context of evaporative index and aridity index, as defined by Budyko (Budyko and Miller, 1974),
324 to assess whether nonconforming watersheds (i.e., those with forest disturbance and decreased
325 streamflow) were more likely to occur in water-limited watersheds than in energy-limited ones.
326 Evaporative index represents the proportion of precipitation that evaporates, on a mean annual
327 basis, and is equal to the quantity $1 - Q/P$. Aridity index is the ratio of mean annual PET to mean
328 annual P. Long-term values of mean annual Q, mean annual P, aridity, and incoming solar
329 radiation for each watershed were obtained from the CAMELS dataset (Addor et al., 2017). We
330 also tested for significant differences in latitude, aridity, and solar radiation among conforming
331 versus nonconforming watersheds using the nonparametric Kruskal-Wallis test for multiple

332 comparisons, which was conducted using the function *kruskal* in R package *agricolae* (de
333 Mendiburu, 2020).

334

335 2.2.3 *Expected streamflow change in watersheds with and without forest disturbance*

336

337 To address the question of whether streamflow has changed as a result of forest
338 disturbance over discrete time periods, we used time trend analysis, which is an analytical
339 framework used to quantify streamflow change resulting from vegetation change (Zhao et al.,
340 2010). The premise of time trend analysis is that expected streamflow can be predicted from a
341 small number of predictor variables for a calibration period, and then applied to a later time
342 period to compare predicted to observed runoff for that time period. Computationally, a linear
343 regression model is calibrated on an initial time period, applied to a second time period, and the
344 residuals (i.e., the difference between the observed and predicted values in the second time
345 period) are assumed to be due to factors not included in the model. Although previous
346 applications of time trend analysis have used a linear regression model, we initially attempted to
347 conduct this analysis using a machine learning model structure, specifically random forests
348 (Breiman, 2001), but found that random forests performed similarly to linear regression but
349 presented the disadvantage of not producing easily interpretable coefficients.

350 For the purposes of time trend analysis, we split our period of record into two time
351 periods: 2000-2009 and 2010-2019. We calibrated and validated the linear regression model for
352 time trend analysis using data from water years 2000-2009. Odd-numbered years were used for
353 calibration, and even-numbered years for validation. Preliminary analysis indicated that our
354 dataset met the assumptions required for linear regression (Helsel et al., 2020). Given that
355 temperature exhibited a significant positive trend at many watersheds (Fig. 2) and was a
356 significant predictor, we included it in our model. Thus, the regression model took the form:

357

$$Q_1 = a_1 * P_1 + b_1 * T_1 + c_1 + e \tag{1}$$

358

359 In Eq. (1), Q=annual streamflow; P=annual precipitation; T=annual mean temperature;
360 subscripts represent values from the calibration/validation period (time 1, or 2000-2009); a, b,
361 and c are coefficients; and e represents model residuals. We also tested whether the model

362 improved when we included the interaction of T and P as a product term, and seasonal rather
 363 than annual T and P; neither of these options improved model fit, so we proceeded with the
 364 simpler Eq. (1). The regression held a and b the same across all watersheds, for two reasons.
 365 First, the processes that relate P and T to streamflow should be consistent across all watersheds,
 366 and second, allowing these coefficients to vary would effectively create a separate model for
 367 each watershed, which would result in many watersheds being omitted due to years with missing
 368 data during the calibration period. The intercept, c, was allowed to vary among watersheds to
 369 capture watershed specific differences with respect to factors that were not included in this linear
 370 model. The application of this model to the evaluation period (time 2) uses time 1 coefficients
 371 and time 2 observations of annual precipitation and temperature to predict annual streamflow
 372 over time period 2 (2010-2019):

$$Q'_2 = a_1 * P_2 + b_1 * T_2 + c_1 \tag{2}$$

375 The difference between observed ($\overline{Q_2}$) and predicted ($\overline{Q'_2}$) mean annual streamflow during the
 376 evaluation period is represented as the quantity:

$$\overline{Q_{obs-exp}} = \overline{Q_2} - \overline{Q'_2} \tag{3}$$

379 where $\overline{Q_{obs-exp}}$ represents the magnitude of streamflow change that cannot be attributed to
 380 precipitation and temperature and thus is typically interpreted to be due to vegetation change
 381 (Zhao et al. 2010).

382 One objective of time trend analysis was to determine how runoff responds to
 383 disturbance. As in our other analyses, we hypothesized that runoff is likely to increase in
 384 disturbed watersheds, although a secondary hypothesis was that runoff response depends not
 385 only on magnitude of disturbance but also on aridity and/or incoming solar radiation. To answer
 386 the question of whether streamflow has increased or decreased in disturbed watersheds, we
 387 interpreted significant change in streamflow, from our time trend analysis results (i.e., deviation
 388 in observed Q from predicted Q) in the context of disturbance. Significant change in annual
 389 streamflow was identified using a one-sample t-test (Biederman et al., 2015), wherein the null
 390 hypothesis was that there has been no change in streamflow due to factors other than

391 precipitation and temperature ($Q_{\text{obs-exp}} = 0$). P-values less than 0.05 were identified as
392 significant deviations in streamflow. Disturbed watersheds were defined as those where tree
393 mortality exceeded 10% of initial live tree volume.

394

395 2.2.4 *Streamflow change as a function of disturbance severity and climate*

396

397 We used multiple regression to address two objectives: 1) to evaluate the relative
398 importance of several factors for predicting change in streamflow (ΔQ), which allowed isolation
399 of the relative contributions of climate versus disturbance to ΔQ , and 2) to determine whether the
400 interaction of forest disturbance severity with aridity or solar radiation affects runoff response to
401 forest disturbance. A regression model was developed to predict ΔQ across two discrete time
402 periods, 2000-2009 versus 2010-2019.

403 To enable disentangling the confounding effects of climate versus vegetation changes, we
404 initially considered a large set of predictor variables encompassing time varying climatic
405 variables (e.g., change in mean annual precipitation) as well as time-invariant climate descriptors
406 (e.g., long-term mean incoming solar radiation) that are specific to each watershed. The initial set
407 of potential predictors included baseline Q and baseline P for 2000-2009 (\overline{Q}_1 and \overline{P}_1 ,
408 respectively), mean watershed aridity and solar radiation, tree mortality during 2010-2019, and
409 change in temperature, precipitation, and potential evapotranspiration (PET) between the two
410 time periods. To meet the assumption of noncollinearity among predictors, we then reduced the
411 number of predictors by evaluating pairwise correlations among all predictors and removing
412 predictors with correlation coefficients with absolute values of 0.6 or greater, where the predictor
413 with the lower correlation with ΔQ was removed. In this manner, PET, solar radiation, and
414 aridity were removed due to their respective correlations with temperature and \overline{P}_1 ; solar radiation
415 and aridity were represented in the model in interaction terms with tree mortality. Due to
416 multicollinearity between the interactions of mortality with solar radiation and aridity, we
417 removed the interaction of mortality with solar radiation as it was a less useful predictor than the
418 interaction of mortality with aridity. Thus, the final regression model took the form:

419

$$\Delta Q = b_0 + b_1 \overline{P}_1 + b_2 \Delta P + b_3 \Delta T + b_4 \text{mortality} + b_5 \text{mortality} * \text{aridity}$$

420

(4)

421 where \bar{P}_1 represents mean annual precipitation for 2000-2009; ΔP and ΔT were differences in
422 mean annual precipitation (mm) and mean annual temperature ($^{\circ}\text{C}$) between 2000-2009 and
423 2010-2019; and b_x refer to coefficients. As before, we tested whether model fit improved with
424 the inclusion of a product term representing interactions between ΔP and ΔT , and also using
425 differences in seasonal rather than annual P and T to consider the effects of precipitation phase
426 and snowpack, and the model did not improve so we implemented Eq. (4) using annual
427 observations of P and T. For this analysis, mortality was standardized by total volume of trees in
428 the watershed, i.e., as the volume of trees that died during the study period relative to initial live
429 tree volume, thus having possible values of 0 to 1 (USDA, 2020). The last term,
430 mortality*aridity, represents the interaction of tree mortality with aridity, which was included to
431 test the hypothesis that streamflow response to forest change is influenced by aridity. We used
432 the p-value associated with the coefficient of each predictor variable in Eq. (4) to assess its
433 significance as a predictor of ΔQ . We then compared standardized regression coefficients for
434 each variable to determine the relative importance of climatic factors, forest disturbance, and
435 interaction of forest disturbance with aridity for predicting ΔQ .

436 Based on the predominant hypothesis that runoff increases following forest disturbance,
437 we expected that tree mortality would have a positive coefficient in the regression model, i.e.,
438 that larger levels of tree mortality would lead to positive ΔQ . Our alternative hypothesis – that
439 disturbance may decrease runoff at high aridity or solar radiation – led to the expectation that the
440 coefficient for the interaction of tree mortality with aridity or solar radiation would be negative,
441 even as the coefficient for tree mortality alone was positive. To interpret the ability of each
442 predictor variable to explain additional variability in ΔQ , we examined partial regression plots
443 for each predictor (Moya-Laraño and Corcobado, 2008). Partial regression plots, also known as
444 added variable plots, isolate the explanatory capability of a single variable relative to that of all
445 other variables (Moya-Laraño and Corcobado, 2008). Although pairwise scatterplots between a
446 predictor and ΔQ would be appropriate for simple (single-variable) regression, in the context of
447 multiple regression, such plots ignore the effects of other variables in the model and can thus be
448 misleading representations of the contribution of each variable to explaining variability in the
449 response variable (Moya-Laraño and Corcobado, 2008). Partial regression plots were developed
450 to address this concern using the R package *car* (Fox and Weisberg, 2019). To visualize the
451 interactive effect of disturbance severity and aridity on streamflow change, we also examined

452 marginal effects of the interaction between mortality and aridity using R package *sjPlot*
453 (Lüdecke, 2021).

454 To interpret our regression model in the context of climatic warming, we used the
455 regression model (Eq. 4) to evaluate the sensitivity of streamflow changes to tree mortality and
456 aridity, both with and without 1° C of warming. We compared our results to those of previous
457 studies that projected decreases in streamflow with climate warming across the western US
458 (McCabe et al., 2017; Udall and Overpeck, 2017),

459

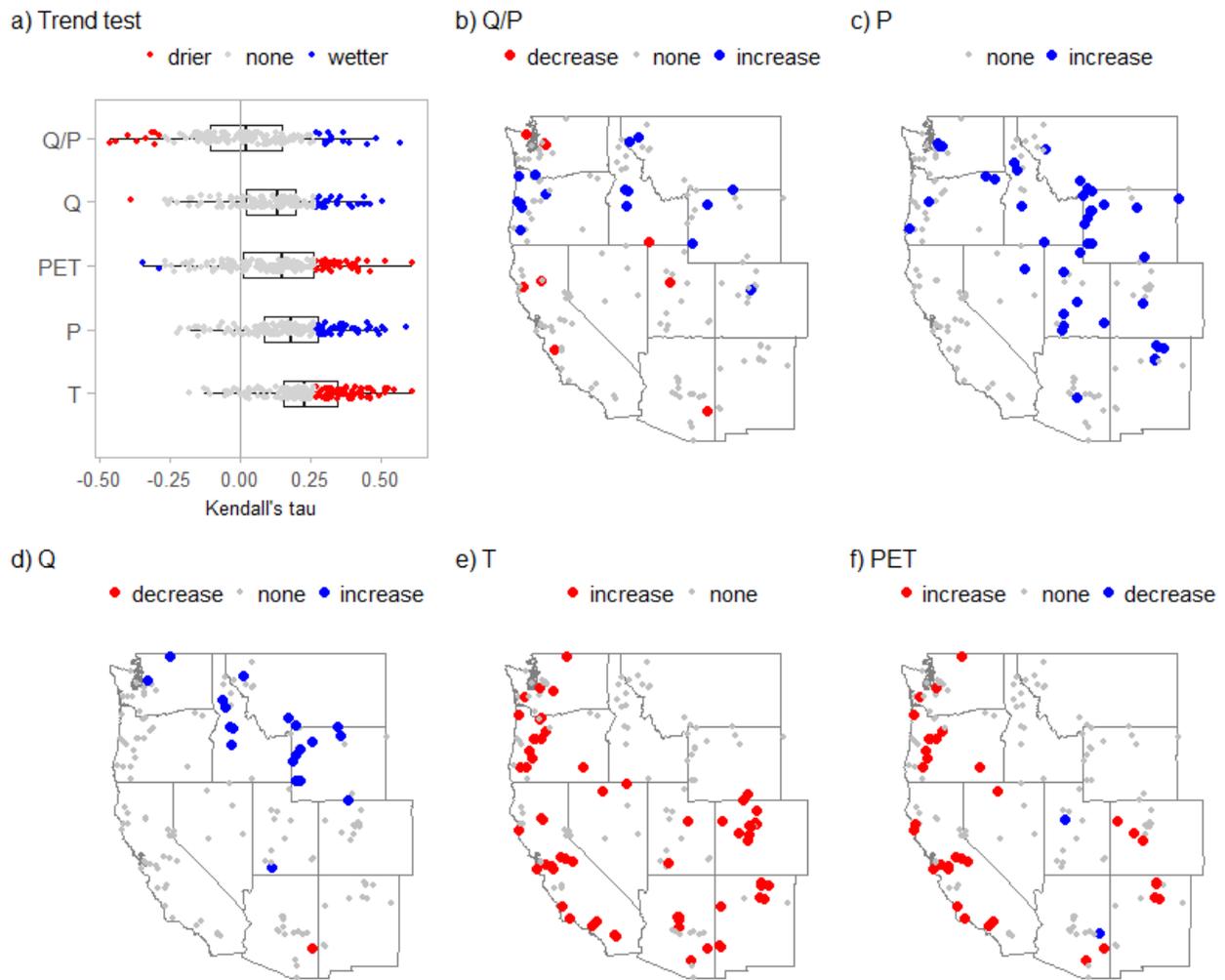
460 **3. Results**

461 *3.1 Trends in water budget components and drivers*

462

463 Most watersheds (>60%) did not experience significant monotonic trends in any water
464 budget components or drivers during 2000-2019 (Fig. 2). P increased significantly between 2000
465 and 2019 in 26% of watersheds, driving some increasing trends in Q (13%) and Q/P (10%). P
466 and Q decreased in <1% of watersheds, and Q/P decreased significantly 6% of watersheds. T and
467 PET increased significantly in 40% and 23% watersheds, respectively, and both decreased in
468 $\leq 1\%$ of watersheds (Fig. 2), which is consistent with general climate warming. Significant
469 changes in Q/P, P, Q, T, and PET were widespread with no clear geographic patterns (Fig. 2a-f).

470 When we repeated the Mann-Kendall trend test for the entire period of record (1980-
471 2019), results were very different than for 2000-2019. More watersheds experienced significant
472 decreases in P, Q/P, and Q (7%, 24%, and 17%, respectively), and only 8% of watersheds
473 exhibited significant increases in Q and Q/P. This pattern coincides with significant increases in
474 T (84%) and PET (81%), both of which decreased in <1% of watersheds. Thus, while an
475 appreciable percentage of watersheds show evidence for long-term (1980-2019) increases in T
476 and PET, only a small percentage show evidence for changes in Q and Q/P.



478

479

480 **Fig. 2. Significant trends in annual water budget components and drivers over the period**
 481 **2000-2019, based on the Mann-Kendall trend test ($p < 0.1$). Q= streamflow; P=precipitation;**
 482 **T=temperature; and PET=potential evapotranspiration.**

483

484 *3.2 Runoff ratio and forest change*

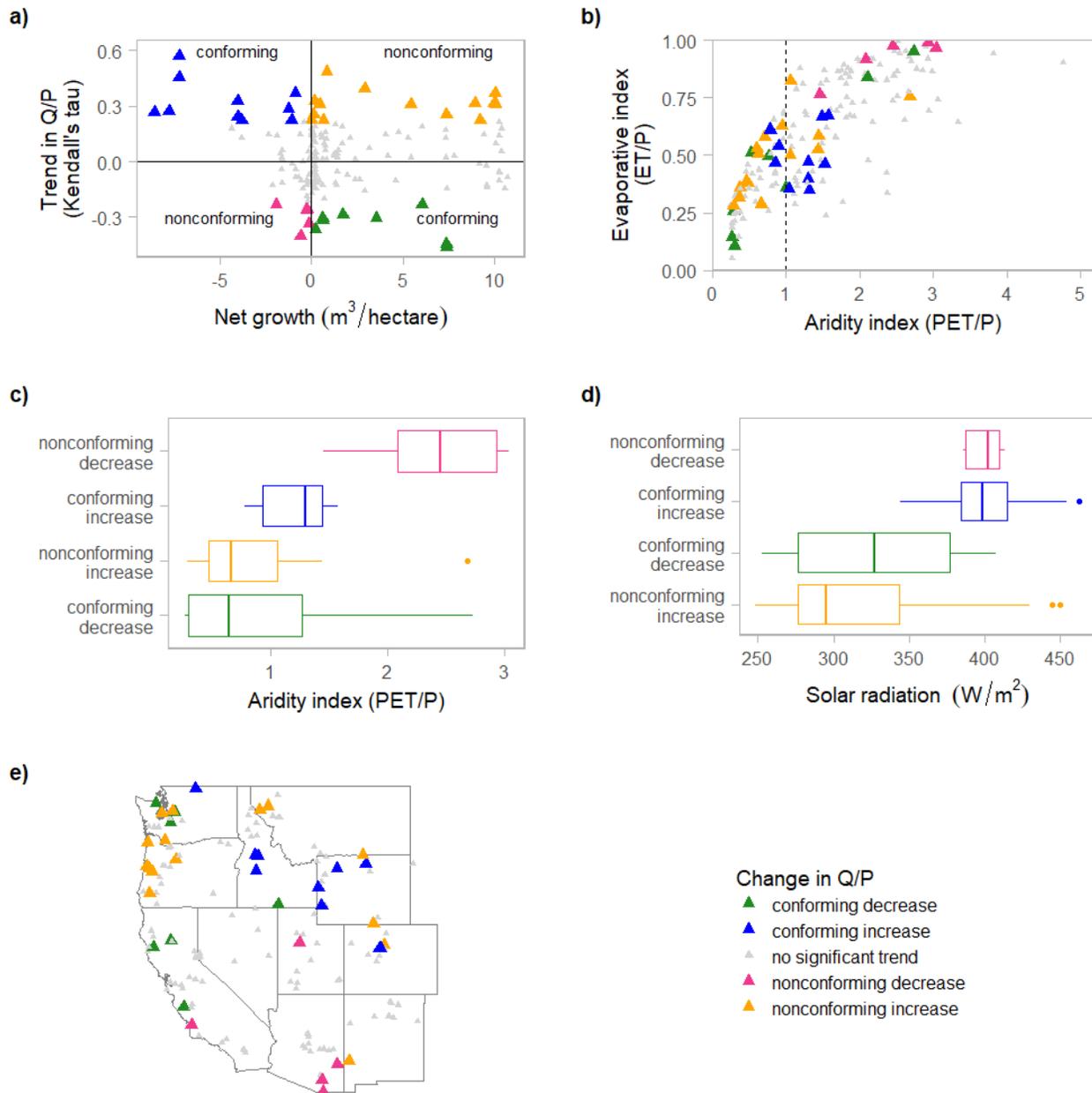
485

486 This analysis sought to test the hypothesis that forest cover is inversely related to runoff,
 487 and comparison of trends in runoff ratio (Q/P) to net tree growth demonstrated only moderate
 488 support for this hypothesis. Slightly less than half of all watersheds (43%) met the expectation
 489 that Q/P is inversely related to change in forest density (Fig. 3, upper left and lower right
 490 quadrants, with 24 and 44 watersheds, respectively), and the remaining watersheds (57%) did not

491 conform to this expectation (Fig. 3, lower left and upper right quadrants). However, a small
492 proportion of watersheds exhibited statistically significant trends in Q/P, as we found in the
493 previous section. Note that in Fig. 3a, watersheds in both left quadrants experienced negative net
494 tree growth, i.e., mortality exceed growth by surviving or newly established trees, which
495 indicates disturbance and decrease in volumetric forest density. To quantify the degree to which
496 estimated net growth might reflect random sample variability or noise, which is higher in smaller
497 watersheds due to smaller sample sizes, we examined the standard errors associated with the
498 estimated net growth in each watershed as produced by the EVALIDator tool. For >75% of
499 watersheds, net growth differed from 0 by more than one standard error. Thus, we inferred that
500 most watersheds have sufficient sample size to reliably indicate positive vs. negative net growth.

501 Trends in Q/P that contradict the expectation that Q/P is inversely related to change in
502 forest density occurred in two situations. First, Q/P decreased in watersheds with negative net
503 tree growth, i.e., greater mortality than live tree growth (Fig. 3a, lower left quadrant). This
504 response was observed mainly in water-limited catchments where $PET/P > 1$ and at lower
505 latitudes in the southwestern US (Fig. 3b-e, magenta symbols). Second, Q/P increased while net
506 tree growth was positive (Fig. 3a, upper right quadrant). This response was generally observed in
507 energy-limited or moderately water-limited ($PET/P < 2$) watersheds at higher latitudes of the
508 Pacific Northwest and northern Rocky Mountains (Fig. 3b-e).

509 Given recent research questioning the inverse relationship between forest cover and
510 runoff (Goeking and Tarboton, 2020), an alternative hypothesis is that runoff ratio is more likely
511 to decrease following forest disturbance in watersheds with high aridity and at lower latitude.
512 However, we found that forest disturbance itself was more widespread and severe within water-
513 limited watersheds, as evidenced by the preponderance of magenta and blue symbols where
514 $PET/P > 1$ (Fig. 3b-c) and where incoming solar radiation is relatively high (Fig. 3d). Results of
515 the Kruskal-Wallis test showed no significant differences in aridity or solar radiation among
516 disturbed watersheds with increased versus decreased runoff ratio, nor were there significant
517 differences among relatively undisturbed watersheds with increased versus decreased runoff ratio
518 (Fig. 3c-d). However, these results do not account for an increasing trend in P over 2000-2019
519 (see previous section). The following two analyses do account for this effect and thus allow
520 better separation of forest disturbance versus climate effects on streamflow.



524 **Fig. 3. (a) Relationship between trend in Q/P (measured as Kendall's tau) and net growth**
 525 **of trees for 2000-2019. Positive values of Kendall's tau indicate a monotonic increase in**
 526 **Q/P. Colors for watersheds with significant trend over time are assigned based on**
 527 **quadrants, where upper left and lower right quadrants conform to expected Q/P response**
 528 **to forest changes, and lower left and upper right exhibit runoff ratio trends do not conform**
 529 **to expectations. (b) Position of watersheds in the Budyko framework of evaporative index**
 530 **(1-Q/P) versus aridity index (PET/P). (c & d) Aridity and incoming solar radiation, with**
 531 **watersheds grouped into the quadrants in (a). Boxes represent interquartile ranges;**
 532 **horizontal bars within boxes represent medians. Boxes were not statistically significantly**

533 different, based on Kruskal-Wallis test ($\alpha=0.1$). (d) Geographic distribution of watersheds,
534 with colors as assigned in (a). Q= streamflow; P=precipitation; ET=evapotranspiration;
535 PET=potential evapotranspiration.

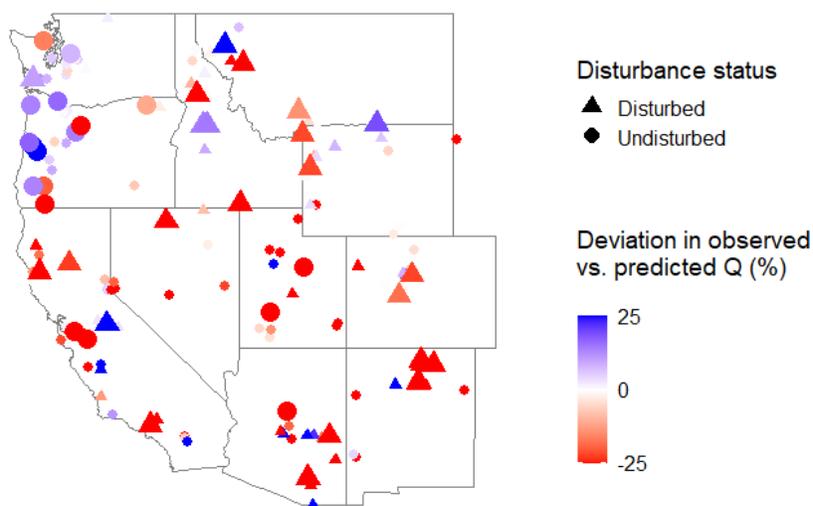
536

537 3.3 Streamflow change as a function of precipitation and temperature vs. other drivers

538

539 Time trend analysis and subsequent t-tests for significant deviations in streamflow
540 indicated that observed streamflow changed significantly in 44 (28% of) watersheds in 2010-
541 2019 relative to 2000-2009 (Fig. 4) due to factors other than precipitation and temperature. Of
542 these watersheds, streamflow decreased and increased by statistically significant magnitudes in
543 30 and 14 watersheds, respectively (Table 3). Validation of the linear model (Eq. 1) had adjusted
544 $r^2=0.98$. As expected, both precipitation and temperature were significant predictors ($p<0.01$ for
545 both variables).

546



547

548

549 **Fig. 4. Percent deviation in observed mean annual streamflow (Q) for 2010-2019, relative to**
550 **Q predicted by time trend analysis (calibrated for 2000-2009). Watersheds with statistically**
551 **significant deviation in Q (large symbols) were identified using on a one-sample t-test**
552 **($p<0.05$); small symbols represent watersheds with no significant deviation in Q ($p\geq0.05$).**
553 **Disturbed watersheds (triangles) are those where tree mortality exceeded 10% of initial live**
554 **tree volume.**

555

556 Only 26 watersheds experienced both disturbance and significant change in streamflow,
557 as determined by time trend analysis, and streamflow decreased in 20 of these watersheds (Table

3). This finding contradicts the hypothesis that streamflow increases following disturbance. The geographic distribution of significant decreases in streamflow in disturbed watersheds (Fig. 4) partially supports our secondary hypothesis that streamflow response to disturbance is influenced by factors such as incoming solar radiation, aridity, or latitude. Additionally, 18 undisturbed watersheds had significant changes in streamflow (10 decreases and 8 increases; Fig. 4). These results imply that deviations in observed vs. expected streamflow, as predicted from a linear model based on precipitation and temperature, cannot be attributed to vegetation change alone, which has commonly been an interpretation of time trend analysis (Biederman et al., 2015; Zhao et al., 2010). However, unlike the univariate trends shown in Fig. 2 and Fig. 3, time trend analysis accounts for changes in P and T over time and evaluates Q relative to those changes.

Table 3. Results of time trend analysis, which predicts mean annual streamflow from observed precipitation and temperature and then compares observed to predicted streamflow for a future time period. Disturbed watersheds are defined as those where tree mortality exceeded 10% of initial live tree volume. Significant change in annual streamflow was identified as $p < 0.05$ from a one-sample t-test.

	<u>Runoff lower than expected (decreased Q)</u>		<u>Runoff higher than expected (increased Q)</u>	
	Any change	Significant change	Any change	Significant change
Disturbed (n=67)	42	20	25	6
Not disturbed (n=92)	56	10	36	8
Total	98	30	61	14

We considered the possibility that our choice of disturbance threshold could affect our results and therefore evaluated the direction of streamflow response given different disturbance thresholds. Among all watersheds, 67 met our initial disturbance criterion of >10% tree mortality during 2010-2019. Different thresholds (5%, 15%, and 20%) did not lead to different conclusions about the proportion of disturbed watersheds that experience decreased versus increased streamflow. For all thresholds of disturbance, a slight majority (>54%) of disturbed watersheds exhibited decreased streamflow, based on observed streamflow compared to that predicted by the time trend analysis model.

585 3.4 Streamflow change as a function of climate and disturbance

586

587 All coefficients in the multiple regression model for ΔQ (Eq. 4) were statistically

588 significant ($p < 0.05$; Table 4) with adjusted model $r^2 = 0.70$ ($p < 0.01$). The average change in

589 runoff (ΔQ) across all 159 watersheds during the time period considered in this analysis was

590 positive (63 mm/yr), consistent with an increase in P (mean ΔP was 91 mm/yr). Standardized

591 regression coefficients indicate the direction and relative impact of each predictor on ΔQ (Fig.

592 5a) and indicate that \bar{P}_1 had the largest impact on ΔQ , which may be due to a positive association

593 of \bar{P}_1 and ΔP between 2000-2009 and 2010-2019 in watersheds that were already relatively wet.

594 \bar{P}_1 , ΔP , and mortality all had positive coefficients and thus positive effects on ΔQ , while ΔT and

595 the interaction of mortality with aridity had negative coefficients (Table 4; Fig. 5a). Partial

596 regression plots (Fig. 5b-f) illustrate the ability of each predictor variable to explain variability in

597 ΔQ that is not specifically accounted for by other predictors. Note that partial regression plots are

598 not scatterplots of pairwise variables but instead represent the effect on model residuals of

599 adding an additional model term to an existing model. The slopes of the lines in the partial

600 regression plots (Fig. 5b-f) are equal to the regression coefficients and are all significantly

601 different than zero (Table 4), which indicates that each predictor provides useful information in

602 predicting ΔQ . Examination of model diagnostics verified that residuals were normally

603 distributed and independent of predictor values. Fig. 5 shows that some observations exert high

604 leverage for some predictors.

605

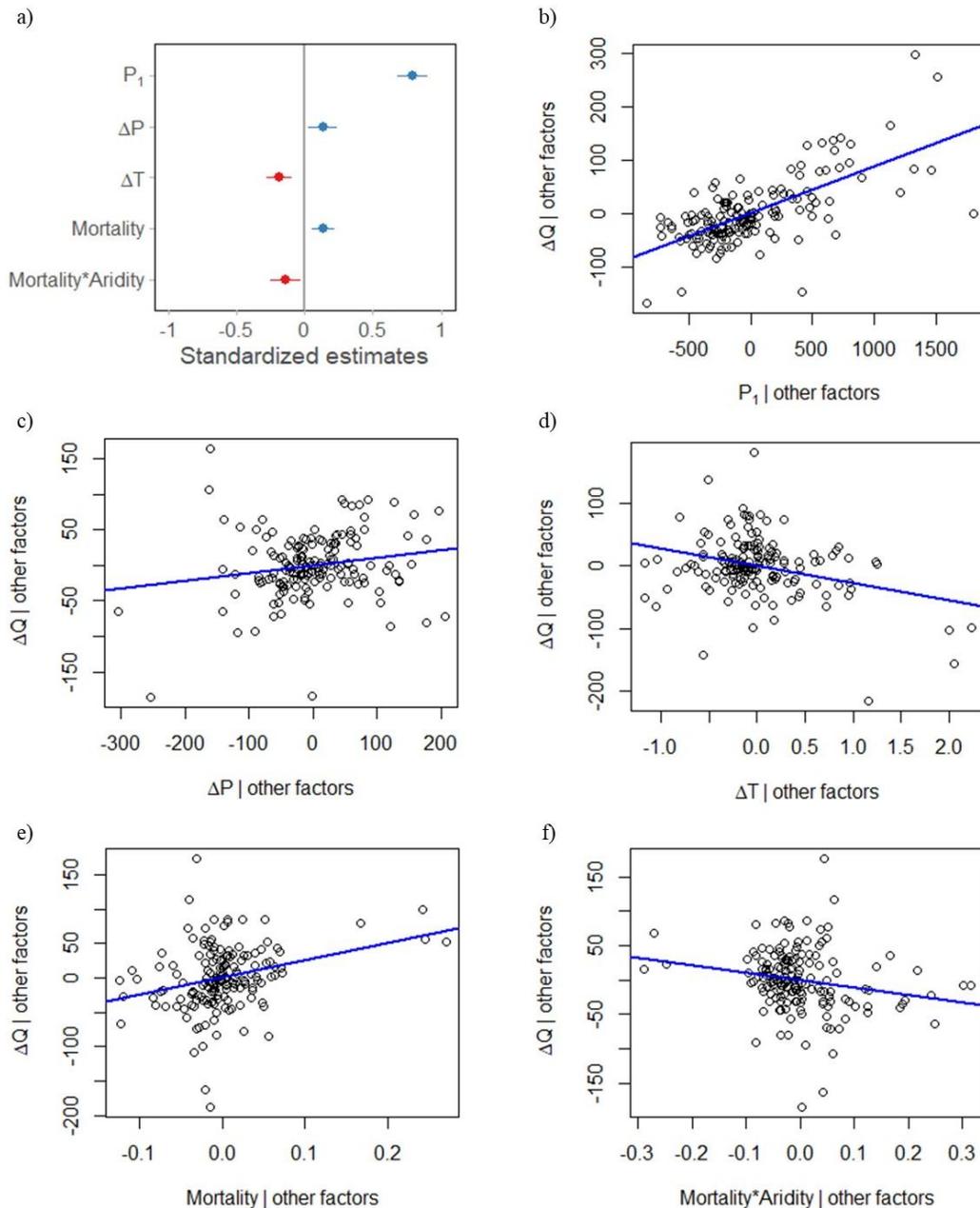
606 **Table 4. Regression coefficients, standard errors, t-statistics, and associated p-values for**

607 **multiple linear regression of ΔQ between 2000-2009 and 2010-2019.**

Variable	Units	Coefficient	Standard error	t-statistic	P-value
Intercept	mm/yr	-29.20	10.20	-2.860	0.005
\bar{P}_1	mm/yr	0.087	0.008	11.473	<0.001
ΔP	mm/yr	0.107	0.047	2.279	0.024
ΔT	°C	-27.85	6.895	-4.038	<0.001
Mortality	proportion	250.3	67.91	3.685	<0.001
Mortality*Aridity	proportion	-108.4	43.59	-2.488	0.014

608

609



610
611

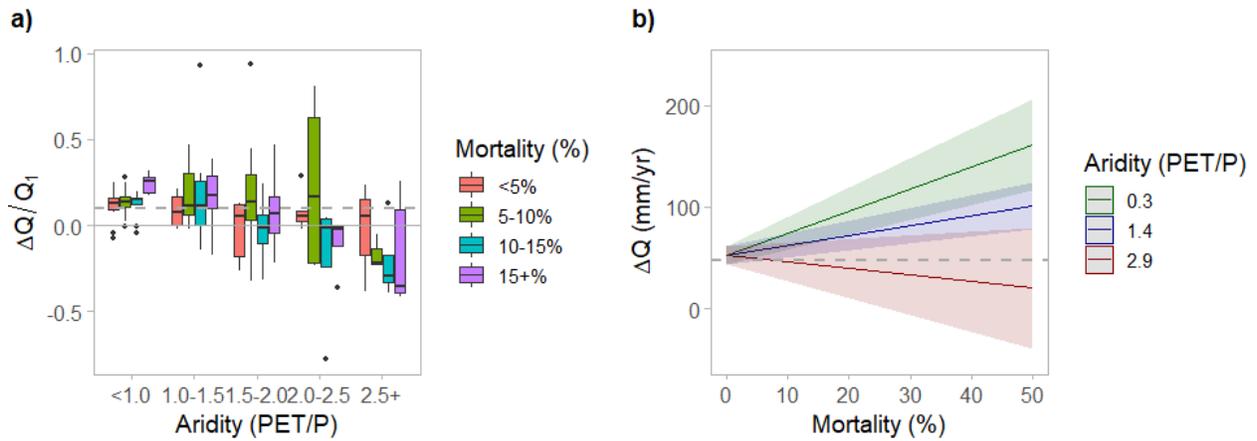
612 **Fig. 5. Effect of each variable on change in annual streamflow (ΔQ), in mm/yr, from 2000-**
 613 **2009 to 2010-2019: a) Unitless standardized coefficient estimates, which indicate the**
 614 **magnitude of change in ΔQ , in standard deviations, for a change equal to one standard**
 615 **deviation of each predictor variable. \bar{P}_1 =mean annual P for 2000-2009, ΔP =change in**
 616 **precipitation, and ΔT =change in temperature. b-f) Partial regression plots for each**
 617 **predictor variable. Each plot depicts the relationship between the named predictor and ΔQ**
 618 **while accounting for the explanatory capability of all other predictors. Values along the x**
 619 **axis of each plot represent the residuals of a model omitting the named variable, values**
 620 **along the y axis represent the residuals of a model of the named predictor as a function of**
 621 **all other predictors, and the slope of the line is equal to the multiple regression coefficient**
 622 **for the named variable.**

623

624 One purpose of this regression analysis was to test the hypothesis that runoff increases
625 following tree mortality, and as an alternative hypothesis, that the sign (positive or negative) of
626 runoff response to disturbance is affected by aridity. Our results provide partial support for both
627 hypotheses. As expected, the coefficient for tree mortality was positive (Table 4; Fig. 5a); the
628 statistical significance of this positive coefficient supports the first hypothesis that runoff
629 increases with decreased forest cover. However, the significant and negative coefficient for the
630 interaction of mortality and aridity also supports our alternative hypothesis that mortality does
631 not result in increased runoff in all cases. In particular, runoff response to disturbance may be
632 negative in very arid watersheds. Fig. 6a illustrates ΔQ as a function of mortality and aridity
633 based on observations (i.e., not modeled values), demonstrating two important results. First,
634 relatively wet watersheds (aridity < 1.5) generally had positive ΔQ , and ΔQ was larger for
635 watersheds with more tree mortality. Second, very dry watersheds (aridity > 2.5) generally
636 experienced negative ΔQ , and higher mortality was associated with larger decreases in Q . In
637 interpreting these results, it is important to note that overall ΔP was positive, which is expected
638 to contribute to positive ΔQ ; thus, the dashed line representing ΔP in Fig. 6a provides a more
639 neutral axis of reference than $\Delta Q = 0$.

640 Fig. 6b illustrates predictions and 90% prediction intervals for ΔQ as a function of tree
641 mortality for aridity at its observed 5th percentile, median, and 95th percentile, assuming that all
642 other variables are held constant at their mean observed values. The value of aridity at which tree
643 mortality was predicted to have a negative effect on Q was 2.35. Thus, for watersheds with
644 $PET/P \geq 2.35$, ΔQ decreased with tree mortality. Thus, in these very water-limited watersheds
645 there is an inverse relationship between ΔQ and tree mortality. Note that 95% of watersheds
646 experienced levels of tree mortality less than 33%, so predictions above this level of mortality
647 are beyond the range of most data and therefore uncertain.

648



649

650

651 **Fig. 6. Interacting effect of tree mortality and aridity on ΔQ (2000-2009 vs. 2010-2019).** a)
 652 **Boxplots of ΔQ (as a proportion of Q_1) based on observed values from 159 watersheds.** b)
 653 **Marginal effects of mortality and aridity, based on the multiple regression model (i.e.,**
 654 **values of ΔQ for different values of mortality and aridity when values of other predictors**
 655 **are held constant); values of aridity represent the 5th percentile (0.3), median (1.4), and**
 656 **95% percentile (2.9) of watersheds examined in this study. In both plots, horizontal dashed**
 657 **lines represent ΔP times P_1/Q_1 , (relative to Q_1 for 6a), which illustrates the expected ΔQ**
 658 **based solely on ΔP .**

659

660 *As shown in Eq. (4), the regression model accounted for changes in precipitation*
 661 *and temperature. The modeled relationship between mortality, aridity, and ΔQ*
 662 *(Fig. 6*

663 **Fig. 6b)** demonstrates the same variable response to disturbance as that shown by
 664 observations (Fig. 6a), illustrating that the response of ΔQ to disturbance and the interaction of
 665 disturbance with aridity is not explained by precipitation and temperature changes alone. Thus,
 666 decreased streamflow in response to increased temperature or decreased precipitation may be
 667 modulated (in wet watersheds) or exacerbated (in dry watersheds) by disturbance.

668 To assess the overall sensitivity of our modeled ΔQ to potential warming, we
 669 summarized ΔQ for several values of mortality and aridity, with and without 1° C of warming
 670 (Table 5) and with no change in precipitation. Specifically, equation 4 was applied with $\Delta P=0$
 671 and $\Delta T=0$ or 1. The model predicted a mean decrease in streamflow of 5.6% for 1° C of
 672 warming. Regression-based estimates for ΔQ at various levels of tree mortality and aridity
 673 generally suggest that streamflow is expected to increase at increasing levels of disturbance for

674 watersheds at low to moderate values of aridity, while the opposite is true in very arid
 675 watersheds, specifically with $PET/P > 2.35$, as manifested in the rightmost column of Table 5.
 676 Left to right in Table 5, the model indicates greater percentage increases in streamflow following
 677 disturbance in more humid watersheds, trending down to a decrease in streamflow for the most
 678 arid watersheds. For $1^\circ C$ of warming, the 5.6% decrease in streamflow is superimposed on these
 679 trends.

680

681 **Table 5. Predicted change in mean annual streamflow (expressed as a percentage of Q_1 , or**
 682 **initial mean Q) for different levels of tree mortality and aridity, with and without a $1^\circ C$**
 683 **temperature increase and assuming no change in precipitation.**

	Tree mortality	Aridity (PET/P)				
		0.30 (5th percentile)	0.77 (25th percentile)	1.44 (Median)	2.08 (75th quantile)	2.93 (95th percentile)
No warming	0%	0.0%	0.0%	0.0%	0.0%	0.0%
	10%	4.4%	3.4%	1.9%	0.5%	-1.3%
	25%	11.0%	8.5%	4.8%	1.3%	-3.4%
$1^\circ C$ warming	0%	-5.6%	-5.6%	-5.6%	-5.6%	-5.6%
	10%	-1.2%	-2.3%	-3.7%	-5.1%	-7.0%
	25%	5.4%	2.8%	-0.9%	-4.4%	-9.1%

684

685

686 4. Discussion

687

688 We found variable runoff response to forest disturbance using multiple analysis methods:
 689 Mann-Kendall trend analysis, time trend analysis of predicted vs. observed streamflow based on
 690 observed precipitation and temperature, and multiple regression using both climatic and
 691 disturbance variables. Collectively, our results confirm, via systematic broad-scale analysis, that
 692 the generally held hypothesis that forest cover and streamflow are inversely related is not
 693 universal in semi-arid western watersheds. Examination of the relationship between Mann-
 694 Kendall trend in Q/P versus net tree growth allowed us to identify two scenarios that do not
 695 conform to this relationship (Fig. 3). First, statistically significant decreases in Q/P occurred
 696 during a period of forest cover loss in a small number of watersheds (four) that occur in areas of
 697 high aridity (PET/P) and high incoming solar radiation. Second, 10 watersheds exhibited
 698 statistically significant increases in Q/P during a period of forest cover growth. Time trend
 699 analysis indicated that among watersheds with significant changes in streamflow, 77% (20 of 26)

700 of disturbed watersheds, and only 56% (10 of 18) undisturbed watersheds, experienced decreased
701 streamflow. Thus, significantly decreased streamflow was more prevalent in disturbed than
702 undisturbed watersheds, counter to commonly held expectations. Increased streamflow in 44% (8
703 of 18) of undisturbed watersheds coincided with higher precipitation overall in 2010-2019
704 compared to 2000-2009. Multiple regression analysis showed that mortality explains some
705 variability in ΔQ that is not explained by climatic drivers, and that the direction of streamflow
706 response to mortality (i.e., increase vs. decrease) is affected by aridity.

707 Among our analysis methods, only the multiple regression quantitatively assessed change
708 in streamflow as a function of both climatic and disturbance variables in a way that allowed
709 isolating and quantifying climate and disturbance effects. Therefore, the finding that disturbance
710 severity (i.e., magnitude of tree mortality) is a significant predictor with a positive coefficient
711 supports the overarching hypothesis that streamflow increases as a result of disturbance, and that
712 disturbance effects on streamflow are separable from climate effects. However, the interaction of
713 mortality and aridity had a negative coefficient, which signifies a decrease in streamflow as a
714 result of disturbance in very arid watersheds. Observational data (Fig. 6a) as well as our multiple
715 regression results (Fig. 6b) provide quantitative evidence that disturbances at high aridity are
716 more likely to result in decreased streamflow than those at lower aridity. These findings are
717 consistent with a recent modeling study (Ren et al., 2021), which concluded that of runoff
718 responds variably to forest disturbance caused by mountain pine beetle, that the response
719 depends on both mortality level and aridity, and that drier years tend toward decreased post-
720 disturbance streamflow. In that study, the inflection from increased to decreased runoff occurred
721 between aridity values of 2.0 and 3.0, or in wetter areas with mortality levels less than 40%, and
722 decreased runoff was explained by either increased canopy evapotranspiration or increased
723 ground transpiration following disturbance (Ren et al., 2021).

724 Independent of forest cover changes, we observed decreased streamflow associated with
725 increased T and PET. Our multiple regression model predicted a mean decrease in streamflow of
726 5.6% for 1° C of warming, which is consistent with the 6% reduction per degree C that is
727 predicted for the entire Colorado River Basin (Udall and Overpeck, 2017) and 6-7% reductions
728 per degree that are predicted for the Upper Colorado River Basin (McCabe et al., 2017; Udall
729 and Overpeck, 2017). Our study period, 2000-2019, coincides with the onset of above-average
730 temperatures in the Colorado River Basin that began in 2000 and contributed to below-average

731 streamflow (Udall and Overpeck, 2017). Although this trend has been previously documented in
732 western US watersheds (Brunner et al., 2020; Udall and Overpeck, 2017), the time trend and
733 multiple regression analyses presented here disentangle climate from vegetation effects and offer
734 a refined understanding of the role of forest change effects on streamflow in these trends.

735 Increasing T and PET are driving not only decreases in streamflow in many western
736 watersheds (Brunner et al., 2020; Udall and Overpeck, 2017) but also increases in tree mortality
737 (Williams et al., 2013). Our analysis of trend in Q/P relative to net tree growth, and our
738 regression model of ΔQ as a function of tree mortality, show relatively high forest disturbance in
739 watersheds with high aridity and solar radiation (Fig. 3c-d). Higher T and PET may affect
740 streamflow both directly, via increased evaporative demand, and indirectly via vegetation-
741 mediated effects such as replacement of trees with vegetation that may actually have higher total
742 evapotranspiration (Bennett et al., 2018; Guardiola-Claramonte et al., 2011; Morillas et al.,
743 2017). Additionally, increases in T and PET that result in increased soil evaporation can increase
744 vegetation moisture stress and susceptibility to disturbance such as wildfire (Groisman et al.,
745 2004).

746 Possible mechanisms for nonconforming decreases in runoff in watersheds with
747 decreased forest cover (i.e., lower left quadrant in Fig. 3a) may be a combination of increased
748 transpiration by surviving or newly established vegetation, as well as increased solar radiation
749 reaching snowpack and soil surfaces, either of which may increase total evapotranspiration. The
750 first mechanism, net increase in evapotranspiration due to increased total transpiration, has been
751 observed following insect outbreaks with rapid growth of surviving trees (Biederman et al.,
752 2014), simulated tree die-off that resulted in increased herbaceous transpiration (Guardiola-
753 Claramonte et al., 2011), and replacement of trees with dense shrubs (Bennett et al., 2018); all
754 three of these studies were conducted in semiarid to arid watersheds. Further, short-term
755 streamflow response may contradict longer-term response as young trees grow rapidly during
756 forest recovery (Perry and Jones, 2017) in a phenomenon known as the Kuczera effect (Kuczera,
757 1987), and the use of net growth as a disturbance metric can quantify the extent to which post-
758 disturbance regrowth may produce this effect. The second mechanism, increased solar radiation
759 as a result of canopy loss, could result in earlier snowpack ablation (Lundquist et al., 2013)
760 driven by increased sublimation (Biederman et al., 2014) and increased evapotranspiration from
761 soil and non-canopy vegetation (Morillas et al., 2017; Reed et al., 2018). Changes to post-

762 disturbance energy budgets have been observed following multiple disturbance types and
763 severities (Cooper et al., 2017; Maness et al., 2013). Just as net increases in evapotranspiration
764 can occur following forest disturbance and lead to decreased streamflow, the converse is that net
765 decreases in evapotranspiration can occur during periods of forest cover growth and thus lead to
766 increased streamflow (i.e., upper right quadrant in Fig. 3a). Independently of forest disturbance
767 or growth, an additional contributing factor to decreased runoff may be a long-term decline in
768 deep soil moisture due to recent droughts (Iroumé et al., 2021; Peterson et al., 2021; Williams et
769 al., 2020).

770 Another potential confounding effect is the type of winter precipitation (rain vs snow). In
771 this study, we accounted for precipitation and temperature at annual and not seasonal time scales;
772 neither the regression model used for time trend analysis nor the multiple regression model for
773 ΔQ improved appreciably when seasonal rather than annual timescales were tested. Previous
774 work has observed both streamflow increases (Hammond and Kampf, 2020) and decreases
775 (Berghuijs et al., 2014) in response to winter precipitation phase (snow to rain) shifts. Warmer
776 temperatures have been observed to result in decreased streamflow in watersheds with high snow
777 fraction, i.e., >0.15 , although the causal mechanism for this observation is unknown (Berghuijs
778 et al., 2014). In contrast, Hammond and Kampf (2020) observed both increased and decreased
779 streamflow following shifts from snow to mixed rain and snow. Streamflow response to snow-to-
780 rain transitions appear to be more strongly associated with the seasonal timing, particularly
781 relative to the seasonal timing of maximum annual evapotranspiration, than the type of
782 precipitation (de Lavenne and Andréassian, 2018; Knighton et al., 2020; Robles et al., 2021). In
783 our study, increasing trends in Q/P and simultaneous increases in tree growth occurred in a wide
784 variety of environments (Fig. 3e), including the temperate Pacific Northwest, where snow
785 fraction may be less than 0.15, as well as high-elevation forested watersheds across the western
786 US where winter precipitation phase change may translate to more rain-on-snow events that
787 produce rapid winter runoff. Because seasonal snowpack represents storage of water that
788 becomes available for transpiration by plants during the growing season, seasonal asynchrony
789 between water availability and the growing season may dampen any relationship between forest
790 cover changes and streamflow response (Knighton et al., 2020).

791 Results of our time trend analysis demonstrate that streamflow has deviated from
792 predictions based on precipitation and temperature at many watersheds across the western US,

793 regardless of forest disturbance (Table 3). An assumption of time trend analysis is that any
794 change not predicted by factors included in the model, typically precipitation and temperature, is
795 due to factors not included in the model, typically vegetation (i.e., land cover) change or land use
796 change (Zhao et al., 2010). However, time trend analysis provides observational but not causal
797 links of change in streamflow to factors such as vegetation change. Incongruities between the
798 subset of watersheds that were disturbed and those with significant streamflow change (Table 3)
799 call into question the underlying premise of time trend analysis that deviations of observed from
800 predicted streamflow are due to vegetation change alone (Zhao et al., 2010). In our exploration
801 of whether changes in streamflow were correlated with changes in T and PET over longer time
802 periods, we found that although T and PET increased in most watersheds, increases in T and PET
803 were not strongly correlated with changes in streamflow or runoff ratio. Given that Mann-
804 Kendall trend tests detected significant increases in T and PET for 1980-2019 that were not
805 detectable during the period covered by our time trend analysis (2000-2019), it is possible that
806 model coefficients for T over multiple decades may not remain constant as temperature increases
807 beyond the range of observed T during 2000-2009. In other words, the assumptions inherent in
808 time trend analysis may not hold in a nonstationary climate as changes may go beyond ranges for
809 which the model was calibrated. Other possible explanations for significant changes in
810 streamflow include shifts in winter precipitation phase (from snow to rain), the timing of
811 seasonal precipitation, longer term increases in T and PET that are occurring beyond the
812 timeframe considered in this analysis, seasonal T and precipitation extremes that are not reflected
813 in annual mean values, and/or forest disturbance below the threshold considered in our analysis.

814 A caveat of this study is that we characterized disturbance across entire watersheds, when
815 in reality, disturbance is typically patchy and may include a combination of stand-replacing and
816 nonstand-replacing disturbances. For example, less severe disturbance may be uniformly
817 distributed throughout a watershed whereas more intense disturbances that may affect only small
818 portions of a watershed, where both scenarios would lead to comparable watershed-scale metrics
819 of forest cover loss or tree mortality. Previous studies illustrated that forest structure affects
820 snowpack (Broxton et al., 2016; Moeser et al., 2020), so this distinction may be important for
821 determining disturbance effects on runoff. The ability to project future changes in streamflow
822 due to both changing climate and forest disturbance will likely improve with enhanced spatial
823 representation of forest characteristics.

824 Several challenges exist in combining observational datasets from different disciplines
825 and using different temporal and spatial sampling frames, and here we describe some of those
826 challenges and potential future solutions. First, the analyses conducted in this study required
827 using forest inventory data collected across multiple years rather than an annual time step. It is
828 not currently possible to produce estimates of the FIA attributes used in this analysis at an annual
829 time step at the scale of individual watersheds, and this constraint undoubtedly dampens
830 observed hydrologic response to acute, episodic disturbances such as severe wildfire. Ongoing
831 work in the area of statistical small area estimation (Coulston et al., 2021; Hou et al., 2021)
832 demonstrates promising capabilities for characterizing forest attributes at finer spatial and
833 temporal scales. Combining FIA-based estimates with other datasets, e.g., the Monitoring Trends
834 in Burn Severity (MTBS) dataset that delineates large wildfires by severity class (Eidenshink et
835 al., 2007), could illuminate how specific disturbances may have unique or compounding effects
836 on streamflow and snowpack. Application of such techniques to future investigations will require
837 identification of appropriate lag effects and legacy effects (e.g., response to recovery from severe
838 disturbance versus persistent response to the initial severe disturbance).

839 Second, most CAMELS watersheds are smaller than the encompassing HUC8 watersheds
840 that we used to summarize forest data, although we found that forest change metrics from the
841 National Land Cover Database (Homer et al., 2020) were statistically similar at the two scales.
842 Compatibility of these datasets could be improved by combining ground observations from forest
843 monitoring plots with remote sensing and other ancillary data, e.g., via the small area estimation
844 techniques described above. Ongoing extension of the period of record and improved precision
845 in estimates for individual watersheds will enhance our ability to relate forest characteristics and
846 dynamics to changes in hydrologic processes and flux magnitudes. In particular, improved
847 precision of future monitoring may help quantify important relationships among modulating
848 factors such as aridity and incoming solar radiation.

849 Correlation is not causation, and therefore we cannot be sure that any observed changes
850 in streamflow are due to forest disturbance or the lack thereof. Our results, which are based on
851 observations across many watersheds, underscore the need for process-based modeling to
852 understand where, why, and to what degree unexpected streamflow responses may occur as a
853 result of the combined effects of forest change and climate change. Although there may indeed
854 be forest disturbance effects on streamflow, hydrologic responses may be modulated, offset, or

855 intensified by factors such as aridity and incoming solar radiation and by changes in forcing such
856 as increasing temperature.

857

858 **5. Conclusions**

859

860 We used a large-sample hydrology approach to combine hydrologic, climatic, and forest
861 data within 159 watersheds in the western US to assess evidence for the hypothesis that forest
862 cover loss leads to increased streamflow. This study expanded on previous studies that have
863 linked streamflow to climatic drivers by also considering quantitative forest disturbance
864 information, which allowed us to disentangle climate effects from forest disturbance effects on
865 streamflow. Multiple analysis methods – including simple trend analysis, time trend analysis
866 accounting for climate variables, and multiple regression – demonstrated that streamflow in
867 some disturbed watersheds was lower than expected based on climatic drivers (i.e., P and T)
868 alone. Results of both observations and multiple regression modeling showed that streamflow
869 response to disturbance was modulated by aridity. Although disturbed watersheds exhibited
870 increased streamflow at low to intermediate aridity, which is consistent with the hypothesis that
871 reduced forest cover produces increased water yield, we found that disturbance in very arid
872 watersheds (aridity>2.35) was associated with streamflow. Disturbance was also more prevalent
873 in watersheds with high solar radiation and high aridity, the very watersheds that are more likely
874 to be vulnerable to decreased streamflow following disturbance. These results suggest that very
875 arid watersheds may be more susceptible to both increased forest disturbance and decreased
876 streamflow in the future.

877

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889

890 **Data and code availability statement**

891 In an effort to make this study reproducible, the data and computational scripts used to produce
892 the study results have been made publicly available in HydroShare (Goeking and Tarboton,
893 2021).

894

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Figure 1.

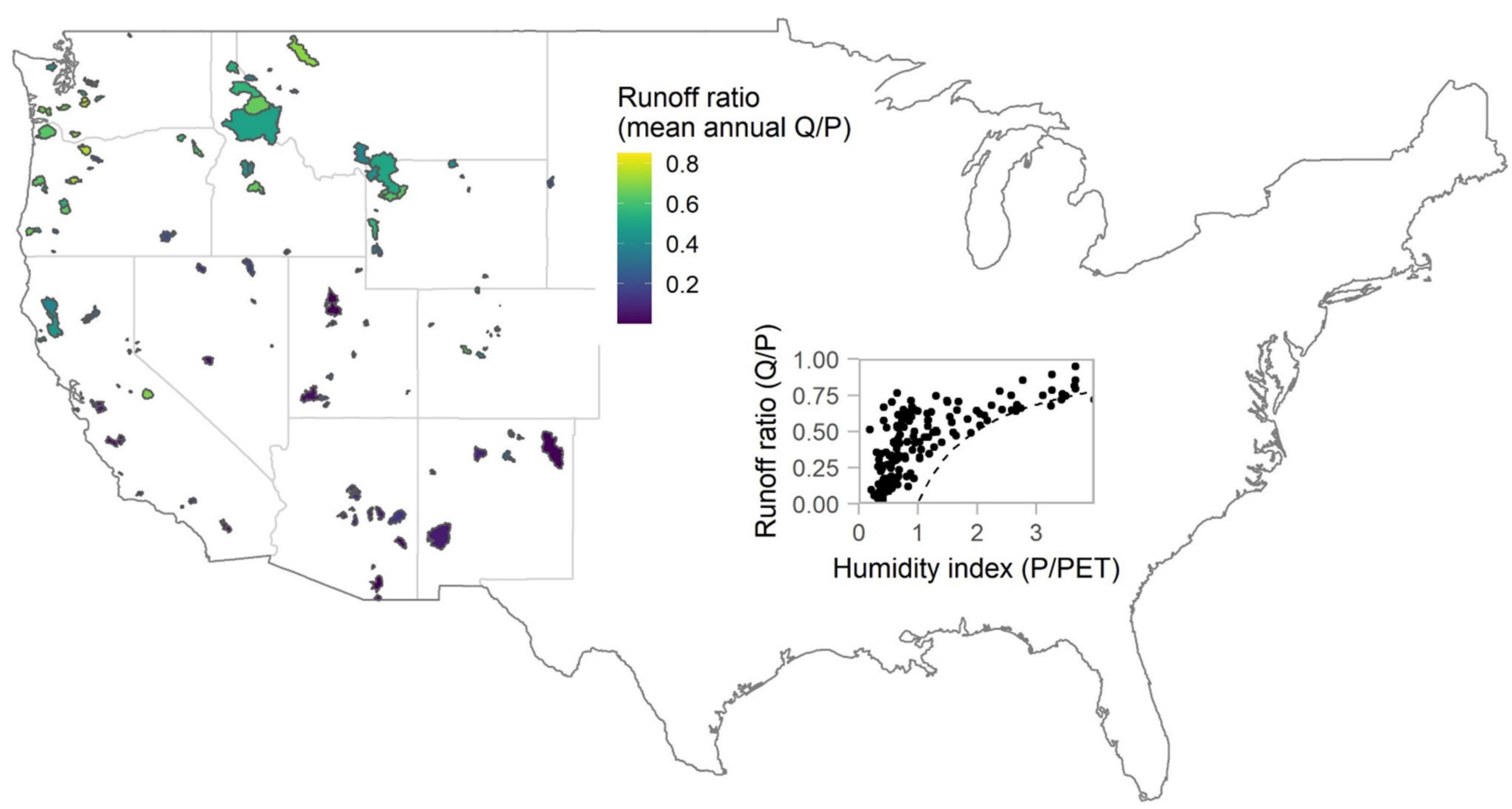
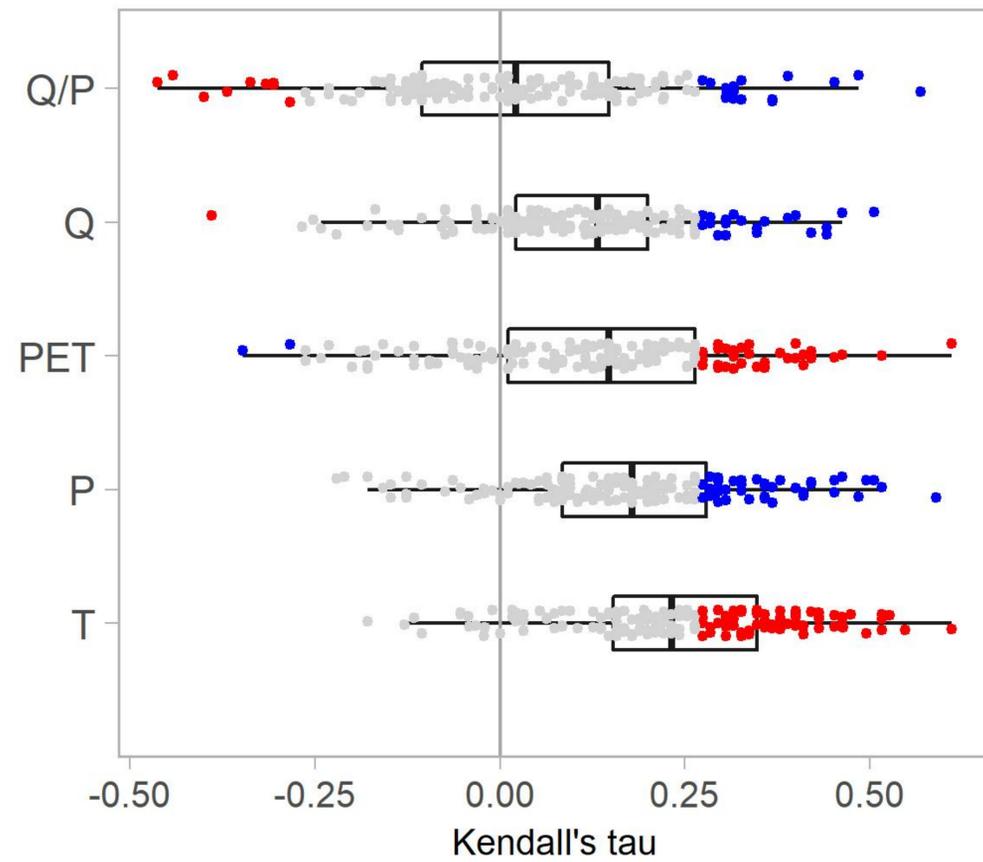


Figure 2.

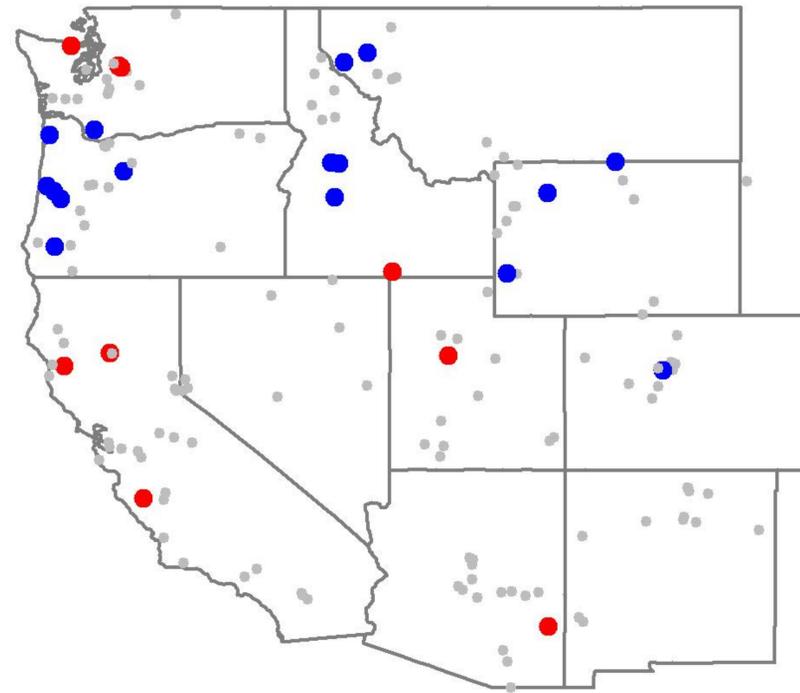
a) Trend test

• drier • none • wetter



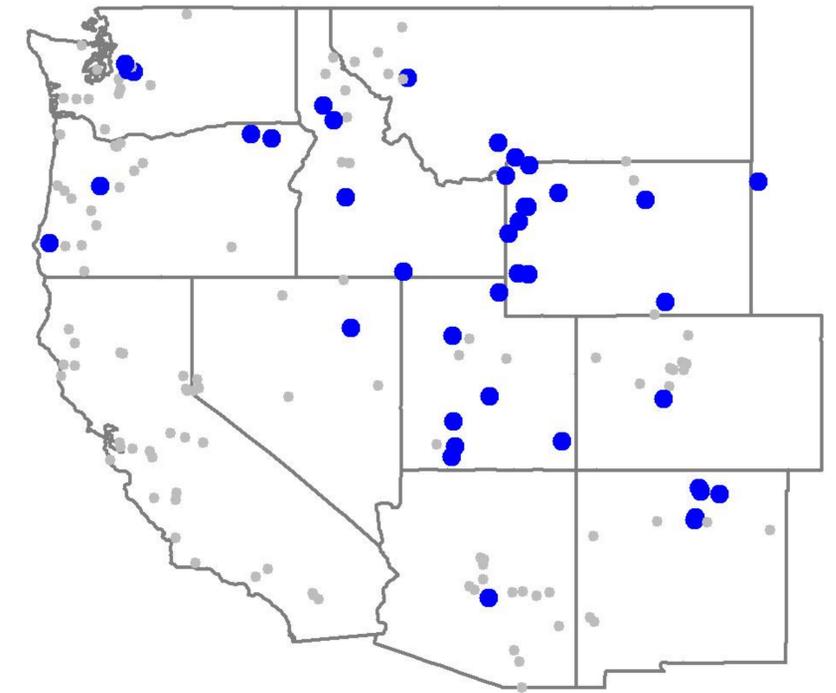
b) Q/P

• decrease • none • increase



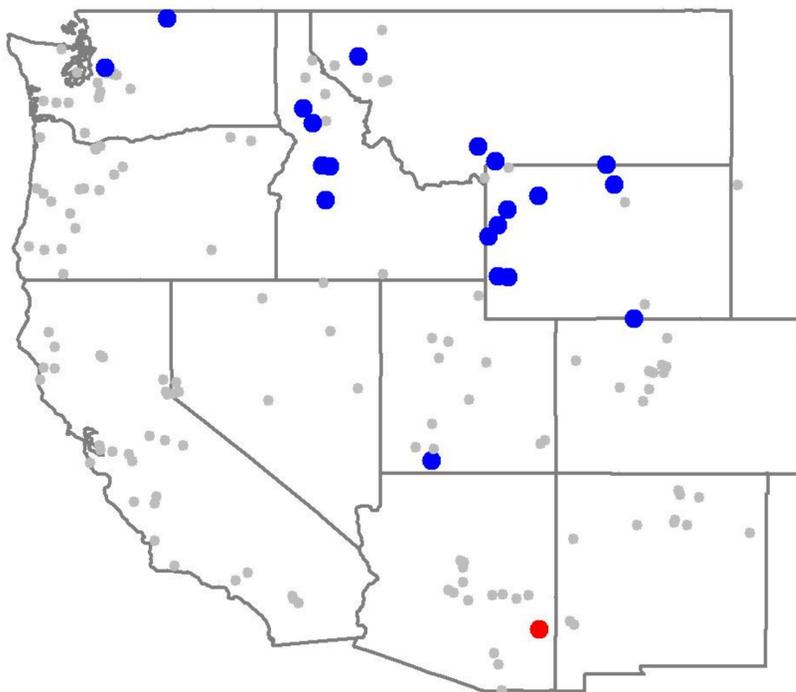
c) P

• none • increase



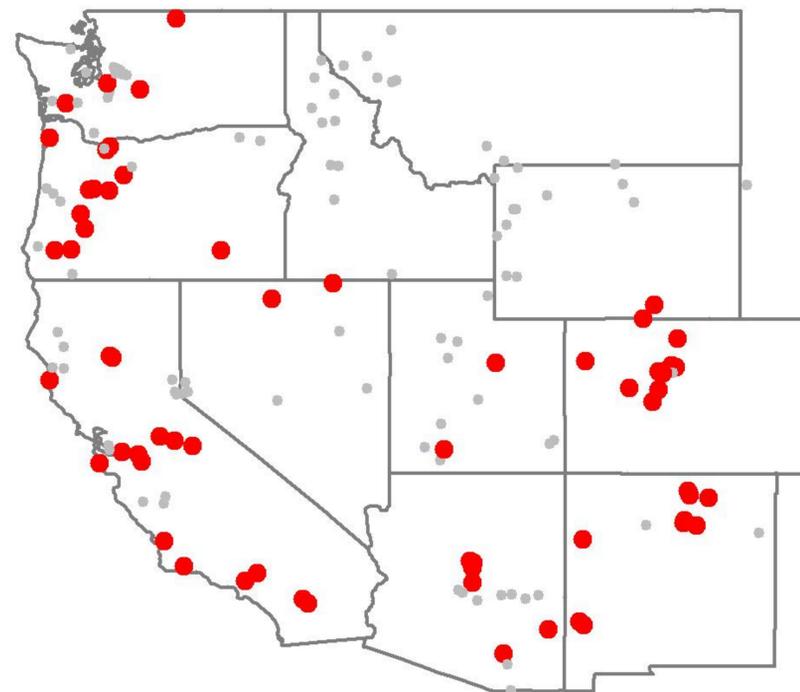
d) Q

• decrease • none • increase



e) T

• increase • none



f) PET

• increase • none • decrease

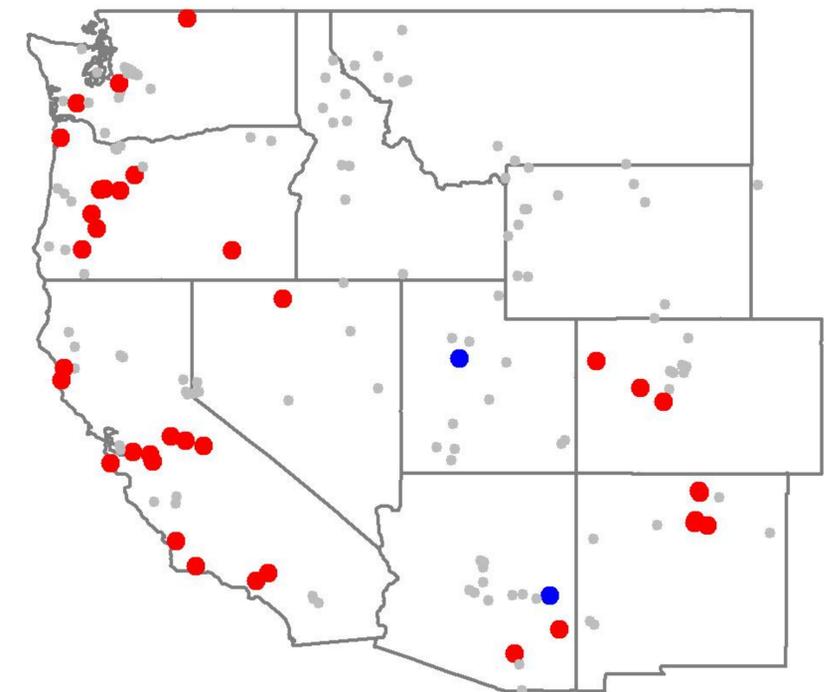
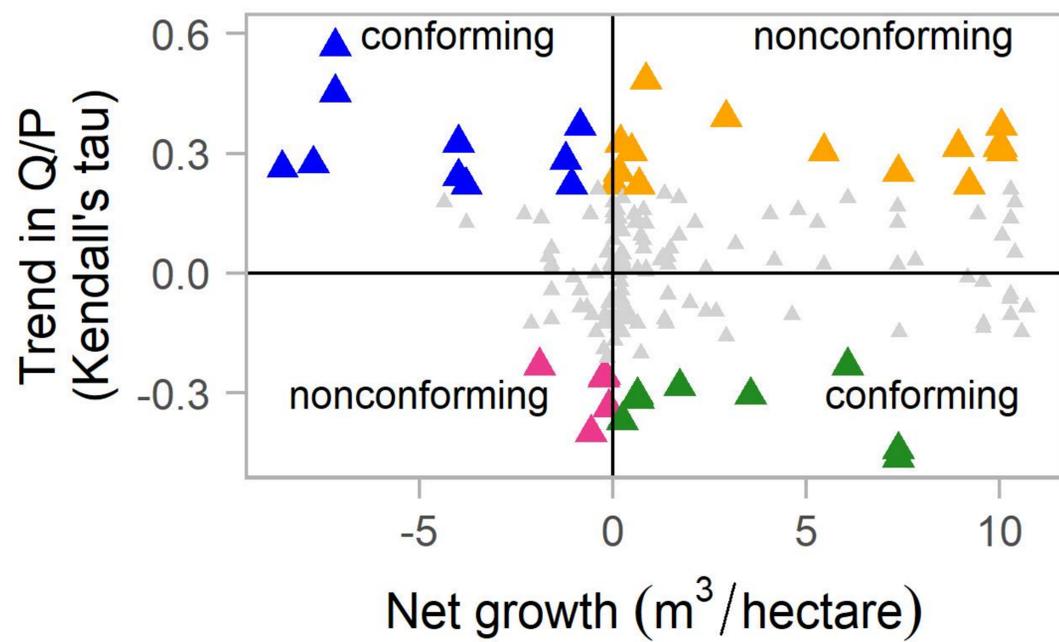
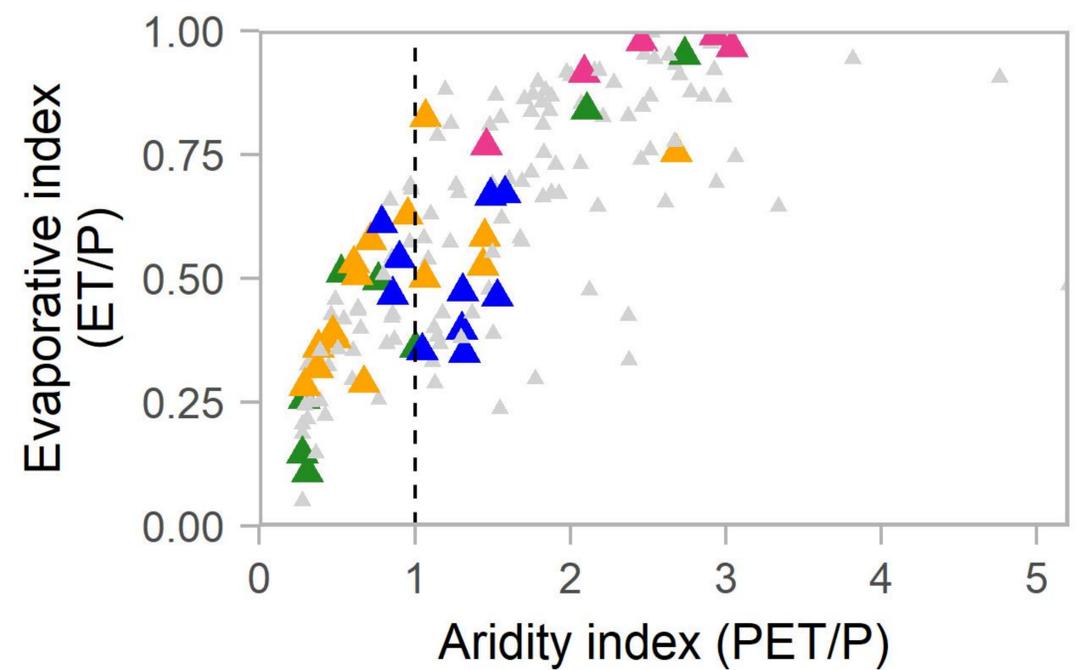


Figure 3.

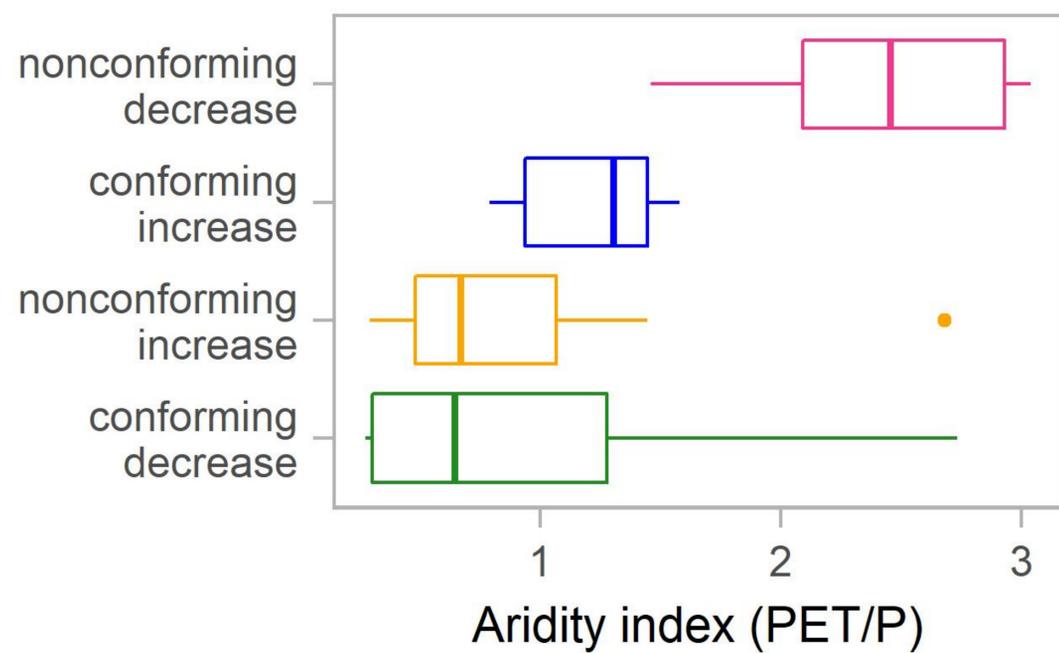
a)



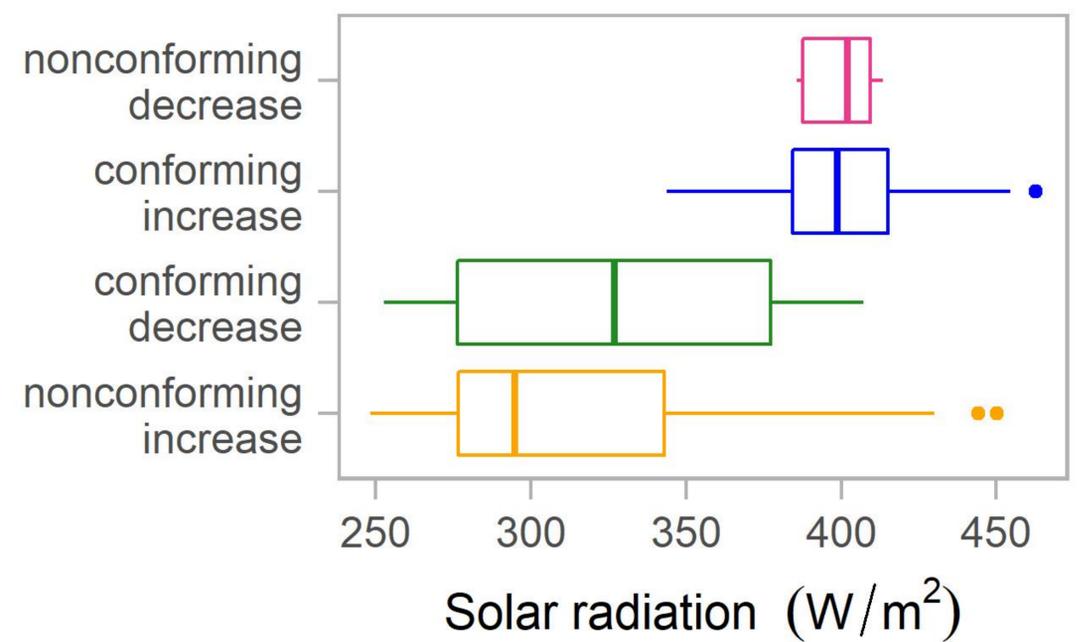
b)



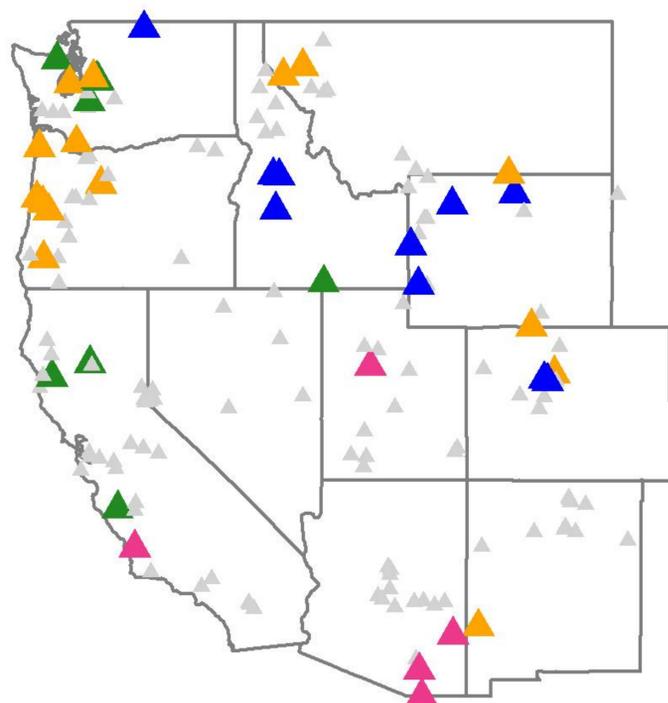
c)



d)



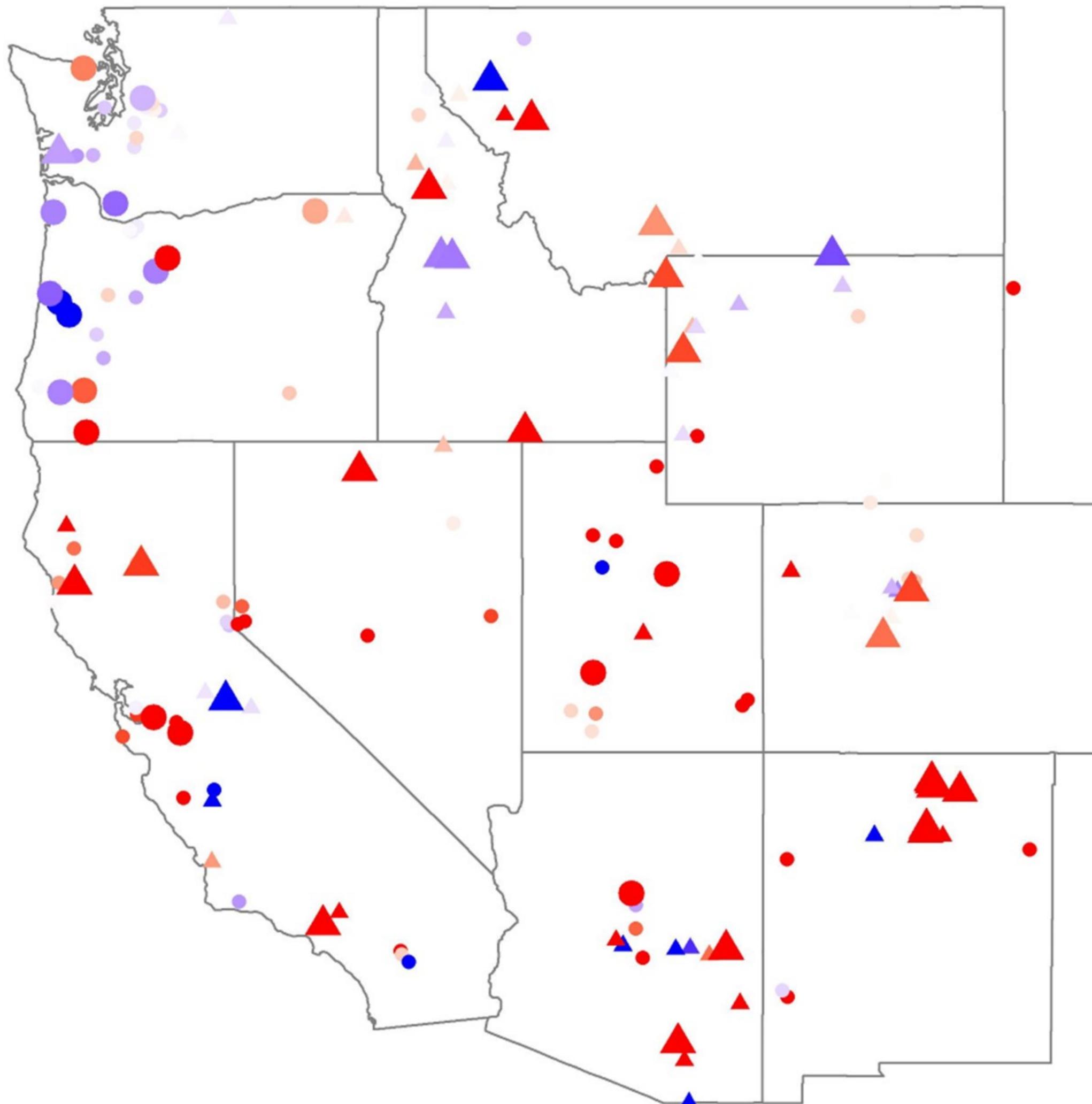
e)



Change in Q/P

- ▲ conforming decrease
- ▲ conforming increase
- ▲ no significant trend
- ▲ nonconforming decrease
- ▲ nonconforming increase

Figure 4.



Disturbance status

- ▲ Disturbed
- Undisturbed

Deviation in observed vs. predicted Q (%)

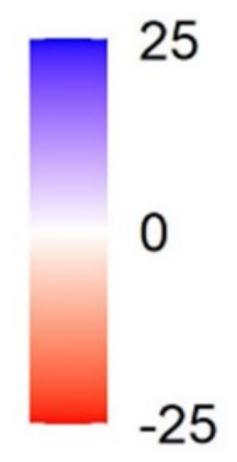
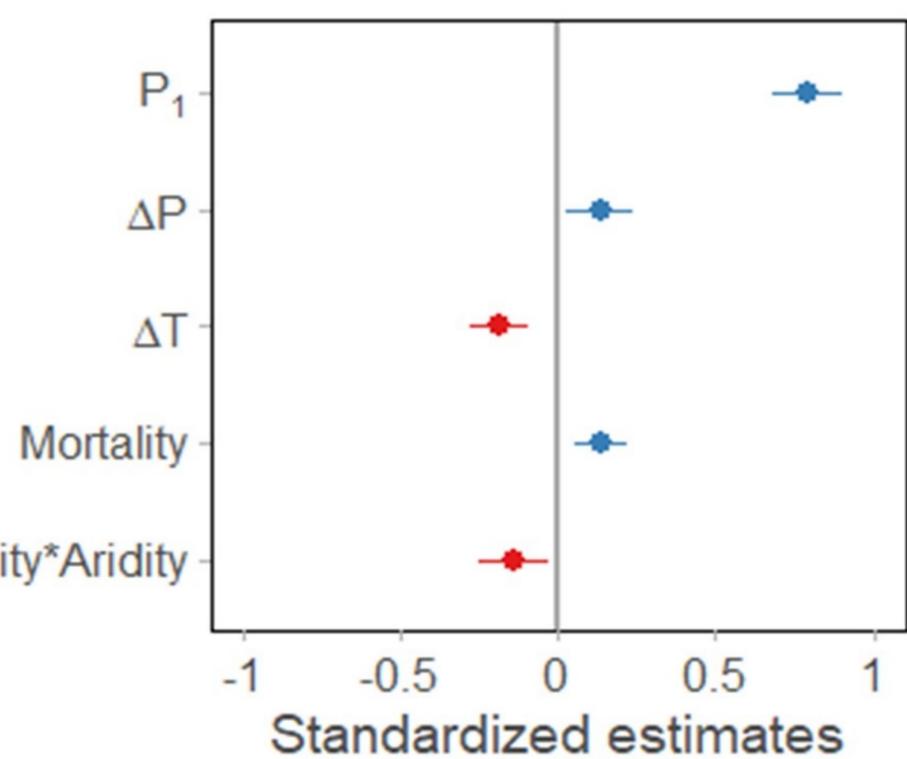
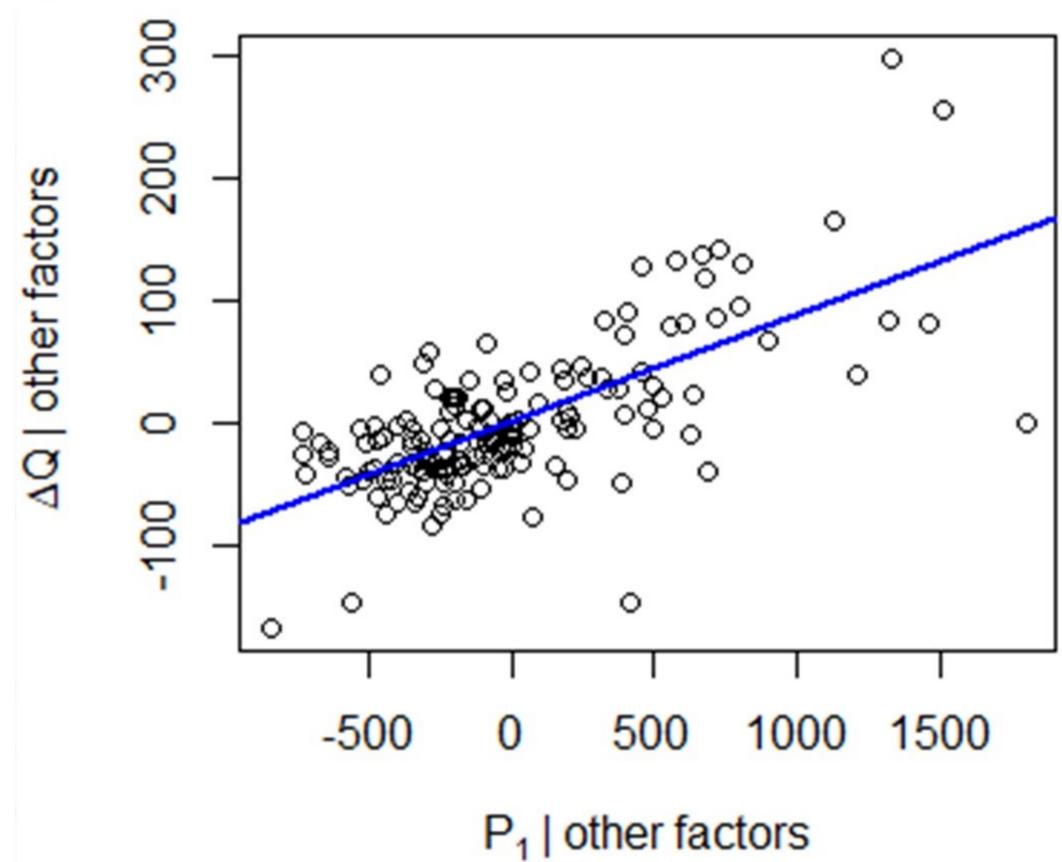


Figure 5.

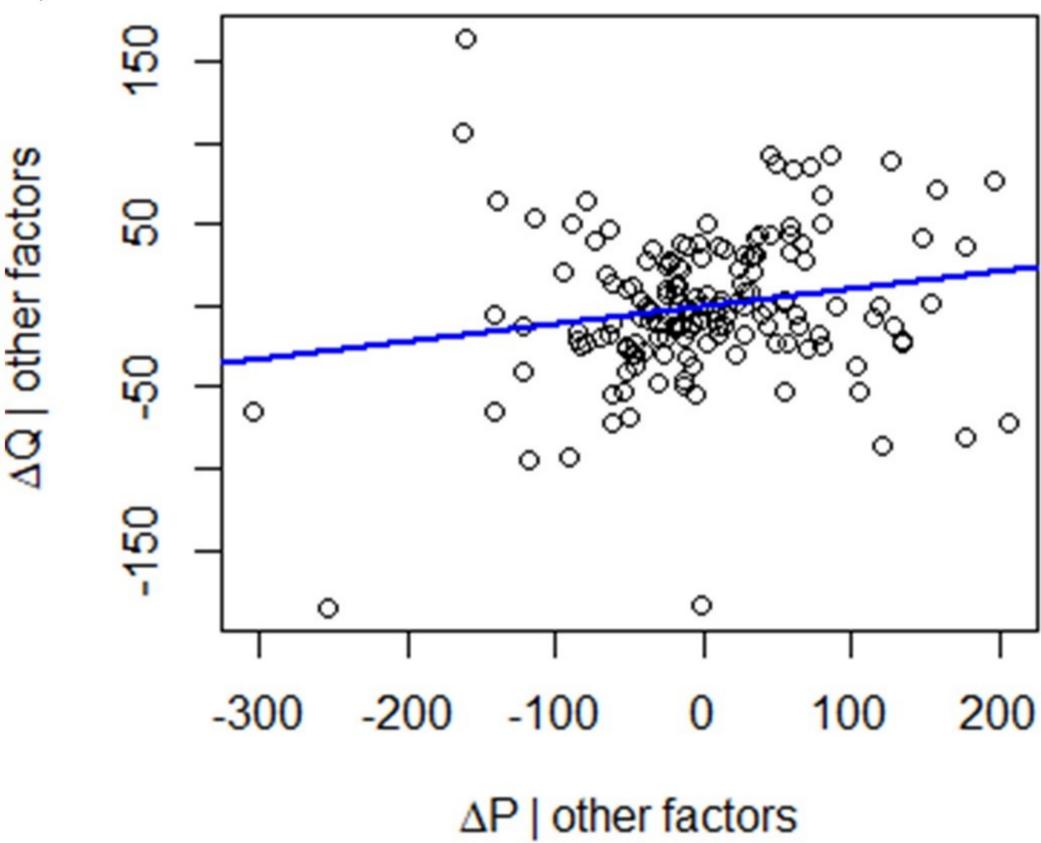
a)



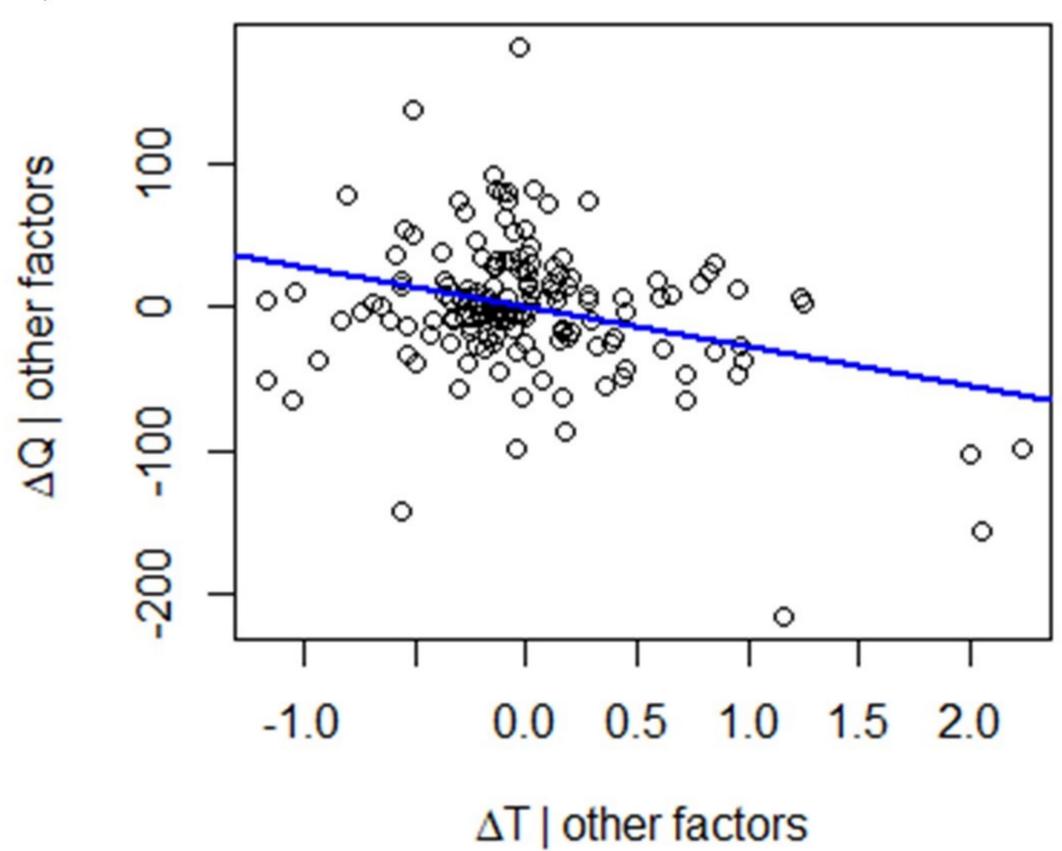
b)



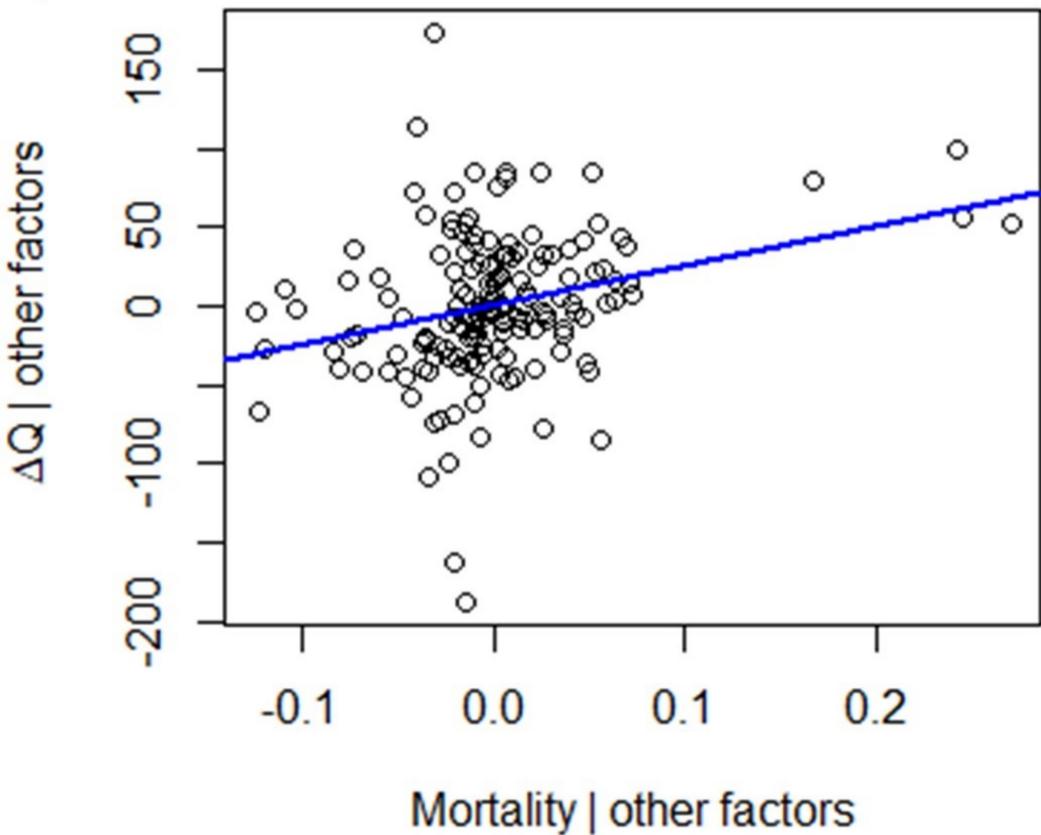
c)



d)



e)



f)

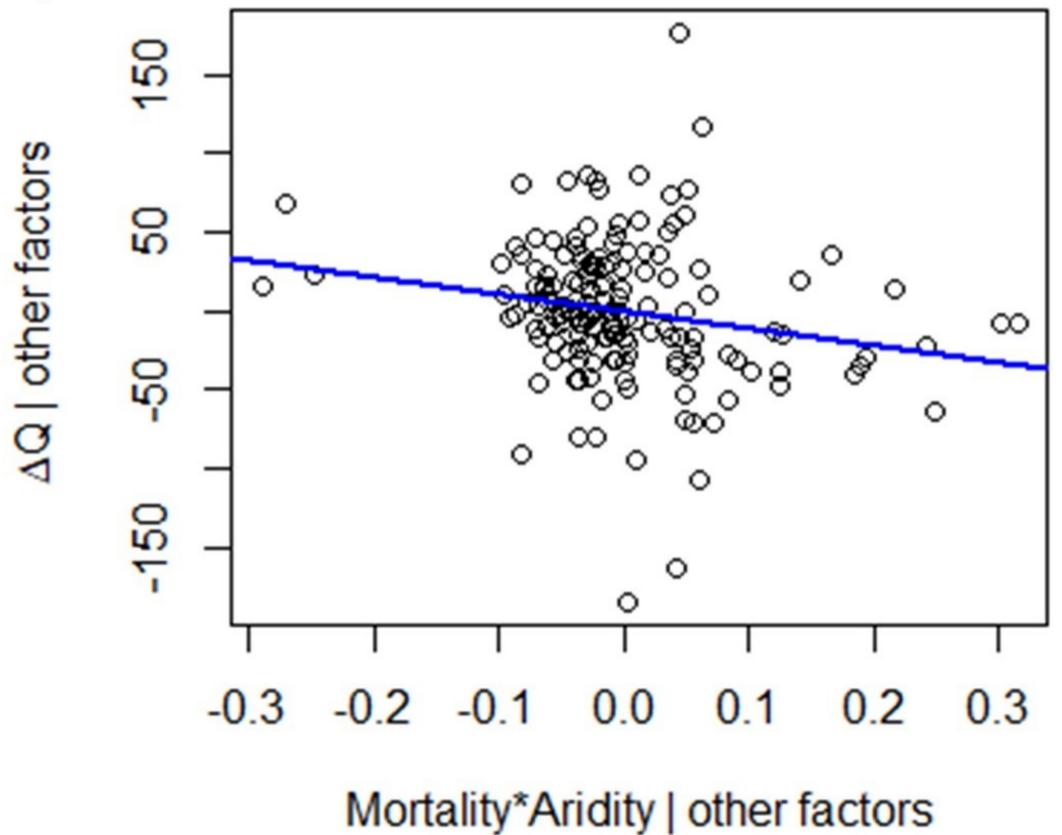
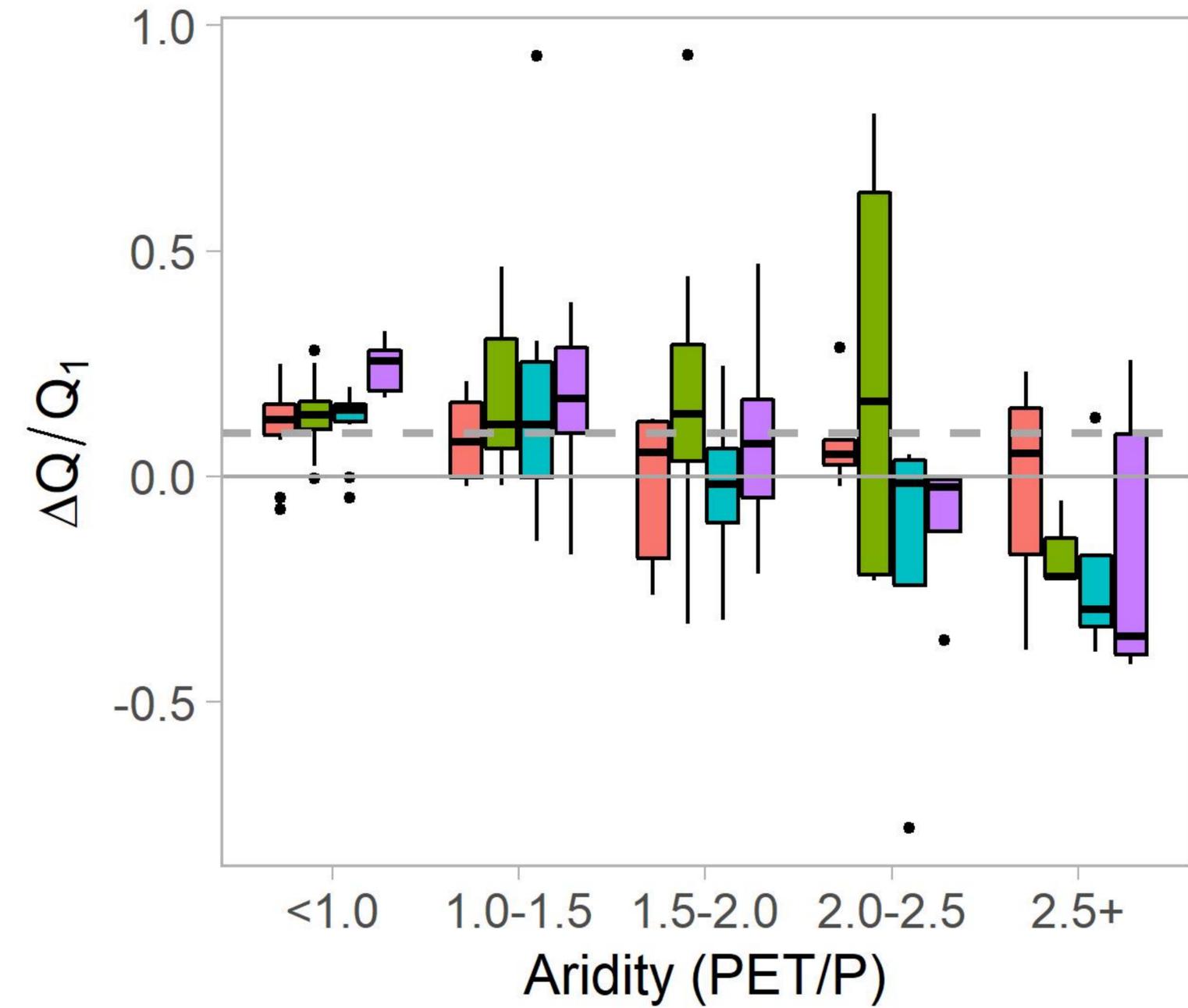


Figure 6.

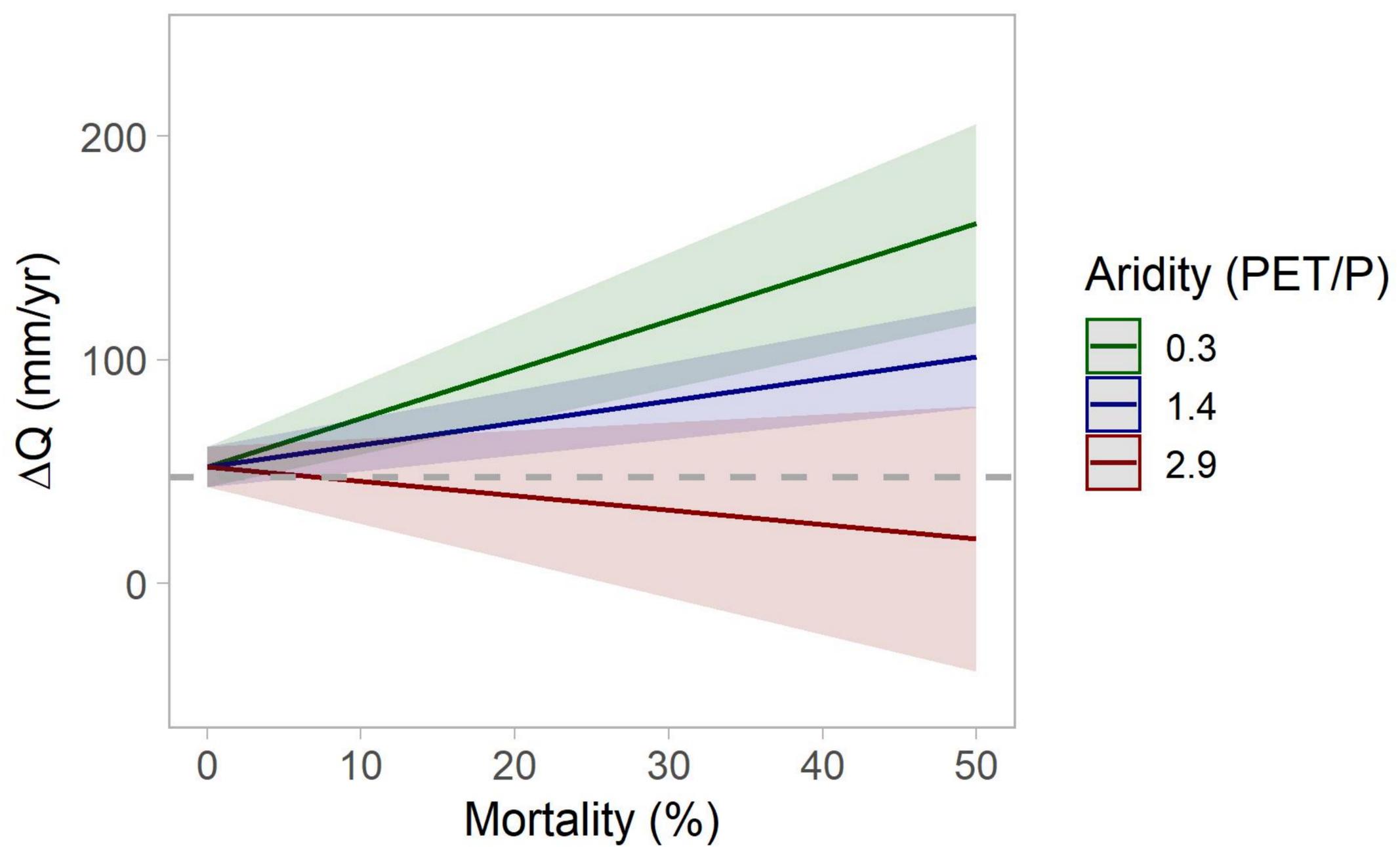
a)



Mortality (%)

- ▭ <5%
- ▭ 5-10%
- ▭ 10-15%
- ▭ 15+%

b)



Aridity (PET/P)

- 0.3
- 1.4
- 2.9