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3 **Article type:** Letter

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5 **Despite a century of warming, increased snowfall has buffered the ice phenology of**
6 **North America's largest high-elevation lake against climate change**

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8 **Running head:** Yellowstone Lake ice phenology

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33 **Author contributions:** LMT, GG, KC, AH, and PF organized the data set and performed
34 exploratory analyses. IAO led the modeling with input from LMT, DLP, and SH. IAO, GG, and
35 SH made the figures with input from LMT and DLP. IAO, DLP, and SH wrote the manuscript
36 with input from LMT and all authors. All authors read and approved the article for submission.

37 **Scientific significance statement:**

38 Climate change is dramatically altering aquatic ecosystems. For lakes in cold climates, one of
39 the most significant climate impacts is altered ice phenology—the timing and duration of ice
40 cover during winter. Under climate change, most lakes are freezing later, melting out earlier,
41 and experiencing a shorter duration of ice cover. Exceptions to this rule are particularly
42 interesting as they shed light on the factors that promote lake resiliency against change. Using a
43 96-year record, we show that the ice phenology of Yellowstone Lake, North America’s largest
44 high-elevation lake, has not changed despite considerable warming in the region due to the
45 buffering effect of increased snowfall. Yet, climate projections suggest that this buffering may
46 soon fade with far-reaching implications for ecosystem function and biodiversity.

47
48 **Data availability statement:** All data sets and code used for this study are available on GitHub:
49 https://github.com/bellaoleksy/NC_YSL_Ice_Phenology

50
51 **Abstract:**

52 Lakes are sentinels of environmental change. In cold climates, lake ice phenology—the timing
53 and duration of ice cover during winter—is a key control on ecosystem function. Ice phenology is
54 driven by a complex interplay between physical characteristics and climatic conditions. Under
55 climate change, lakes are generally freezing later, melting out earlier, and experiencing a
56 shorter duration of ice cover; however, few long-term records exist for large, high-elevation
57 lakes which may be particularly susceptible to climate impacts. Here, we quantified ice
58 phenology over the last century (1927-2022) for North America’s largest high-elevation lake—
59 Yellowstone Lake. We linked ice phenology to precipitation and temperature, and show that
60 while air temperatures have risen, no change in the timing nor duration of ice cover has
61 occurred due to buffering by increased snowfall. Our findings paired with climate projections
62 suggest that Yellowstone Lake may be on the precipice of change with far-reaching
63 implications.

64
65 **Keywords:** Yellowstone Lake, climate change, Greater Yellowstone Ecosystem, winter
66 limnology

67
68 **Introduction:**

69 Lakes are sentinels of environmental change as they accumulate and reflect changes to local
70 and regional watersheds through time (Adrian et al. 2009; Moser et al. 2019). Most lakes are
71 located at temperate to arctic latitudes in the Northern Hemisphere (Verpoorter et al. 2014) and
72 experience strong seasonal phenology as they annually transition from open water to a frozen
73 surface. Ice phenology has been recorded on a wide range of lakes around the world and shifts
74 in ice duration have become a hallmark of climate change impacts on lakes (Magnusson et al.
75 2000; Sharma et al. 2019). Generally, warming temperatures are leading to later ice-on and
76 earlier ice-off dates, expanding ice-free periods (Lopez et al. 2019), and in some cases
77 eliminating ice cover intermittently or entirely (Sharma et al. 2019). For instance, across spatially

78 and morphologically distinct lakes in the Northern Hemisphere, ice-on is occurring on average
79 11.6 days later per century with ice-off shifting ahead by 8.1 days (Magnuson et al. 2000;
80 Woolway et al. 2020). The duration of ice cover influences the timing and duration of
81 stratification, which controls nutrient mixing and oxygenation in lakes, making it one of the most
82 critical drivers of biological activity (Woolway et al. 2021). Thus, changes in ice phenology can
83 have cascading implications extending from physical characteristics to food webs, and from
84 microfauna to higher trophic levels.

85
86 Although ice duration is declining for most lakes due to climate change, substantial variation
87 exists in ice phenology trends over space and time (Weyhenmeyer et al. 2011). Predicting
88 changes in phenology remains challenging, particularly for lakes with unique characteristics
89 (e.g., at exceptionally high elevation or extremely large in size). For instance, deeper lakes take
90 longer to cool in fall and thus are more susceptible to intermittent ice cover (Woolway et al.
91 2020). Surface area also matters; larger fetch yields more wave action which can inhibit or delay
92 ice formation (Magee and Wu 2017). High elevations, which show large gradients in weather
93 over small distances (Mountain Research Initiative EDW Working Group 2015), are expected to
94 be particularly susceptible to warming, although few long-term records of high elevation lake ice
95 phenology exist. This complex interplay between environmental factors is further complicated by
96 the importance of both temperature and precipitation to ice formation and persistence. While
97 most regions of the globe are experiencing warming, changes in precipitation are more
98 heterogeneous over small spatial scales with higher uncertainty in future projections (Lopez-
99 Cantu et al. 2020).

100

101 In this study, we evaluated links between climate and ice phenology at Yellowstone Lake, North
102 America's largest lake above 2000 m. Yellowstone Lake is located in Yellowstone National
103 Park, the centerpiece of the ~8-million hectare Greater Yellowstone Ecosystem (GYE). Since

104 1950, the GYE has experienced steady warming with temperatures rising by 1°C in the
105 watershed that includes Yellowstone Lake (Upper Yellowstone; Hostetler et al. 2021).
106 Elevations above 2100 m in the GYE are warming even faster with a rise of 1.4°C from 1980-
107 2018 (Hostetler et al. 2021). Given the high-elevation of Yellowstone Lake paired with rapid
108 contemporary warming, we expected strong shifts in ice phenology, with later ice formation and
109 earlier break-up over time. To test this prediction, we addressed two questions: (1) Has ice
110 phenology changed in Yellowstone Lake over the last century (1927-2022)? And, (2) how are
111 climate factors linked to interannual variability and long-term trends in ice phenology?
112 Surprisingly, we found no change in timing nor duration of ice cover at Yellowstone Lake over a
113 96-year record. For now, an increase in snowfall is buffering the lake's ice phenology against
114 change. However, projections of how future temperature and precipitation regimes will shift
115 above 2100 m in the Upper Yellowstone River watershed (i.e., Hostetler et al. 2021) suggest we
116 are approaching an abrupt shift where snowfall will no longer buffer Yellowstone Lake against
117 significant change to its seasonal ice cover. Collectively, our study highlights the power of long-
118 term data for tracking environmental change and the value of such a long record for a high-
119 elevation, montane lake.

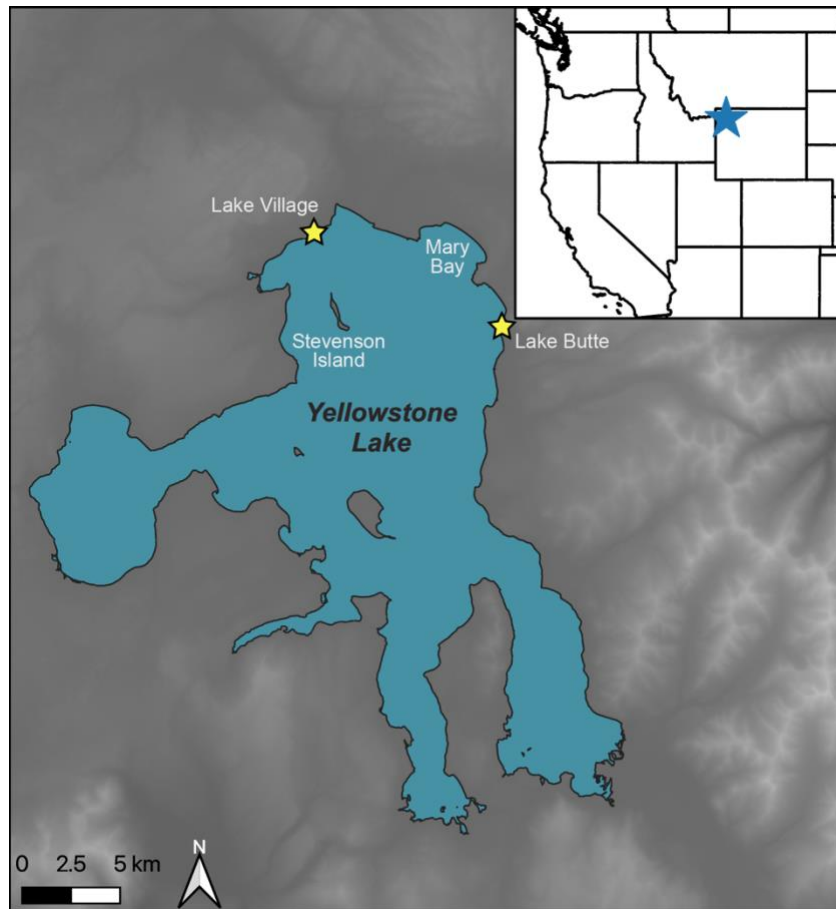
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121 **Methods:**

122 *Study area*

123 Yellowstone Lake is located at a moderate latitude (~44.5°N) in Yellowstone National Park in
124 northwestern Wyoming, USA. With a surface area of 341 km², a maximum depth of 120 m, a
125 volume of 14.9 km³, and an elevation of 2,357 m, Yellowstone Lake is the largest high-elevation
126 lake in western North America (Kaplinski 1991). Yellowstone Lake mixes twice a year and has
127 been typically ice-covered from late December through May (Gresswell & Varley 1988). Water
128 chemistry of Yellowstone Lake is influenced by underlying geothermal activity, including
129 hydrothermal vents in the northern regions of the lake (Anderson & Harmon 2002; Morgan et al.

130 2007). Surface water temperatures are 9-18°C during the ice-free season (Koel et al. 2019,
131 2020).
132



133
134 **Figure 1.** Map of Yellowstone Lake in northwestern Wyoming, USA, with yellow stars and labels
135 indicating key landmarks where ice phenology was assessed. Inset map: Blue star indicating the location
136 of Yellowstone Lake in the western United States.

137
138 *Long-term data acquisition*

139 The ice-off date for Yellowstone Lake has been recorded each year by Lake Village Ranger
140 Station staff since 1927. The ice-on date has also been recorded since 1931. For this record,
141 ice-on is defined as the date when ice cover is continuous across the northern section of the
142 lake (i.e., from Mary Bay to Stevenson Island) when viewed from the Lake Butte overlook

143 (Figure 1). For ice-off, the opposite is true; it is the date each year when ice was no longer
144 continuous from the same overlook. We compiled these records from a combination of sources
145 including the Yellowstone National Park archives, Yellowstone National Park Resource
146 Management, and staff records from ranger stations. We obtained corresponding climatic data
147 for the same time period (1927-2022). Daily air temperatures (maximum and minimum) and
148 precipitation were retrieved from the Water Resources Data Systems which is maintained by the
149 State Climate Office at the University of Wyoming (<http://www.wrds.uwyo.edu/>) for the
150 Yellowstone Lake weather station (#485345) at the Lake Village Ranger Station (Figure 1).
151 From these data, we calculated annual and seasonal air temperatures. Daily precipitation
152 amounts were converted into rainfall and snowfall based on an empirically derived snow
153 probability function (Dai et al. 2008; see Supporting Information for details).

154

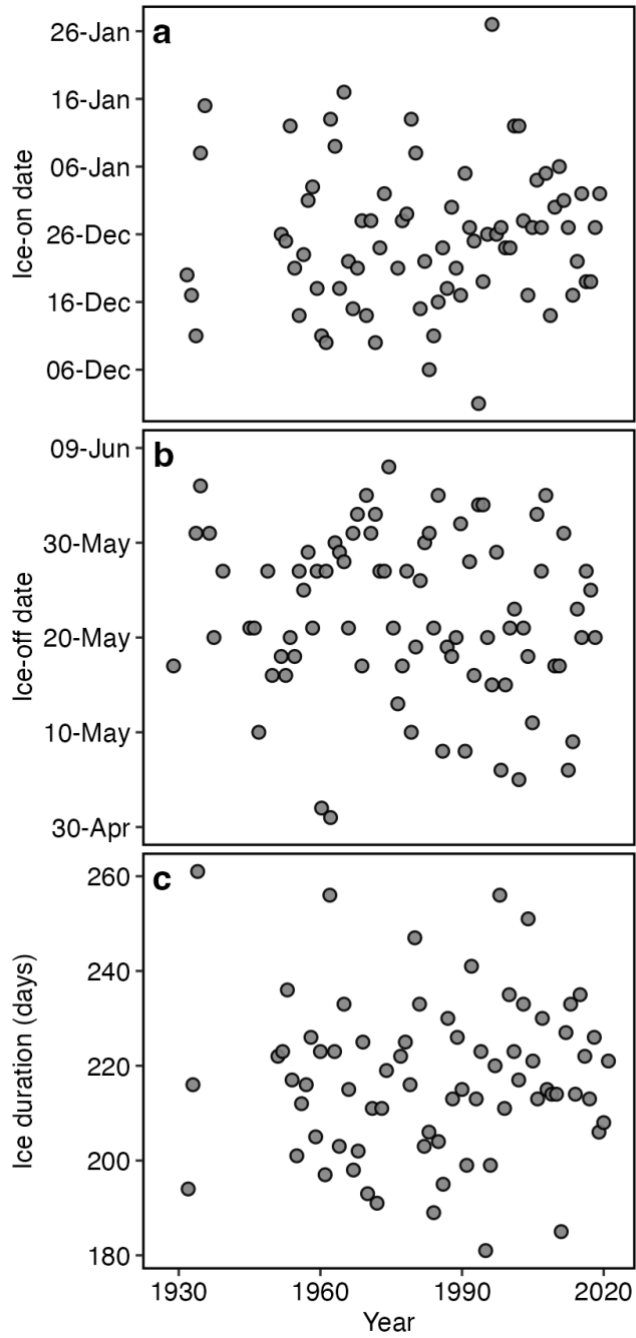
155 *Data analysis*

156 All statistical analyses and data visualizations were conducted in R version 4.2.1 (R Core Team
157 2022). We constructed time series models to test whether the timing of ice formation and
158 breakup changed over a century and to investigate potential climatic drivers. We tested how
159 weather conditions of the preceding months impacted ice phenology (ice-on, ice-off), such that
160 only data prior to the mean date of ice-on or ice-off were included in models. For ice-on models,
161 we considered summer (June-August) and fall (September-November) minimum, maximum,
162 and cumulative mean daily air temperatures and precipitation totals (as rain or snow). For ice-off
163 models, we considered spring (April-June) and winter (January-March) minimum, maximum,
164 and cumulative air temperature and precipitation totals as well as the maximum observed
165 snowpack depth of the preceding winter.

166

167 We modeled the drivers of ice-on and ice-off using generalized additive models (GAMs; Hastie
168 & Tibshirani 1990; Wood et al. 2017) using a gamma family with a logistic link function via the

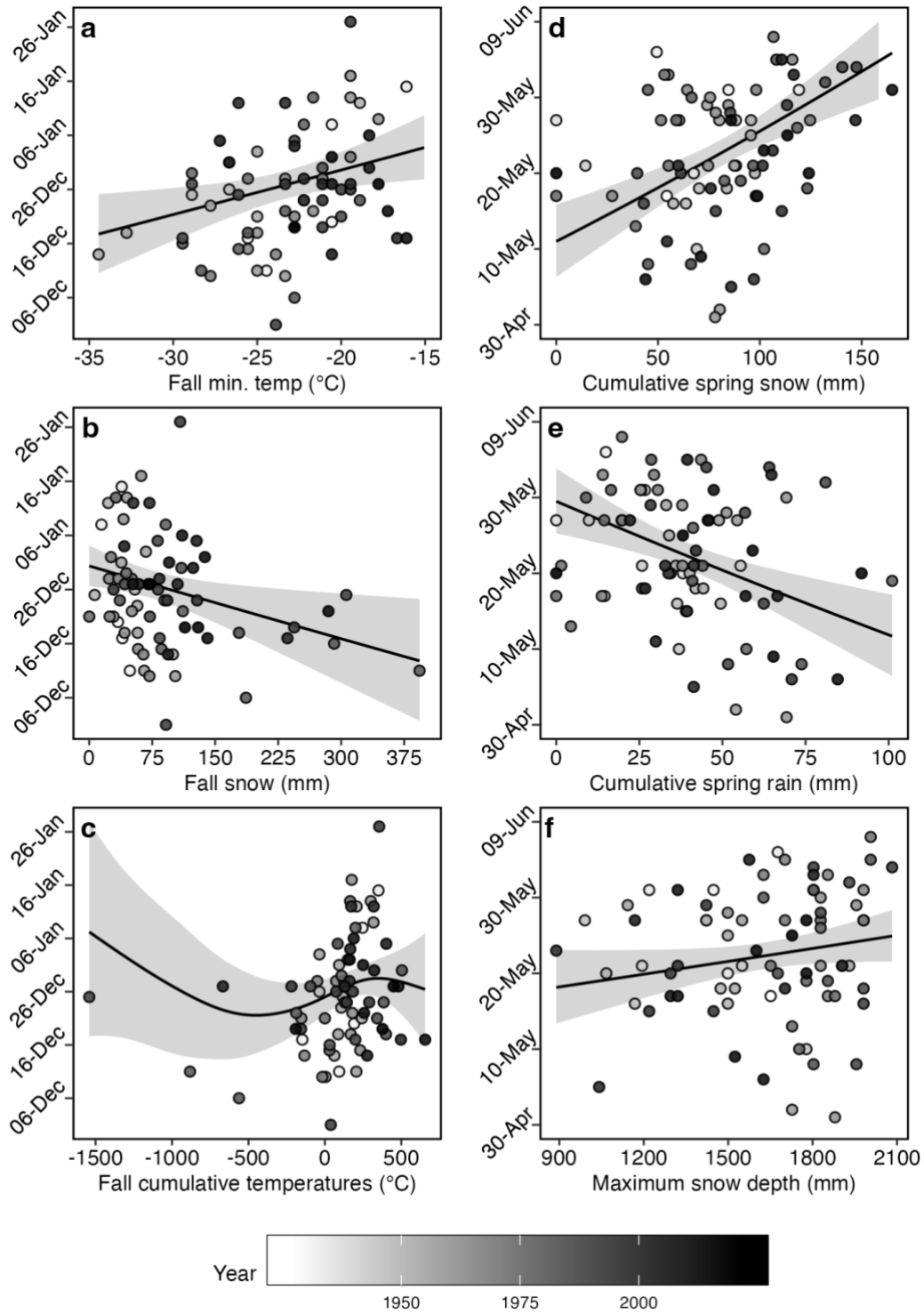
169 mgcv package (version 1.8-40; Wood 2019). Model diagnostic checks indicated that we did not
170 need to account for temporal autocorrelation in our models. For both ice-on and ice-off, we
171 began with a “full” model that included all predictors and only used uncorrelated variables in
172 models ($|r| < 0.7$; Table S1). We ultimately report the models that balance parsimony and
173 deviance explained; many models performed similarly and are listed in Table S1 for
174 comparison. Similarly, for all climatic variables, we analyzed the time series using GAMs to test
175 for changes over time. For each time series, we additionally calculated the first derivatives in the
176 GAMs time series to test for an acceleration or deceleration in the trend; a period was significant
177 if the confidence intervals around the first derivative did not overlap with zero.



178

179 **Figure 2.** Raw annual data for the timing of (a) ice-on, (b) ice-off, and (c) ice duration at Yellowstone Lake
 180 from 1927-2022. Lack of trend lines indicate a lack of statistical significance at $P < 0.05$.

181



182

183 **Figure 3.** General Additive Model (GAM) results for the date of (a-c) ice-on and (d-f) ice-off. Ice-on date
 184 was best explained by (a) minimum fall air temperatures, (b) cumulative fall snow, and (c) cumulative fall
 185 air temperatures (deviance explained = 28.9%). Ice-off date was best explained by (d) cumulative spring

186 snowfall, (e) cumulative spring rain, and (f) maximum snow depth of the previous winter (deviance
187 explained = 37.2%). For all panels, the points represent raw data, and the fitted curves are the predictions
188 when holding all other predictors at their median value.

189

190 **Results:**

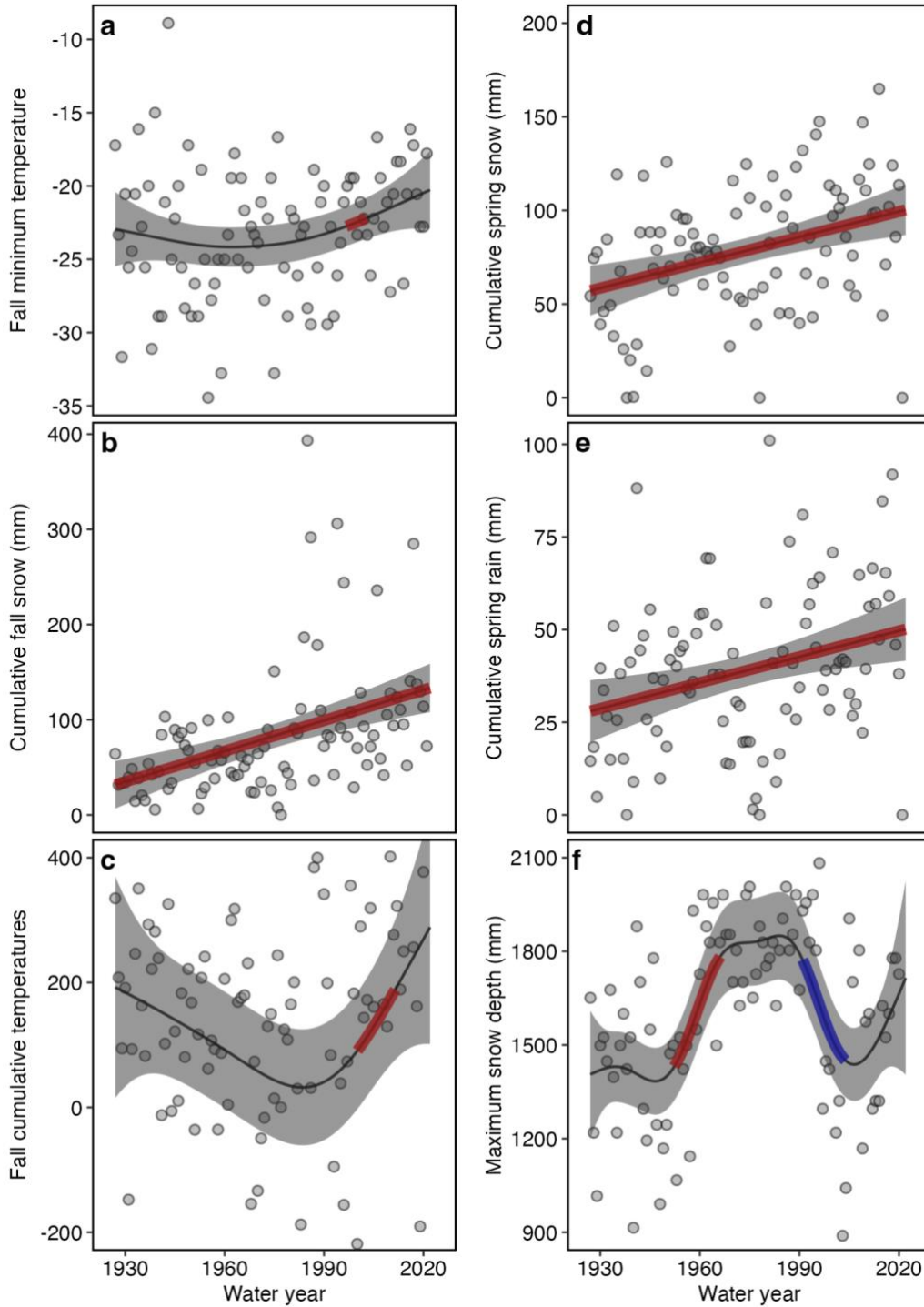
191 Our data set included 75 and 83 years of data for ice-on and ice-off, respectively, which
192 translated to 21% and 13% missing data for each metric. For our study period, the average ice-
193 on date for Yellowstone Lake was 25 December with the earliest ice-on occurring on 30
194 November and the latest on 26 January. We found no evidence for a shift in the timing of ice-on
195 (edf = 1.001, $F = 0.23$, $P = 0.633$; Figure 2a). For ice-off, the average ice-off date was 22 May
196 with the earliest break-up occurring on 28 April and the latest on 12 June. We found no
197 evidence for a shift in the timing of ice-off (edf = 1, $F = 0.008$, $P = 0.93$; Figure 2b). The average
198 ice duration was 217 days with a minimum of 181 and maximum of 261. Similarly, we found no
199 evidence of changing ice duration over the period of record (edf = 1.041, $F = 0.032$, $P = 0.987$;
200 Figure 2c).

201

202 The best-fit model for ice-on included minimum fall air temperatures, cumulative fall snow, and
203 cumulative fall air temperatures (deviance explained = 28.9%; Figure 3a-c). Generally, later ice
204 formation was associated with warmer minimum fall temperatures, early build-up of winter
205 snowpack, and colder cumulative air temperatures. Ice-off date was best explained by
206 cumulative spring snowfall, cumulative spring rain, and maximum snow depth of the previous
207 winter (deviance explained = 37.2%; Figure 3d-f). Ice-off was positively correlated with
208 cumulative spring snow and the maximum observed snow depth of the preceding winter, and
209 negatively correlated with cumulative spring rain.

210

211 All of the top predictors of ice phenology show evidence of change over the period of record,
212 although the strength and direction of those trends varied, and not all trends were linear (Figure
213 4). Indeed, minimum fall air temperatures have increased slightly since the mid-20th century
214 (edf = 2.132, $P = 0.0676$; Figure 4a), with an acceleration in the trend from ~1996-2002.
215 Cumulative fall snowfall has been increasing linearly since the 1930s (edf = 1.001, $P < 0.001$;
216 Figure 4b) and cumulative fall temperatures have also increased more recently with an
217 accelerating trend from ca. 2000-2011 which continues increasing to present day (edf = 2.051,
218 $P < 0.001$). We observed pronounced changes in spring precipitation, with linear increases over
219 the entire record in both cumulative snow (edf = 1.001, $P < 0.001$; Figure 4d) and rainfall (edf =
220 1.001, $P = 0.003$; Figure 4e). Finally, maximum winter snow depth displayed highly non-linear
221 patterns (edf = 6.003, $P < 0.001$), with an accelerating trend between ca. 1950-1966, followed
222 by relatively stable conditions, and a decelerating trend between ca. 1990-2003; since the early
223 2000s, there is evidence that maximum snow depth is again increasing (Figure 4f). For
224 transparency, trends for all predictors that were assessed are included in the Supporting
225 Information and organized by focal period: annual (Figure S1), winter (Figure S2), spring (Figure
226 S3), summer (Figure S4), and fall (Figure S5).



227

228 **Figure 4.** Time series of the top predictors of the date of (a-d) ice-on and (e-g) ice-off. Grey points are
 229 raw data and lines are fitted trends from generalized additive models (GAMs). Shading around trend-lines
 230 represents 95% confidence intervals. Red or blue lines indicate periods of a significant increase or
 231 decrease in the trend, respectively, as indicated by the first derivative of the GAMs.

232

233 **Discussion:**

234 Globally, most lakes are experiencing shifts in ice phenology due to climate change
235 (Magnusson et al. 2000; Sharma et al. 2019). Exceptions to this trend are interesting as they
236 can reveal factors that promote resilience in lake ecosystems against climate-induced shifts in
237 ecosystem functioning. Here, using a 96-year record, we show that Yellowstone Lake has been
238 remarkably resistant to changes in ice phenology despite long-term warming in the region.
239 Shifts in local precipitation, especially increases in fall and spring snow, appear to be buffering
240 the lake's ice phenological shifts against warming temperatures.

241

242 The lack of long-term directional change in ice phenology at Yellowstone Lake was unexpected
243 given regional and local evidence for warming. Since 1950, annual temperatures have
244 increased by 1°C throughout the Greater Yellowstone Ecosystem (Hostetler et al. 2021). These
245 changes are particularly pronounced at the high elevation (above 2000 m) of Yellowstone Lake
246 where air temperatures increased by 1.4°C in less than 40 years (1980-2018; Hostetler et al.
247 2021). Using local weather data, we found some evidence for increased summer, fall, and
248 spring temperatures, primarily in the last three decades. Given the key role of air temperatures
249 in driving ice formation and break-up (Kirillin et al. 2012), it is noteworthy that we did not find
250 evidence for directional shifts in ice phenology in association with spring and fall temperature
251 increases. One possible explanation is that fall minimum temperatures—which were important in
252 predicting ice formation—are not rising as quickly as overall temperature trends in the region. A
253 more likely explanation, however, likely lies in how precipitation regimes are concurrently
254 changing at Yellowstone Lake.

255

256 Snow cover, particularly in spring, can delay ice break-up. Cumulative spring snow, which was
257 strongly correlated with delayed ice-off dates, has nearly doubled over the last century at

258 Yellowstone Lake (Figure 4d). In general, precipitation has increased in spring and fall in the
259 region. Conversely, snowfall has declined or been relatively stable at high elevations in the
260 Upper Green River basin to the south (Hostetler et al. 2021). Ice-off timing of other high
261 elevation lakes is strongly correlated with spring snowfall (e.g., Caldwell et al. 2021; Preston et
262 al. 2016) and increased snowfall has been suggested as a primary cause in other lakes where
263 ice phenology is not shifting with warming temperatures (e.g., Korhonen 2006; Ñoges & Ñoges
264 2013; Yao et al 2013). Our results further emphasize the importance of considering interactions
265 between air temperature and precipitation patterns in predicting changes in ice phenology.

266
267 Looking ahead, our results paired with recent analyses of climate projections suggest a ‘tipping
268 point’ may be coming soon when ice cover duration abruptly changes for Yellowstone Lake.
269 This tipping point will largely stem from the ongoing shift from snow- to rain-dominated
270 precipitation regimes in the fall and spring. Spring rainfall was strongly correlated with earlier
271 ice-off dates and also showed an increasing temporal trend over the last century (Figure 4e).
272 Increased spring rainfall has not yet caused a detectable long-term trend towards earlier ice
273 break-up, potentially because of the counteracting effects of increased spring snow. As
274 temperatures warm further, and fall and spring snowfall decreases, it is possible that ice
275 phenology will rapidly change on Yellowstone Lake. Future temperature projections under an
276 RCP4.5 scenario across all seasons suggest an increase of around 2.8°C by 2061-2080 for the
277 Greater Yellowstone region (Hostetler et al. 2021). More concerning are projections under the
278 same scenario for the dominant precipitation regime across elevations in the Upper Yellowstone
279 watershed. At present, the elevation band that contains Yellowstone Lake (1800-2400m) sits
280 between “snow-dominant” and “rain-snow mix.” By 2040, this is projected to shift firmly to “rain-
281 snow mix” and trending towards “rain-dominated” (Hostetler et al. 2021).

282

283 If Yellowstone Lake experiences an abrupt shift in ice phenology, there may be wide-ranging
284 consequences for nutrient cycling, lake productivity, fisheries, and recreation. Abrupt shifts in
285 lake ecosystem functioning have increased in recent decades (Huang et al. 2022) and often
286 result in significant consequences for cultural values and ecosystem services. Early warning
287 signs of abrupt shifts in ecosystem functioning—e.g., increases in the variance of ecosystem
288 properties—will be useful to monitor moving forward (Ratajczak et al. 2018). Yellowstone Lake,
289 although relatively isolated, has a history of nonnative species introductions (e.g., lake trout)
290 and may experience future change due to atmospheric nitrogen deposition (Nanus et al. 2017;
291 Koel et al. 2019). Understanding ways in which multiple drivers interact will be critical in
292 predicting future shifts in lake functioning and provisioning of ecosystem services for
293 Yellowstone Lake and other large lakes globally.

294

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301

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Supporting Information:

Despite a century of warming, increased snowfall has buffered ice phenology of North America's largest high-elevation lake against climate change

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Methods:

Estimating Daily Rainfall and Snowfall

We converted the daily precipitation values into snowfall and/or rainfall amounts using a function that generates proportions of snow and rain based on air temperature (Dai *et al.*, 2008). The daily mean temperature was calculated as the mean of the maximum and minimum temperatures on each day. When the mean daily temperature is near the threshold at which precipitation changes from snow to rain, it is likely that both types of precipitation fell within the same 24 hr period for which daily precipitation was measured. Following Dai *et al.*, (2008), we used the function:

$$\text{Snow Probability} = -50 * [\tanh(0.4 * (\text{Mean Temp} - 1.75))] - 1$$

We parameterized the function to have a threshold temperature of 1.75°C (when precipitation is 50% rain and 50% snow) and a slope of 0.4, which is consistent with empirically observed values at high altitudes (Dai *et al.*, 2008). We applied the function over all of the daily temperature and precipitation values. We then multiplied the resulting daily snow probabilities by the total daily precipitation to calculate daily snowfall, and used 1 minus the snow probability to calculate daily rainfall.

References:

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Tables:

Table S1. Summary of all GAMs built in the analysis (four models for ice-on and five for ice-off). In the main text, we focus our model interpretation on the model that minimized AIC, maximized deviance explained (% Dev.), and was the most parsimonious.

rank	y	term	edf	ref.df	F statistic	p	% Dev.	logLik	AIC
<i>ice-on</i>									
1	iceOn	s(FallMin)	1	1	6.87	0.011	0.289	-262	540
		s(FallSnow)	1	1	6.39	0.014			
		s(FallTempSum)	2.89	3.62	1.19	0.235			
2	iceOn	s(FallMin)	1	1	10.2	0.002	0.207	-266	540
		s(FallSnow)	1	1	7.24	0.009			
3	iceOn	s(FallMin)	1	1	6.84	0.011	0.287	-262	542
		s(FallMax)	1	1	0.371	0.545			
		s(FallSnow)	1.13	1.24	4.75	0.019			
		s(FallTempSum)	2.63	3.31	0.975	0.339			
4	iceOn	s(FallMin)	1	1	7.28	0.009	0.284	-263	544
		s(FallMax)	1	1	0.681	0.412			
		s(FallRain)	1	1	0.492	0.486			
		s(FallSnow)	1.18	1.33	2.33	0.087			
		s(FallTempSum)	2.36	2.97	0.864	0.409			
<i>ice-off</i>									
1	iceOff	s(SnowDepth)	1	1	3.29	0.074	0.372	-266	546
		s(SpringRain)	1	1	15.4	0			
		s(SpringSnow)	1	1	26.3	0			
		s(WinterMin)	1	1	2.37	0.128			
		s(SpringMax)	1	1	1.04	0.312			
2	iceOff	s(WinterSnow)	1.58	1.97	1.6	0.242	0.416	-263	547
		s(SnowDepth)	1	1	4.03	0.049			
		s(SpringSnow)	1	1	24.9	0			
		s(SpringRain)	1	1	17.5	0			
		s(WinterMin)	1	1	4.43	0.039			
		s(SpringMin)	1	1	2.03	0.159			
		s(SpringMax)	1	1	0.999	0.321			
3	iceOff	s(WinterSnow)	1.71	2.17	1.34	0.307	0.402	-264	547
		s(SnowDepth)	1	1	3.29	0.074			
		s(SpringRain)	1	1	15.2	0			
		s(SpringSnow)	1	1	23.8	0			
		s(WinterMin)	1	1	2.73	0.103			
		s(SpringMax)	1	1	1.1	0.297			
4	iceOff	s(SnowDepth)	1	1	3.11	0.082	0.346	-274	560
		s(SpringRain)	1	1	16.8	0			
		s(SpringSnow)	1.06	1.12	24.1	0			
		s(WinterMin)	1	1	2.57	0.113			
5	iceOff	s(SnowDepth)	1	1	4.12	0.046	0.323	-275	560
		s(SpringRain)	1	1	19.8	0			
		s(SpringSnow)	1	1	26.9	0			

Figures:

Annual trends

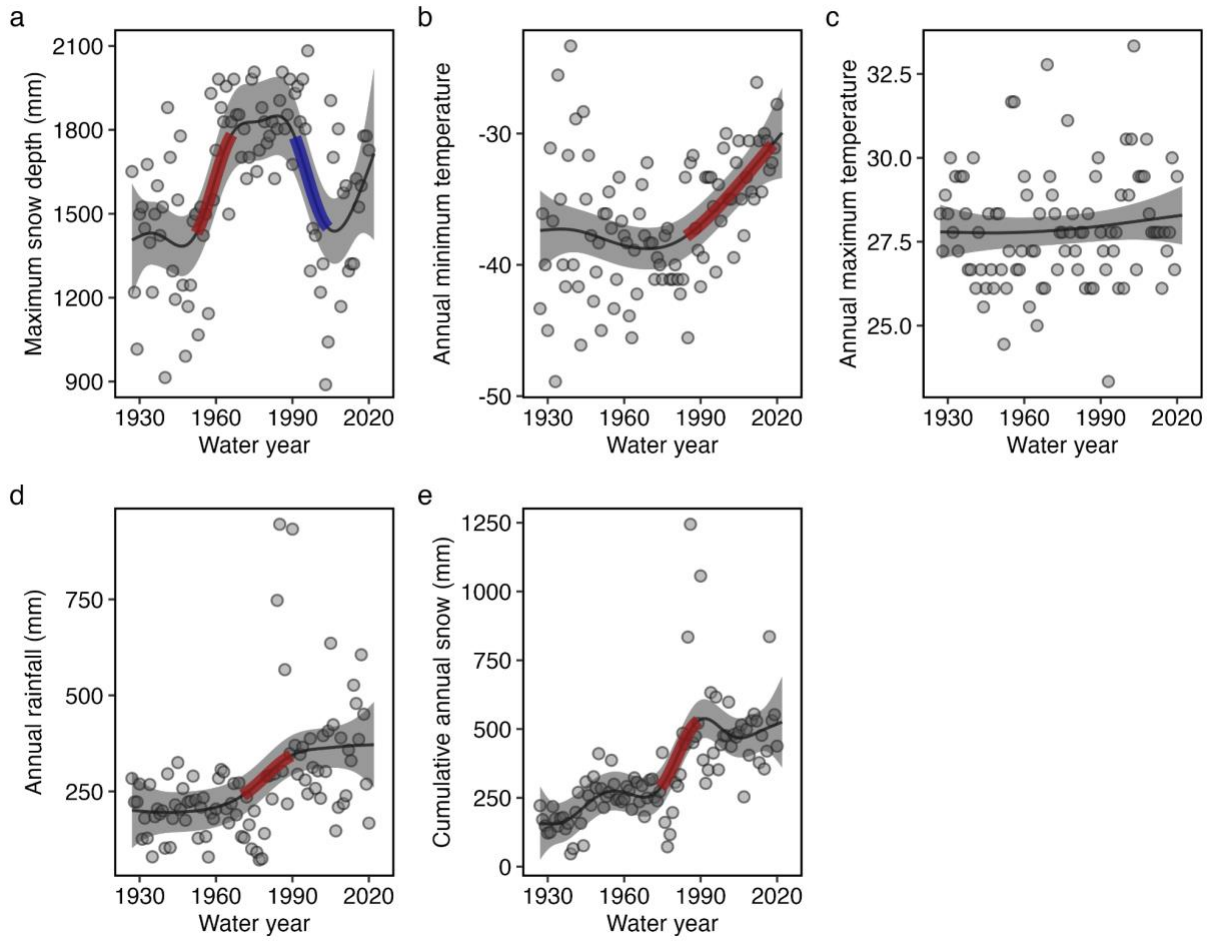


Figure S1. GAMs timeseries for annual climatic trends. Red or blue lines indicate periods of a significant increase or decrease in the trend as indicated by the first derivative of the GAMs.

Winter trends

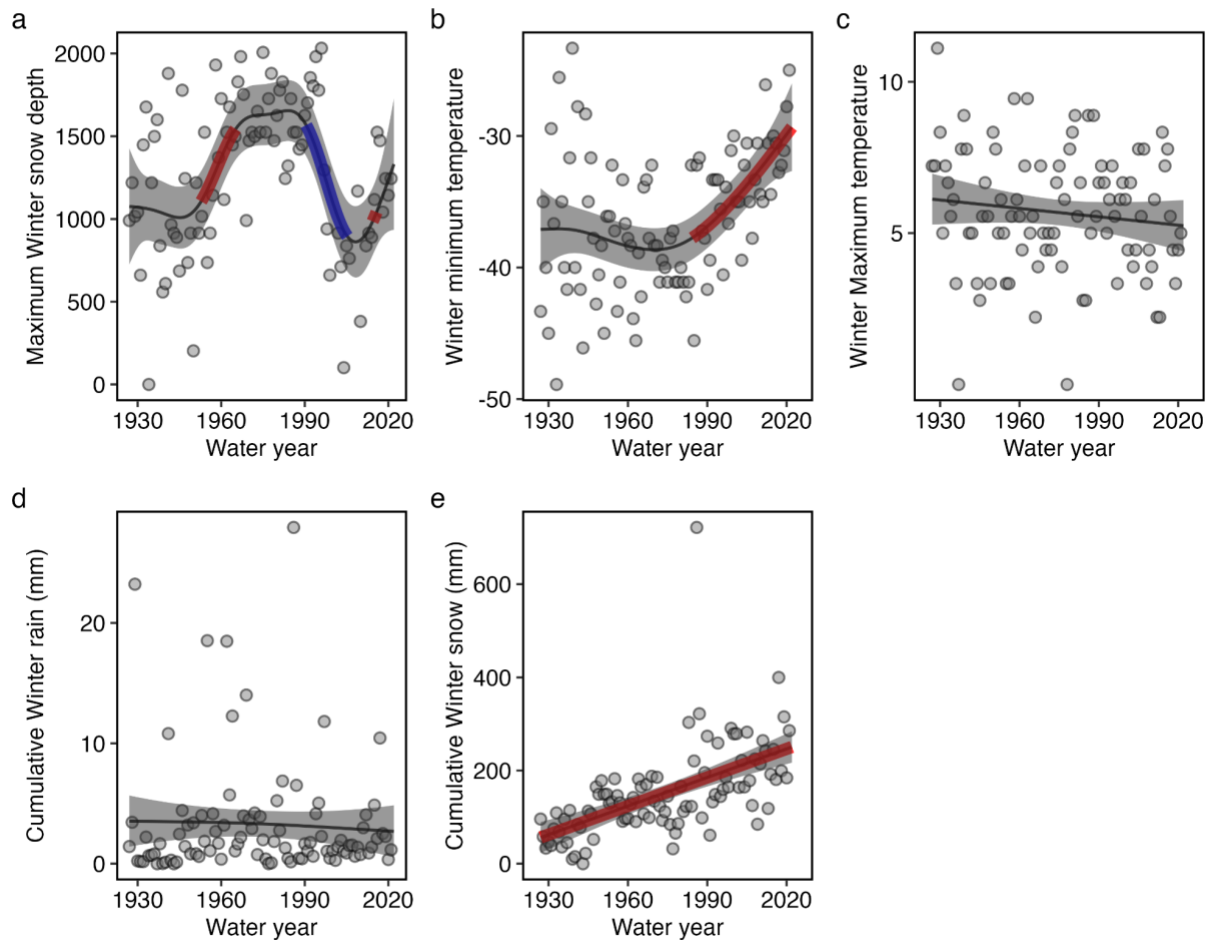


Figure S2. GAMs timeseries for winter climatic trends. Red or blue lines indicate periods of a significant increase or decrease in the trend as indicated by the first derivative of the GAMs.

Spring trends

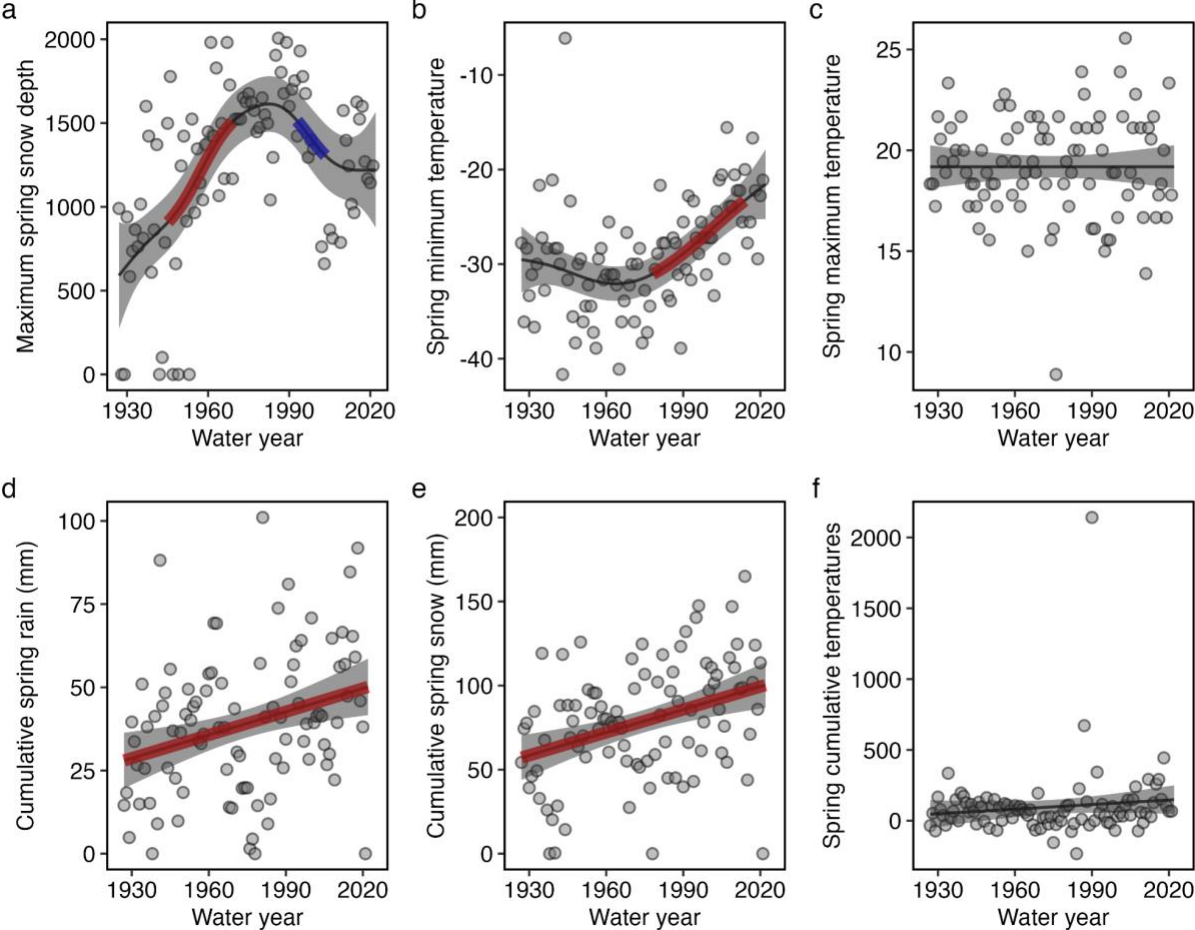


Figure S3. GAMs timeseries for spring climatic trends. Red or blue lines indicate periods of a significant increase or decrease in the trend as indicated by the first derivative of the GAMs.

Summer trends

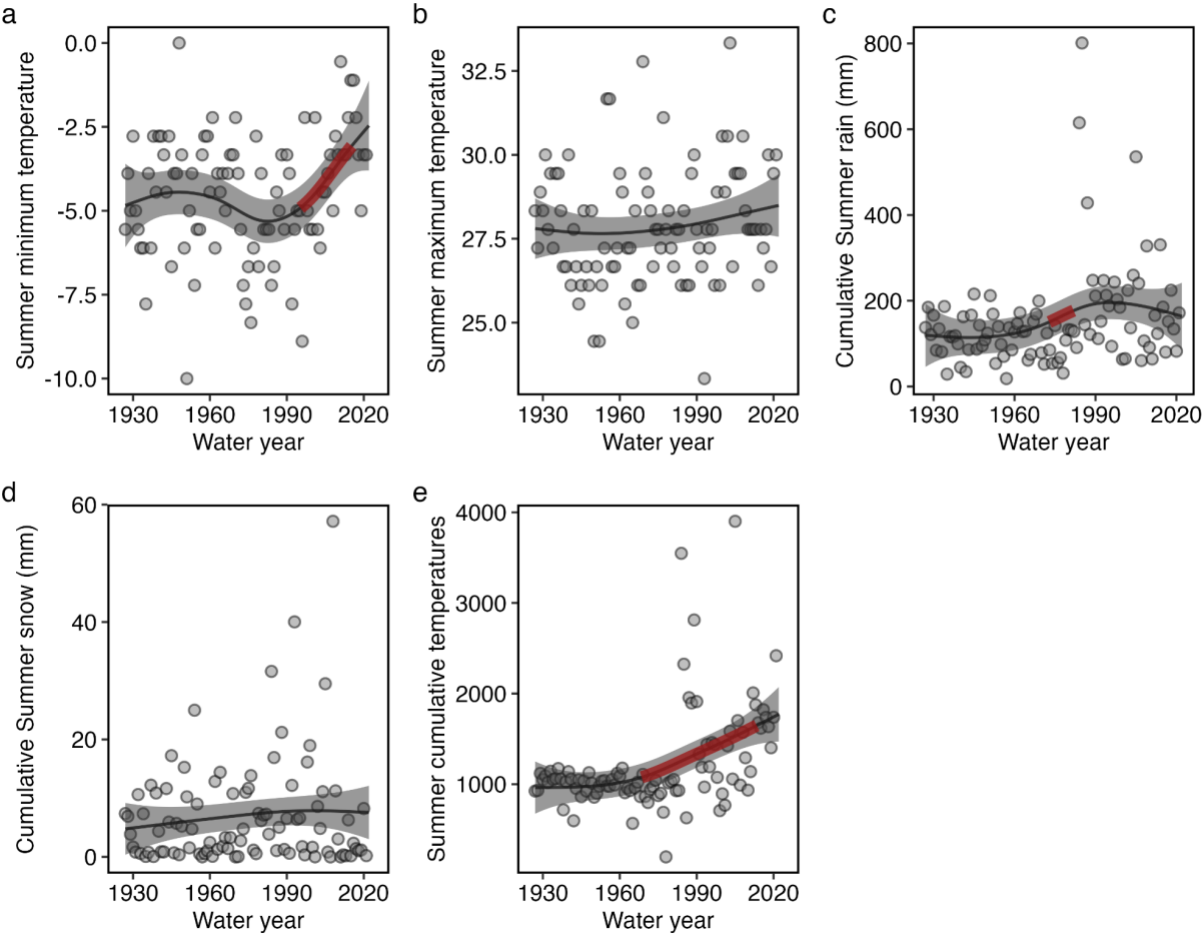


Figure S4. GAMs timeseries for summer climatic trends. Red or blue lines indicate periods of a significant increase or decrease in the trend as indicated by the first derivative of the GAMs.

Fall trends

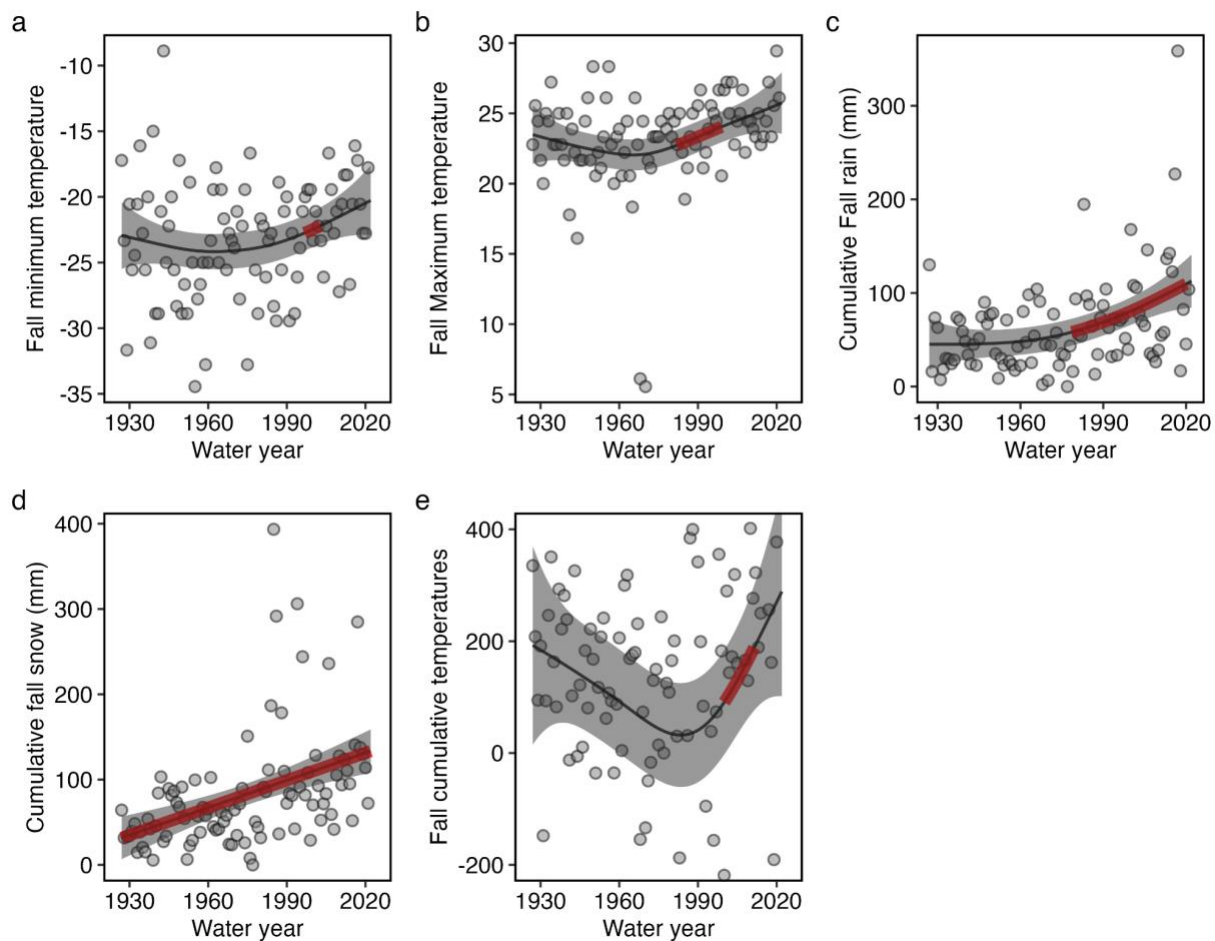


Figure S5. GAMs timeseries for fall climatic trends. Red or blue lines indicate periods of a significant increase or decrease in the trend as indicated by the first derivative of the GAMs.