



The human factor in seasonal streamflows across natural and managed watersheds of North America

Nitin K. Singh¹✉ and Nandita B. Basu^{1,2,3}

While it is established that climate change and human activities (for example, urbanization, dams) alter streamflows, there exists considerable uncertainty regarding the relative magnitude of their contributions. Most studies have focused on annual flows and found trends to be dominated by climate. Here we compare trends in seasonal flow totals for 315 natural and 1,957 managed watersheds across North America over 60 years (1950–2009). We find an amplification of seasonal flow trends in 44% of the managed watersheds, while 48% of the watersheds exhibit flow dampening. The magnitudes of amplification (20–167%) and dampening (5–52%) are substantial and vary seasonally. Multivariate models reveal that while rainfall, slope and forest cover are the key drivers of seasonal trends in natural watersheds, canals, impervious areas and dam storage dominate the responses in managed watersheds. Our findings of human-driven seasonal flow alterations highlight the need to develop adaptation strategies that mitigate the associated negative impacts.

Water availability is critical to human sustenance, ecosystem function and geophysical processes^{1,2}. Concurrently, water availability is sensitive to human and natural forcings^{3,4}. In the past century, the demand for freshwater has soared exponentially to meet the necessities of the growing population⁵. This relentless demand for freshwater has led to the installation of dams, reservoirs and canals to store, extract and transport water from rivers⁶. As a consequence, more than two-thirds of river systems and associated flows have been altered globally⁷. At the same time, changes in climate patterns, temperature trends and both timing and magnitude of precipitation, as well as snowmelt dynamics⁸, are altering streamflow patterns across the world⁹. Given societal water needs, it is critical to quantify the relative importance of climate versus anthropogenic drivers for streamflow patterns.

Numerous studies have explored the long-term trends in streamflow across North America^{9–11}, across Europe^{12,13} and globally^{2,14}. Most of these have focused on natural or pristine watersheds, with minimal anthropogenic alterations, to isolate the effect of a changing climate on streamflow patterns^{10,15}. The few studies that have explored streamflow patterns in managed watersheds across the conterminous United States (CONUS) have reported somewhat contradictory results^{16–18}. Ref. ¹⁶ reported greater changes in annual streamflow trends in managed watersheds compared with natural watersheds over a 60-year time frame (1940–2009) across the CONUS. They used a boosted tree regression approach to attribute the trends to geographic location, topography and hydroclimatic variables¹⁶. Similarly, more frequent changes in annual low flows have been noted in managed than in natural watersheds, over a 50- to 100-yr period (1916–2015) at the CONUS scale, and they attributed it to land-use changes¹⁸. A decline in low flows and increases in high flows have been documented in 53 urbanized watersheds compared with their natural counterparts over 77 years (1939–2016) across the United States¹⁹, and authors ascribed the flow trends to urbanization and increase in infrastructure¹⁹. By contrast, no changes in annual streamflow metrics (for example,

low, median and extreme flows) between managed and natural watersheds have been reported over 35 years (1989–2015) across the United States and Canada, and thus authors concluded that climate is the primary driver of streamflow trends, with management playing a minimal role¹⁷.

While these studies focused on annual trends, a smaller subset of work has focused on seasonal trends in natural watersheds at regional and continental scales^{10,11,20}. These studies have highlighted that seasonal flow extremes increase and decrease in spatially coherent patterns at the continental scale, highlighting the influence of large-scale climatic drivers. However, none of these studies has compared seasonal variations in streamflow trends between natural and managed watersheds at the continental scale. Indeed, anthropogenic interventions probably impact seasonal flow trends more substantially than annual trends as various water resources management decisions (for example, withdrawal for irrigation, inter-basin transfer, reservoir operations) occur at sub-annual timescales²¹. For example, using a reservoir routing model in three watersheds, a study showed that reservoir operations affected predominantly trends in seasonal flows but not annual flows²¹.

There is also limited work on the attribution of climate versus anthropogenic influences of streamflow trends at the continental or global scale^{1,22–25}. Some of these studies have attributed the changes in streamflows solely to climate forcings²⁵, while others have highlighted the role of anthropogenic stressors^{22,23}. It is worth acknowledging that most of the work in this domain has been done at the annual scale. Recently, a study used a global hydrological model to show the extent of influence of land-use change, reservoir operations and irrigation withdrawals on seasonal water availability at the global scale for four decades (1971–2010)²⁴. Thus, there remains a need for attribution studies based on observational evidence to demonstrate the relative importance of climate and anthropogenic forcings on streamflows.

In this article, we analyse seasonal streamflow trends in natural and managed watersheds across North America over the past

¹Earth and Environmental Sciences, University of Waterloo, Waterloo, Ontario, Canada. ²Civil and Environmental Engineering, University of Waterloo, Waterloo, Ontario, Canada. ³Water Institute, University of Waterloo, Waterloo, Ontario, Canada. ✉e-mail: nksingh01@gmail.com

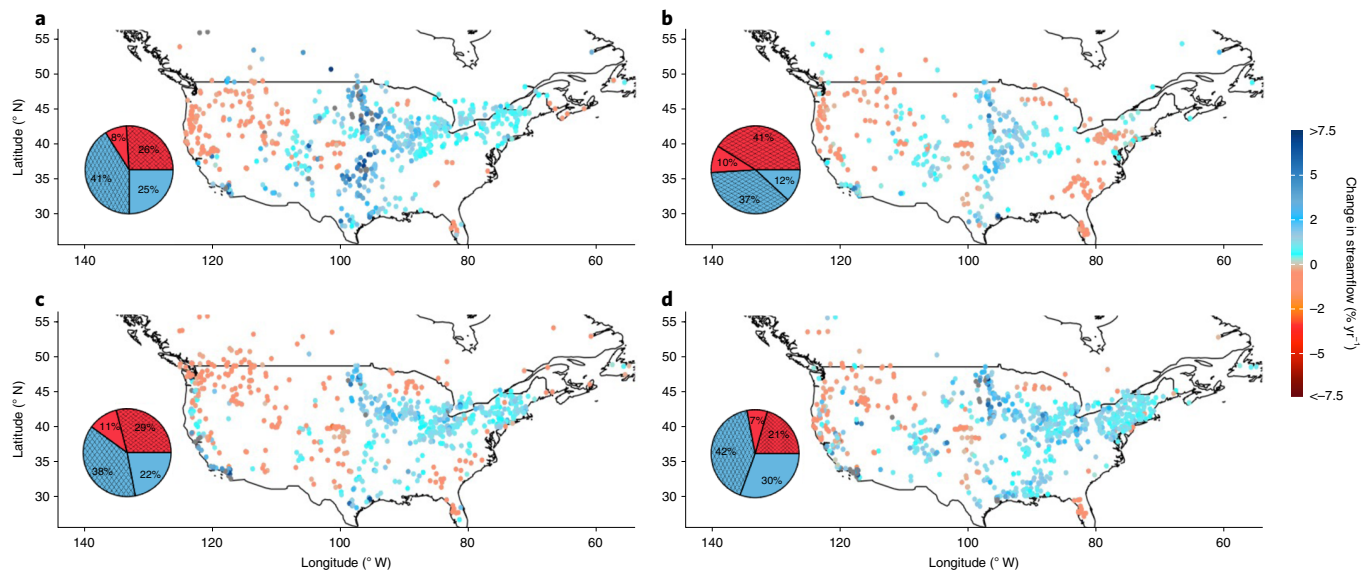


Fig. 1 | Seasonal streamflow trends over 60 years (1950–2009). **a**, Winter (December, January and February). **b**, Spring (March, April and May). **c**, Summer (June, July and August). **d**, Fall (September, October and November). Map shows natural and managed watersheds with significant trends ($P < 0.05$), where blue and red colours represent increasing and decreasing trends, respectively. Pie graphs show the distribution of significant ($P < 0.05$; solid) and nonsignificant ($P > 0.05$; hatched) trends. The United States and Canada boundary outlines can be obtained from <https://www.census.gov/> and <https://www12.statcan.gc.ca/>.

60 years (1950–2009). Further, we build random forest (RF) models to reveal the key natural (for example, climate, topography) and anthropogenic (for example, reservoir storage, canal density, impervious cover) drivers of seasonal flow trends in natural and managed watersheds. Our work addresses three key questions. (1) What are the trends in seasonal streamflows across North America? (2) How do the seasonal trends differ between natural and managed watersheds? (3) What climate, landscape and management factors control these trends, and how do the hierarchies of these controls differ between natural and managed watersheds?

Results and discussion

We describe the seasonal streamflow trends, how trends vary between natural and managed watersheds and the dominant controls of these trends in the following subsections.

Seasonal streamflow trends across North America. The trend analysis revealed seasonally and regionally varying patterns in streamflow trends across North America (Fig. 1). Increasing flows across all four seasons (blue colour in Fig. 1) was apparent in the central plains, while decreasing flows across all seasons (red colour in Fig. 1) occurred in the western mountains (United States), south-east coastal plains (United States), northern forests (United States and Canada) and prairies (Canada). Regions such as the northeast (United States), southeast plains (United States) and boreal plains (Canada) show a decreasing trend in spring but increasing trends in fall and winter. Significant ($P < 0.05$) increase in flow was observed in 30% of the watersheds in fall (692 watersheds), 25% (561) and 22% (504) of watersheds in winter and summer, respectively, and only 12% (273) of the watersheds in spring (Fig. 1). By contrast, significant ($P < 0.05$) decreasing trends in flow occurred in 7% (~170) of the watersheds in fall and winter and in 11% (244) and 10% (217) of the watersheds in summer and spring, respectively. We further find that responses in spring are distinctly different compared with other seasons, with almost an equal proportion of watersheds showing significant ($P < 0.05$) increasing and decreasing trends, while the majority of the watersheds (78%) showed no statistically significant ($P > 0.5$) trend (pie graphs in Fig. 1). By

contrast, fall, winter and summer flows are dominated by increasing trends. While the rest of the paper focuses primarily on significant ($P < 0.05$) trends, the pie graphs in Fig. 1 highlight that both the significant ($P < 0.05$) and nonsignificant ($P > 0.05$) trends tell the same story. These differences in seasonal trends have strong implications for management of our water resources and are missed in annual-scale trend analysis.

Our results are consistent with other studies that have explored annual trends at continental scales and seasonal trends at regional scales^{10,26,27}. For example, ref.¹⁰ showed increasing winter flow trends for the central and northern regions of the United States between 1948 and 1988. Our findings align with the annual-scale studies showing declining flow trends in the western region of the United States^{16,26} and upward flow trends in central plains¹⁶. For the stations in Canada, studies have reported increasing flows in few winter months and decline in summer and fall flows during 1947–1996²⁸, and we found increasing winter flows and declining summer and fall flows in Canada.

Comparing seasonal trends in natural and managed watersheds.

We then compared flow trends between managed watersheds and their natural neighbours and found that 18–24% of the managed watersheds had significant ($P < 0.1$) trends, while trends in their natural neighbours were nonsignificant (Supplementary Table 1). By contrast, the opposite (significant ($P < 0.1$) trends in natural and nonsignificant ($P > 0.1$) trends in managed) was true for only 8–13% of the managed watersheds. The larger proportion of watersheds with significant ($P < 0.1$) trends in the managed basins highlights the role of human water management in these trends, as has been observed by others²⁹. For the rest of the paper, we have focused on the watersheds where trends were significant ($P < 0.1$) in both natural and managed watersheds (10–28% of the managed watersheds; Supplementary Table 1) and focused on comparing the magnitudes and the directions of the trends. Note that percentages hereafter are specific to the category of significant ($P < 0.1$) trends in both natural and managed watersheds.

We found the alteration patterns to be dominated by R_{pp} (PP indicates that flows in both managed and natural watersheds are

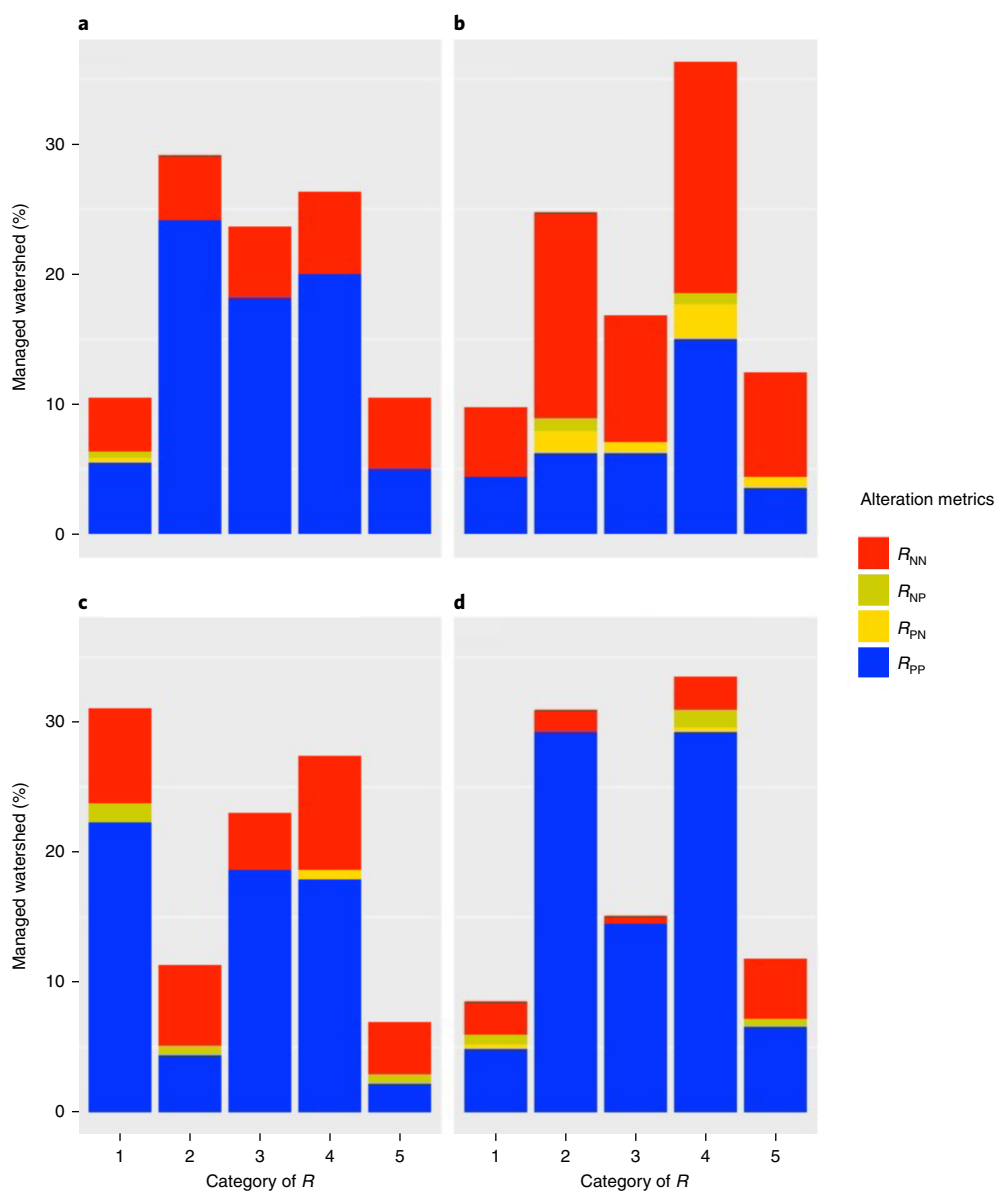


Fig. 2 | The distribution of managed watersheds across the magnitudes of the four alteration metrics for each season. a, Winter. b, Spring. c, Summer. d, Fall. The y axis denotes the percentage of watersheds in each season that has the particular combination of direction and magnitude for R (the magnitude of R is the absolute value of the ratio of the significant ($P < 0.1$) flow trend in the managed to the natural watershed). The numbers represent categories of R : 1, highly dampened ($R < 0.48$); 2, moderately dampened ($0.95 > R > 0.48$); 3, low impact ($0.95 < R < 1.2$); 4, moderately amplified ($1.2 < R < 2.67$); 5, highly amplified ($R > 2.67$). Only significant trends ($P < 0.1$) are used to calculate the R values.

increasing, with significant ($P < 0.1$) trends; P stands for a positive change) on average in 65% (35–85% across the four seasons) of the managed watersheds or R_{NN} (NN indicates that flows in both managed and natural watersheds are decreasing, with significant ($P < 0.1$) trends; N stands for a negative change) on average in 32% (12–57% across the four seasons) of the managed watersheds (Figs. 2 and 3 and Supplementary Table 2). The lack of R_{NP} (NP indicates that flows in managed watersheds are decreasing while flows in their natural neighbours are increasing) and R_{PN} (NP indicates that flows in managed watersheds are increasing while flows in their natural neighbours are decreasing) gauges is interesting and highlights that while climate is the dominant factor that alters the direction of the trend (increasing or decreasing), the human element strengthens or dampens the climate trend.

We further found that the distribution of the proportion of the watersheds across the four categories of R (Supplementary Table 2)

varies seasonally. Simultaneous declines in flows (R_{NN}) are most abundant in spring (57% of the watersheds), while simultaneous increases in flows (R_{PP}) are most abundant in fall (85% of the watersheds) and winter (73% of the watersheds) seasons. This is clearly a broad-scale climatic trend, where spring flows have both an increasing and a decreasing trend, while winter and fall flows have been predominantly increasing. These findings align with the recent work that explored seasonal flow trends from natural watersheds^{11,20}.

Note, however, that even when the flows in the managed and their nearby natural watersheds are changing in the same direction, there can be a remarkable difference in the magnitude of the change, as captured in the R metric. We find that 15–24% of the watersheds have a low degree of anthropogenic alteration (Category 3 in Fig. 2, 40th percentile $< R < 60$ th percentile; $0.95 < R < 1.2$), with $R = 1$ indicating that climate is possibly the most important driver of change. What was especially interesting was that in 26–36% of

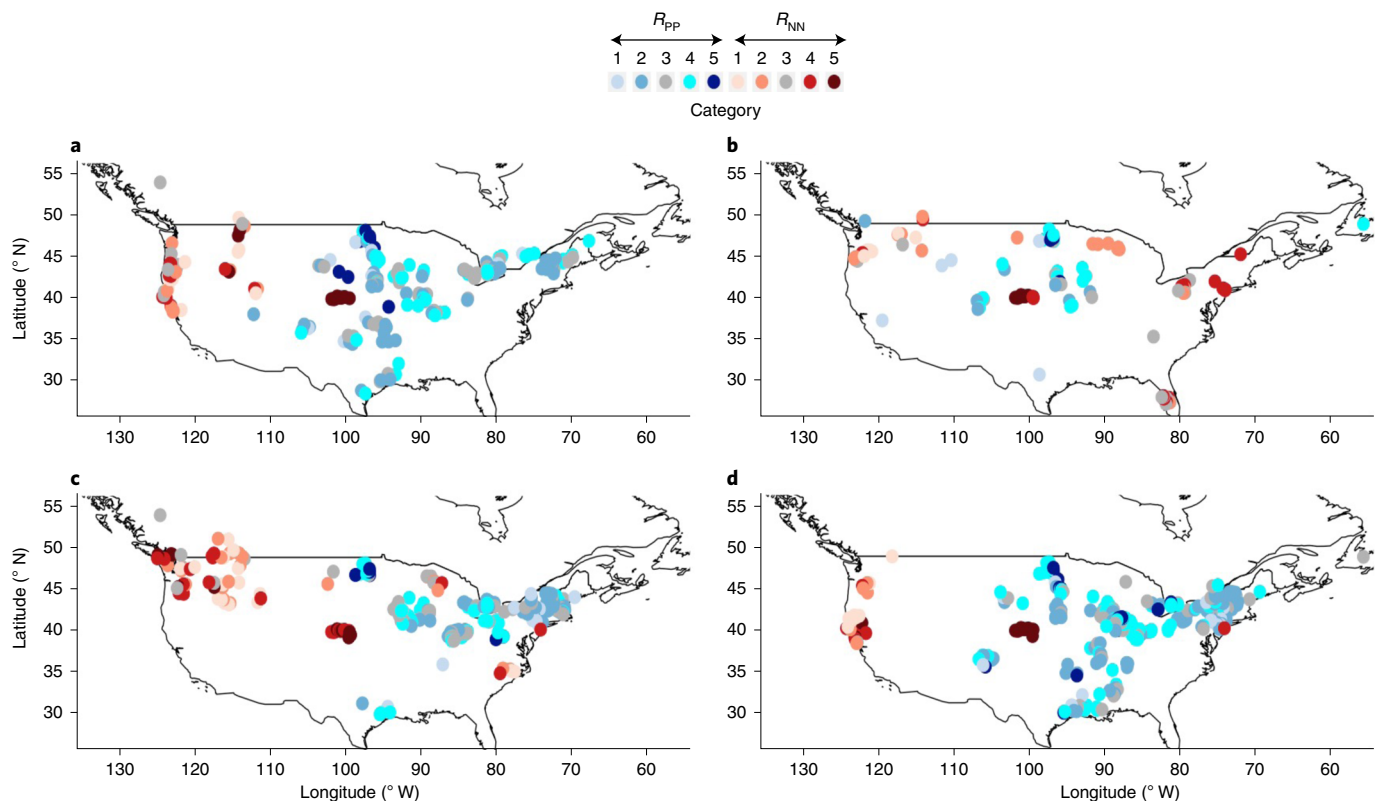


Fig. 3 | Spatial patterns of alteration over 60 years (1950–2009). **a**, Winter. **b**, Spring. **c**, Summer. **d**, Fall. Four shades of colour (blue and red) represent four categories of alteration metric R . Blue colour represents R_{PP} ; red colour represents R_{NN} ; grey colour represents low-impact alteration ($0.95 < R < 1.2$). Only significant trends ($P < 0.1$) are used to calculate R values. The subscripts of R define the direction of flows in the natural and managed watersheds; NN indicates that both managed and natural flows are decreasing, PP indicates that both managed and natural flows are increasing. The United States and Canada boundary outlines can be obtained from <https://www.census.gov/> and <https://www12.statcan.gc.ca/>.

the watersheds, flow trends are 20–167% (Category 4 in Fig. 2; 60th percentile $< R < 90$ th percentile; $1.2 < R < 2.67$) greater in the managed than the nearby natural watersheds, while 7–12% documented flow trends $> 167\%$ higher (Category 5 in Fig. 2; $R > 90$ th percentile; $R > 2.67$) in managed compared with nearby natural watersheds (Fig. 2). In spring, such flow amplifications occurred primarily in watersheds with declining trends, while in all other seasons such amplifications occurred primarily in watersheds with increasing trends. Flow trends were moderately dampened (Category 2 in Fig. 2; 10th percentile $< R < 40$ th percentile; $0.48 < R < 0.95$) in 11–31% of the watersheds and highly dampened (Category 1 in Fig. 2; 10th percentile $> R$; $R < 0.48$) in 9–31% of managed watersheds (Fig. 2). Overall, our findings imply that anthropogenic impacts are not necessarily constant throughout the year and point to the potential role of seasonally variable anthropogenic alterations in mediating flow trends over the long term.

The spread of the R values across the CONUS demonstrates that the anthropogenic influence on flows is highly localized and sensitive to the watershed (Fig. 3). Watersheds with minimal anthropogenic alterations ($0.95 < R < 1.2$) in at least one season are located in central plains (69 watersheds), northeast (41 watersheds) and west mountains (21 watersheds). We find hotspots of highly amplified ($R_{NN} > 2.67$) negative flow trends in the western plains (35 watersheds), where flows in managed watersheds are declining at a significantly ($P < 0.1$) greater rate than for their natural neighbours (Fig. 3). Amplification of declining flow trends can be attributed to increasing human water use to compensate for the climate trends in these arid landscapes. From an ecosystem management perspective, this can lead to loss of environmental flows and impact biodiversity of the riverine ecosystems (Fig. 4)³⁰. Highly amplified positive flow

trends ($R_{PP} > 2.67$) were apparent in the central plains (32 watersheds) (Fig. 3). These changes are more apparent in the fall and winter seasons and are possibly driven by a combination of land-use and dam-storage dynamics, specifically reservoir water release to support irrigation³¹, and a greater proportion of impervious area in the managed watersheds. Such amplification of flow trends in the managed watersheds highlights the possibility of greater flood-related damages as extreme events are expected to increase in the future climate (Fig. 4)³².

We find evidence of dampened declining response ($R_{NN} < 0.48$) in the western mountains, indicating that declining trends in managed watersheds are lower than in their natural neighbours, and this can be attributed to seasonal carry-over of storage that buffers climate trends²¹. The dampening of declining flows in the managed watersheds can be useful in buffering droughts that are likely to intensify in the next few decades (Fig. 4). However, increasing flow trends have dampened ($R_{PP} < 0.48$) mostly in the northeast (20 watersheds), where flows in the managed watersheds have been increasing at a 50% lower rate than their natural counterparts. This dampening of flow increases may allude to the role of human water management in alleviating the vagaries of a changing climate through the construction of water storage structures³³. It is highly likely that these storage structures may buffer the extreme flow events in the near future in the managed watersheds (Fig. 4).

Overall, these findings indicate that within the same region, human modifications can amplify, dampen or have low impact on streamflows. This spatial heterogeneity in the magnitude of alteration complicates our understanding and emphasizes the importance of continental-scale studies to highlight the role of anthropogenic drivers on flows.

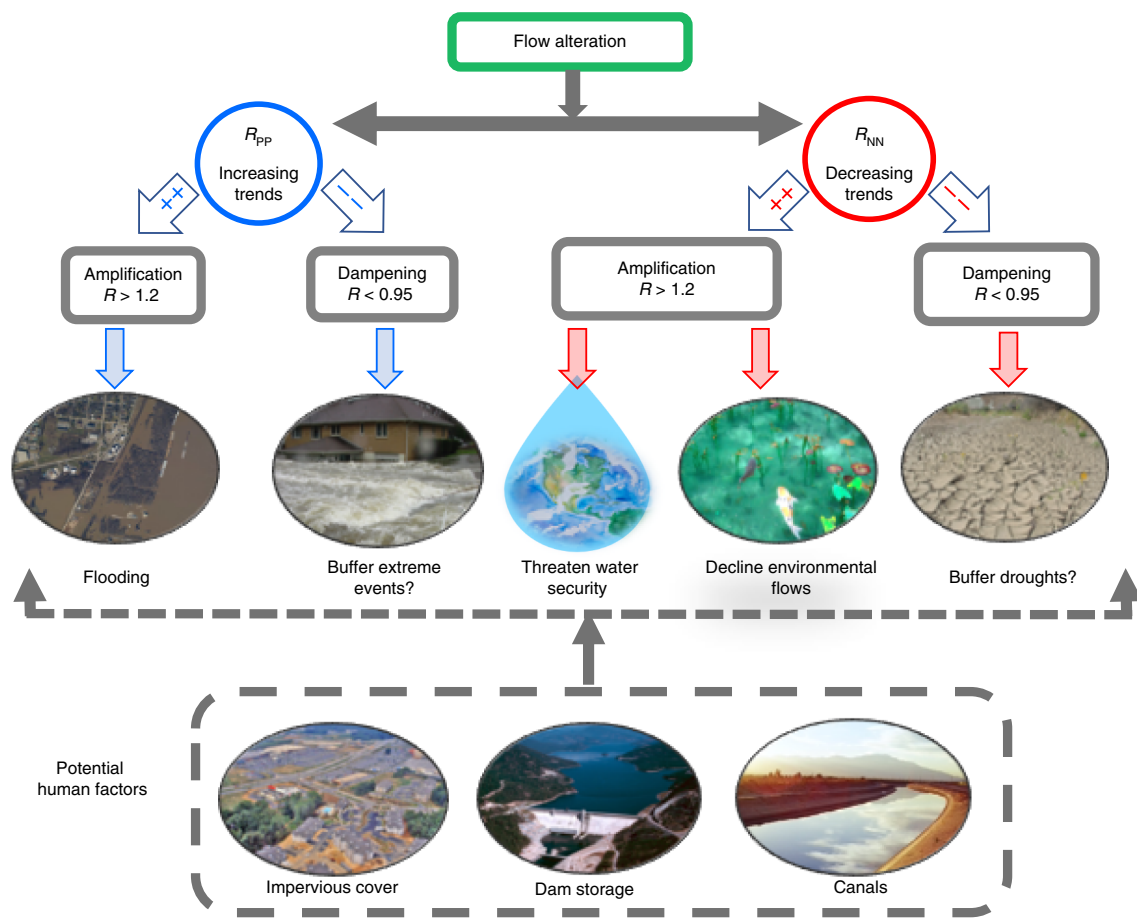


Fig. 4 | Implications of flow amplification and dampening (R_{PP} and R_{NN}) in managed watersheds on water security (floods and droughts), and the potential human factors that drive such flow alterations. An $R_{PP} > 1$ indicates that the flows in both the managed and natural watersheds are increasing over time, but the increase is greater (amplified) in the managed watershed compared with its natural neighbour. This can be attributed to an increase in impervious area that can contribute to flooding. Conversely, an $R_{NN} > 1$ indicates that the flows in the neighbouring natural and managed watersheds are both decreasing over time, but the decrease is greater (amplified) in the managed watershed compared with its natural neighbour. This can be attributed to factors such as human water use (irrigation and so on) that can reduce environmental flows. Credits: (images in centre and bottom rows, left to right) NOAA/USGS, NOAA/USGS, Flaticon (droplet) and Elena Mozhvilo/Unsplash, Sora Sagano/Unsplash, Alan M. Cressler/USGS, USACE/USGS, USGS.

Controls on flow trends in natural and managed watersheds.

RF models were able to describe seasonal flow trends in natural watersheds more accurately than in managed watersheds (Supplementary Table 3), which is consistent with others that have found human interventions to decrease predictability of hydrologic models. Indeed, model results highlight that dominant controls on seasonal flow trends are significantly ($P < 0.1$) different between natural and managed watersheds (Fig. 5). Despite differences, season emerged as the most important variable for both natural and managed watersheds, and this is reasonable given that we are exploring seasonal trends. Interestingly, however, the partial dependence plots show how season modulates the response differently in natural versus managed watersheds (Supplementary Fig 3). For natural watersheds, winter has the strongest effect on increasing flows, followed by fall and summer, while a small decrease in flow is visible in spring. By contrast, in managed watersheds spring plays a much larger role in decreasing flows, followed by summer, while winter and fall play a much smaller role in increasing flows. Managed watersheds often have dams that hold floodwater back in spring and summer, possibly contributing to their stronger role in declining flows. Managed watersheds can also buffer increasing winter flows by holding water back.

After accounting for season, climatic driver and catchment attributes (for example, seasonal precipitation totals, topographic slope and forest cover) emerged as the most important variables for the natural watersheds (Fig. 5). A positive relationship between the flow and precipitation trends in the partial dependence plot suggest that seasonal flow has increased due to increase in seasonal precipitation over time (Supplementary Fig 3). Seasonal flow trends decline with increase in topographic slope, suggesting that flows have declined more in steep watersheds. It is likely that most of these steep watersheds are headwater streams that have been experiencing a rapid decline in seasonal flows in many regions across North America³⁴. These results underscore the need for better monitoring and management of natural headwater streams that serve as ‘water towers’³⁵ and represent more than 60% of the streams in the United States and are highly vulnerable to climate change³⁶.

By contrast, in managed watersheds, the most important drivers of seasonal trends are changes in dam storage, canal density and impervious area (Fig. 5). Changes in dam storage occur due primarily to the construction of new reservoirs that store and release water on the basis of seasonal needs, and thus alter seasonal trends. The partial dependence plot of storage highlights that increases in dam storage have led to declines in seasonal

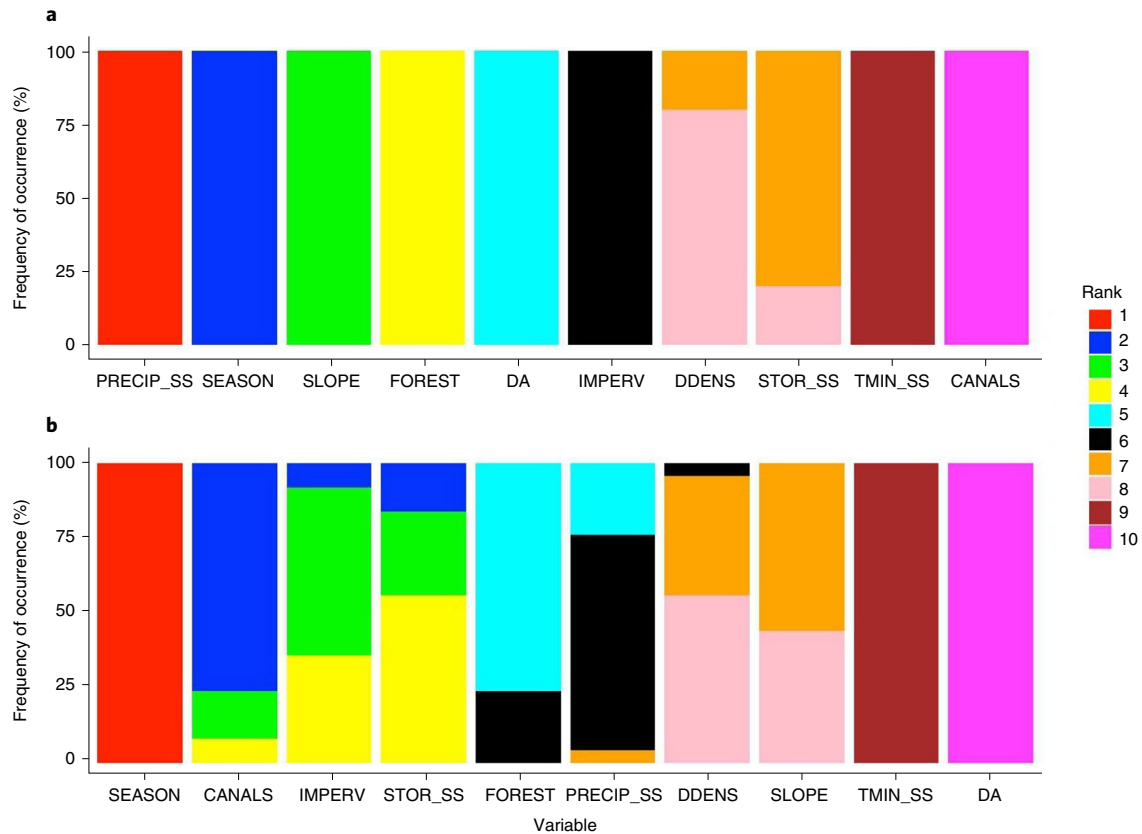


Fig. 5 | The ranking of key variables derived from RF models of seasonal flow trends in natural and managed watersheds. a, Natural watersheds. **b**, Managed watersheds. The frequency of occurrence of rank 1 is 100 for changes in seasonal precipitation (PRECIP_SS), suggesting that the variable attained the same rank 1 across all runs. The abbreviations used here can be gleaned from Supplementary Table 4.

flows (Supplementary Fig 3). This result is further supported by a negative relationship between increase in storage and flow trends during winter ($P < 0.0001$) and spring ($P < 0.0001$), indicating increase in storage has possibly led to the decreased winter and spring flows, while a positive relationship exists between dam-storage trends and summer flow trends ($P < 0.05$), and there is no significant ($P > 0.1$) relationship during fall. Thus, reservoirs in managed watersheds decrease streamflows in winter and spring by holding back snowmelt run-off and increase streamflows in fall by releasing stored run-off. Our findings are consistent with others who reported how storing water in reservoirs in the wet season and releasing it during dry periods could influence flow trends in the managed watersheds³⁷. Indeed, our hotspots of alteration metrics ($R > 2.67$) in the western United States and southeast coastal United States correspond to watersheds with some of the highest dam density (per unit area) and storage (per unit area)⁶. Overall, these findings emphasize some of the ways in which dam and reservoir operations can contribute to the spatio-temporal heterogeneity in anthropogenic influence on flows. Our work calls for more sustainable management of dam storage and argues for optimizing our storage needs to minimize its impact on flow regimes, people and biodiversity downstream³⁸.

Our RF model also shows that canal density is one of the key drivers of streamflow trends in the managed watersheds (Fig. 5). Broadly, canal density is reflective of development and land-use change, driven mostly by intensive agricultural practices as canals are heavily used for irrigation, water diversion and transportation of water via inter-basin transfers to other regions. In other words, higher canal density may suggest greater water consumption and extraction from rivers.

Finally, another critical driver of streamflow trends in the managed watershed is the impervious cover (Fig. 5), which increases streamflow by reducing infiltration and evapotranspiration^{19,39}. The partial dependence plot shows an increase in seasonal flows with impervious cover implying that managed watersheds with greater impervious area are more likely to experience an increase in seasonal flows (Supplementary Fig 3). Our findings are consistent with others that have explored the linkages between the impervious cover and streamflow trends¹⁸. Note, however, that unlike the change in the dam-storage metric, the impervious-cover metric is a static variable that is related to the cover in the year 2006. It would be interesting to explore the relationship between change in impervious cover and increasing flow trends; however, such data were not available for our current study. Nevertheless, our finding of flow amplification in urbanized watersheds is important since with the rise of extreme events due to climate change, flow amplification due to urbanization might make the watersheds more vulnerable to flooding (Fig. 4)⁴⁰. These findings highlight a need for using grey and green infrastructure to minimize flooding damage in urbanized regions.

Humans are dramatically altering the global water cycle, with floods and droughts threatening water security and our well-being. We argue for more targeted interventions to mitigate the effect of diverse anthropogenic drivers on flow regimes (Fig. 4). Our work joins the growing body of literature that demonstrates the influence of anthropogenic influences on streamflow^{22–24}. The difference is that we compare seasonal flow trends between natural and managed watersheds to understand how human activity can both amplify and dampen climate trends in different seasons and in different regions. We found seasonal flow trends to be significantly

($P < 0.1$) different between natural and managed watersheds, in contrast to previous work that found no remarkable difference in annual flow trends¹⁷. Our results further suggest that while climate and topography explain the seasonal flow trends of flows in natural watersheds, impervious cover, canal density and change in dam storage drive flow trends in managed watersheds. These findings highlight the need to consider adaptation strategies to mitigate the negative impact of human disturbance on flows. Specifically, in water-stressed regions of the western United States where flows are declining at a much faster rate than can be attributed to climate, stream ecosystems are at risk due to loss of environmental flows. Conversely, in more humid regions in the central and eastern United States, where flows are increasing at a greater rate than can be attributed to climate, adaptation strategies need to be designed to address flooding-related risks³⁰. Overall, with more extreme events and increasing human water needs, watershed management efforts should focus on mitigating and adapting to a changing climate.

Methods

The data sources and the statistical methods used in the study are discussed in the following subsections.

Data sources. We obtained streamflow data from 1950 to 2009 from the United States Geological Survey (USGS) for US streamflow and from Water Survey of Canada for Canadian streamflow. We selected sites that have data for at least 90% of the months over 55 years, with each month having data for at least 55 out of 60 years. These criteria led to the selection of 2,272 gauges across North America (Supplementary Fig 1). The gauges thus selected were classified as natural (minimally impacted by human disturbance) or managed on the basis of the classification system developed by the USGS Gauges II dataset in the United States⁴¹ and the Reference Hydrometric Basin Network in Canada⁴². To identify natural watersheds, the USGS Gauges II dataset quantified disturbance on the basis of a combination of three key items of information⁴¹: (1) hydrologic disturbance index, (2) qualitative assessment of images to detect human intervention near stream gauge and (3) expert scrutiny of local USGS annual reports. The hydrologic disturbance index is based on seven geospatial variables indicating human disturbance of flows: presence of major dams in the watershed, change in reservoir storage, percentage of canals, road density, distance to nearest pollutant discharge site, freshwater withdrawal and fragmentation of undeveloped land. Watersheds were provided scores based on these variables, and the scores were aggregated to identify the least disturbed (natural) watersheds. In addition, topographic maps and imagery were used to detect small interventions, such as diversion structures and small dams, and local USGS annual data reports were used to ascertain local water management decisions such as regulations and diversions. The methodology led to the identification of 263 natural and 1,826 managed watersheds in the United States. For the Canadian dataset, stations with pristine conditions over time were obtained from the Canadian Reference Hydrometric Basin Network dataset⁴². These reference sites (52 watersheds) have minimal human impacts as defined by the agricultural and urban lands, road density, population density and presence and significance of flow structures^{30,42}. The remaining watersheds were classified as managed.

Daily flow data were used to compute seasonal run-off totals (mm season⁻¹). Seasons were defined as winter (December, January, February), spring (March, April, May), summer (June, July, August) and fall (September, October, November). Streamflow datasets were accessed in R 4.0.2 using dataRetrieval package and tidyHydat package for the US and Canadian gauges, respectively.

We extracted monthly rainfall totals and monthly minimum (T_{\min}) and maximum (T_{\max}) temperatures from PRISM climate datasets, which provided data at a resolution of 4 km² from 1950 to 2009 at CONUS scale⁴³. The gridded raster data were spatially averaged over the watershed boundary (obtained through Gauges II) to generate monthly scale values for each watershed. Finally, monthly scale rainfall was summed to calculate seasonal rainfall totals, and monthly scale temperatures were averaged to get mean seasonal T_{\min} and T_{\max} temperatures.

Trend analysis. The Mann–Kendall test was conducted to quantify trends in seasonal streamflow, climate variables (precipitation and temperature) and dam-storage datasets over 60 years. Broadly, the Mann–Kendall test is a widely known⁴⁴ non-parametric and rank-based method to detect trends in climatic and hydrologic datasets⁴⁵. Generally, trend detection approaches are sensitive to auto-correlation in time series and can lead to spurious trends⁴⁶. We used one of the commonly used variance correction approaches to address auto-correlation in time series⁴⁶. Sen slope was used to compute the rate of change of flows, precipitation and temperature individually for all seasons⁴⁷. To show change (% yr⁻¹) in flows, we divided the Sen slope with seasonal mean flows of the first ten years (1950–1960).

RF model. We used the RF model for predicting seasonal flow trends as a function of climate and anthropogenic drivers. We limit this analysis to US scale (~2,100 watersheds) since watershed attributes needed to develop the model were not easily accessible for Canada. RF is a non-parametric, multivariate, machine-learning-based tool that utilizes a decision tree framework to model responses⁴⁸. The RF algorithm integrates bagging with decision tree splitting criterion and randomization⁴⁸. Bagging (bootstrap aggregation) is an ensemble approach that generates out-of-bag data with replacement from the training set. The RF algorithm randomly selects out-of-bag data and a set of independent variables, resulting in numerous trees (determined by *n*tree parameter). The random selection of predictors (determined by *m*try parameter) and out-of-bag data assures trees are uncorrelated. Later, predictions from all trees are averaged to avoid overfitting by the model. The RF approach has been widely used in hydrological science to conduct variable importance analysis that ranks the key drivers of hydrological responses such as streamflow⁴⁹.

In this study, we developed two separate RF models to explore the drivers of seasonal streamflow trends (Sen slopes) in natural and managed watersheds. We explored 21 independent variables (Supplementary Table 4) and selected the ten climatic and anthropogenic variables that were least correlated among themselves (Supplementary Fig 2). Given that our goal was to identify the drivers of seasonal flow trends, we also used the categorical variable 'season' as one of the independent variables in RF models. The climate drivers used were the seasonal Sen slopes of the precipitation and temperature that were estimated from the PRISM datasets. The watershed attributes included impervious cover, forest cover, drainage area, mean topographic slope, mean elevation, percentage of canals, population density, road density and dam storage and were available from the USGS Gauges II⁵⁰ (Supplementary Table 4). Of these attributes, time series data were available for the dam-storage dataset in the Gauges II database that we used as one of the predictors in the RF model. Although variables such as impervious cover are expected to change over time, we did not have the information to include this for our analysis. We acknowledge that this is a limitation of our study, and temporal trends in variables such as the impervious area would be able to improve the RF modelling and interpretation.

Following variable selection, variable importance analysis⁵¹ was used to rank the key variables that may have the most influence on the seasonal flows trends. The importance of variables is estimated by tracking change in mean square error of model predictions when the variable of interest is permuted and the rest of the predictors are held constant⁵¹. This was done by running the RF model 25 times and ranking the drivers during each iteration. We then calculated the frequency of occurrence of each rank, for each variable and among all 25 iterations. For example, if the frequency of occurrence of rank 1 for any variable is 100, it suggests that the variable attained the same rank 1 across all runs.

To understand the marginal behaviour of the key variables on the RF model predictions, we made use of the partial dependence plots⁵². The partial dependence plots explore the change in average predictive response of the model with the variable of interest while keeping the remaining predictors at their average values⁵². The RF model parameters included the number of trees generated (*n*tree = 2,000, default: 500) and *m*try = 3 (number of independent variables/3). However, it is worth mentioning that these parameters have minimal effect on RF model outputs⁵¹. We estimated Nash–Sutcliffe efficiency, coefficient of determination and mean square error to assess the RF model performance in simulating both magnitude and direction of seasonal flow trends. The RF modelling was conducted with randomForest 4.6–12, and partial dependence plots were generated with pdp in R 4.0.2.

Comparing seasonal flow trends in natural and managed watersheds. To compare streamflow trends between natural watersheds and their managed neighbours, we used the approach developed by ref. 17, where natural and managed watersheds that were within a 115 km radius were considered to be climatologically similar to each other. Trends from managed watersheds that were within a 115 km radius of a natural watershed were extracted and compared with the trends from the natural watersheds. The 115 km radius was based on an analysis of the distance where the correlation between the trends in the natural and managed watersheds was the highest, indicating that the gauges belonged in a similar climate regime. This methodology allowed us to do a direct comparison between natural and nearby human-modified streamflow trends. This pairing of watersheds resulted in approximately 1,151 pairs of managed and natural watersheds. The number of managed gauges that were proximal to a natural gauge ranged from 1 to 42 with a median of 4. We focus our comparison on watershed pairs that exhibited significant ($P < 0.1$) Sen slopes in seasonal flows in both natural and managed watersheds.

We developed a suite of four alteration metrics (R_{NN} , R_{PP} , R_{NP} , R_{PN}): the magnitude of the metric is the absolute value of the ratio of the significant ($P < 0.1$) flow trend in the managed to the natural watershed, while the subscripts represent the direction of change. Specifically, NN indicates that both managed and natural flows are decreasing, PP indicates that both managed and natural flows are increasing, NP indicates that managed is decreasing and natural is increasing and PN indicates managed is increasing and natural is decreasing. To highlight the extent of change in the managed watersheds, we categorized the alteration

metrics into five classes on the basis of the percentile of R values: highly dampened ($R < 10$ th percentile), moderately dampened ($10\text{th} \leq R < 40\text{th}$ percentile), low impact ($40\text{th} \leq R < 60\text{th}$ percentile), moderately amplified ($90\text{th} > R \geq 60\text{th}$ percentile) and highly amplified ($R \geq 90\text{th}$ percentile). An R value < 1 indicates that flow trend in the managed watershed is lower than that in the natural watershed, and these are classified as dampened. For example, $R = 0.5$ indicates that the flow trend in a managed watershed is 50% lower than the trend in its nearby natural neighbour. Similarly, an R value > 1 indicates that flow trend in the managed watershed is higher than that in the natural watershed, and these are classified as amplified. An $R = 1.5$ indicates that the flow trend in a managed watershed is 50% greater than the trend in its nearby natural neighbour. We acknowledge that the categorization is somewhat arbitrary, but it allowed us to quantify the extent of anthropogenic influence in the managed watersheds.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Flow datasets used in the study are publicly available from the United States Geological Survey (<https://waterdata.usgs.gov/nwis/rt>) and the Water Survey of Canada (https://wateroffice.ec.gc.ca/mainmenu/historical_data_index_e.html). The Gauges II datasets are publicly available through the USGS (https://water.usgs.gov/GIS/metadata/usgswrd/XML/gagesII_Sept2011.xml#stdorder). The climatic datasets used in the study are publicly available from Oregon State University (<https://prism.oregonstate.edu/>).

Received: 16 July 2021; Accepted: 10 January 2022;

Published online: 24 February 2022

References

- Vörösmarty, C. J., Green, P., Salisbury, J. & Lammers, R. B. Global water resources: vulnerability from climate change and population growth. *Science* **289**, 284–288 (2000).
- Milly, P. C. D., Dunne, K. A. & Vecchia, A. V. Global pattern of trends in streamflow and water availability in a changing climate. *Nature* **438**, 347–350 (2005).
- Barnett, T. P. et al. Human-induced changes in the hydrology of the western United States. *Science* **319**, 1080–1083 (2008).
- Berghuijs, W. R., Woods, R. A. & Hrachowitz, M. A precipitation shift from snow towards rain leads to a decrease in streamflow. *Nat. Clim. Change* **4**, 583–586 (2014).
- Vörösmarty, C. J. et al. in *Ecosystems and Human Well-Being: Current State and Trends* (eds Rijberman, F. et al.) Ch. 7 (Island Press, 2005); <https://www.millenniumassessment.org/documents/document.276.aspx.pdf>
- Graf, W. L. Dam nation: a geographic census of American dams and their large-scale hydrologic impacts. *Water Resour. Res.* **35**, 1305–1311 (1999).
- Dynesius, M. & Nilsson, C. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* **266**, 753–762 (1994).
- Adam, J. C., Hamlet, A. F. & Lettenmaier, D. P. Implications of global climate change for snowmelt hydrology in the twenty-first century. *Hydrol. Process.* **23**, 962–972 (2009).
- Burn, D. H. & Whitfield, P. H. Changes in cold region flood regimes inferred from long-record reference gauging stations. *Water Resour. Res.* **53**, 2643–2658 (2017).
- Lettenmaier, D. P., Wood, E. F. & Wallis, J. R. Hydro-climatological trends in the continental United States, 1948–88. *J. Clim.* **7**, 586–607 (1994).
- Sagarika, S., Kalra, A. & Ahmad, S. Evaluating the effect of persistence on long-term trends and analyzing step changes in streamflows of the continental United States. *J. Hydrol.* **517**, 36–53 (2014).
- Birsan, M. V., Molnar, P., Burlando, P. & Pfaundler, M. Streamflow trends in Switzerland. *J. Hydrol.* **314**, 312–329 (2005).
- Stahl, K. et al. Hydrology and Earth system sciences streamflow trends in Europe: evidence from a dataset of near-natural catchments. *Hydrol. Earth Syst. Sci.* **14**, 2367–2382 (2010).
- Dettinger, M. D. & Diaz, H. F. Global characteristics of stream flow seasonality and variability. *J. Hydrometeorol.* **1**, 289–310 (2000).
- McCabe, G. J. & Wolock, D. M. A step increase in streamflow in the conterminous United States. *Geophys. Res. Lett.* **29**, 8–11 (2002).
- Rice, J. S., Emanuel, R. E., Vose, J. M. & Nelson, S. A. C. Continental US streamflow trends from 1940 to 2009 and their relationships with watershed spatial characteristics. *Water Resour. Res.* **51**, 6262–6275 (2015).
- Ficklin, D. L., Abatzoglou, J. T., Robeson, S. M., Null, S. E. & Knouft, J. H. Natural and managed watersheds show similar responses to recent climate change. *Proc. Natl Acad. Sci. USA* **115**, 8553–8557 (2018).
- Dudley, R. W., Hirsch, R. M., Archfield, S. A., Blum, A. G. & Renard, B. Low streamflow trends at human-impacted and reference basins in the United States. *J. Hydrol.* **580**, 124254 (2020).
- Bhaskar, A. S., Hopkins, K. G., Smith, B. K., Stephens, T. A. & Miller, A. J. Hydrologic signals and surprises in US streamflow records during urbanization. *Water Resour. Res.* **56**, 1–22 (2020).
- Dethier, E. N., Sartain, S. L., Renshaw, C. E. & Magilligan, F. J. Spatially coherent regional changes in seasonal extreme streamflow events in the United States and Canada since 1950. *Sci. Adv.* **6**, eaba5939 (2020).
- Adam, J. C., Haddeland, I., Su, F. & Lettenmaier, D. P. Simulation of reservoir influences on annual and seasonal streamflow changes for the Lena, Yenisei, and Ob' rivers. *J. Geophys. Res. Atmos.* **112**, D24114 (2007).
- Haddeland, I. et al. Global water resources affected by human interventions and climate change. *Proc. Natl Acad. Sci. USA* **111**, 3251–3256 (2014).
- Jaramillo, F. & Destouni, G. Local flow regulation and irrigation raise global human water consumption and footprint. *Science* **350**, 1248–1251 (2015).
- Veldkamp, T. I. E. et al. Water scarcity hotspots travel downstream due to human interventions in the 20th and 21st century. *Nat. Commun.* **8**, 15697 (2017).
- Gudmundsson, L. et al. Globally observed trends in mean and extreme river flow attributed to climate change. *Science* **371**, 1159–1162 (2021).
- Luce, C. H. & Holden, Z. A. Declining annual streamflow distributions in the Pacific Northwest United States, 1948–2006. *Geophys. Res. Lett.* **36**, 2–7 (2009).
- Kim, J. S. & Jain, S. High-resolution streamflow trend analysis applicable to annual decision calendars: a western United States case study. *Climatic Change* **102**, 699–707 (2010).
- Zhang, X., Harvey, K. D., Hogg, W. D. & Yuzyk, T. R. Trends in Canadian streamflow. *Water Resour.* **37**, 987–998 (2001).
- Yang, Y. et al. Streamflow stationarity in a changing world. *Environ. Res. Lett.* **16**, 064096 (2021).
- Vörösmarty, C. J. et al. Global threats to human water security and river biodiversity. *Nature* **467**, 555–561 (2010).
- Magilligan, F. J. & Nislow, K. H. Changes in hydrologic regime by dams. *Geomorphology* **71**, 61–78 (2005).
- Wing, O. E. J., Pinter, N., Bates, P. D. & Kousky, C. New insights into US flood vulnerability revealed from flood insurance big data. *Nat. Commun.* **11**, 1444 (2020).
- Chalise, D. R., Sankarasubramanian, A. & Ruhi, A. Dams and climate interact to alter river flow regimes across the United States. *Earths Future* **9**, e2020EF001816 (2021).
- Rood, S. B. et al. Declining summer flows of Rocky Mountain rivers: changing seasonal hydrology and probable impacts on floodplain forests. *J. Hydrol.* **349**, 397–410 (2008).
- Viviroli, D., Dürr, H. H., Messerli, B., Meybeck, M. & Weingartner, R. Mountains of the world, water towers for humanity: typology, mapping, and global significance. *Water Resour. Res.* **43**, 7447 (2007).
- Freeman, M. C., Pringle, C. M. & Jackson, C. R. Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales. *J. Am. Water Resour. Assoc.* **43**, 5–14 (2007).
- Lorenzo-Lacruz, J., Vicente-Serrano, S. M., López-Moreno, J. I., Morán-Tejada, E. & Zabalza, J. Recent trends in Iberian streamflows (1945–2005). *J. Hydrol.* **414–415**, 463–475 (2012).
- Dams and Development: A New Framework for Decision-Making* (World Commission on Dams, 2016).
- Suttles, K. M. et al. Assessment of hydrologic vulnerability to urbanization and climate change in a rapidly changing watershed in the Southeast US. *Sci. Total Environ.* **645**, 806–816 (2018).
- IPCC *Climate Change 2021: The Physical Science Basis* (eds Masson-Delmotte, V. et al.) (Cambridge Univ. Press, 2021); <https://www.ipcc.ch/report/ar6/wg1/#SPM>
- Falcone, J. A., Carlisle, D. M., Wolock, D. M. & Meador, M. R. GAGES: a stream gage database for evaluating natural and altered flow conditions in the conterminous United States. *Ecology* **91**, 621–621 (2010).
- Brimley, B. et al. *Reference Hydrometric Basin Network* (Government of Canada, 1999); <https://www.canada.ca/en/environment-climate-change/services/water-overview/quantity/monitoring/survey/data-products-services/reference-hydrometric-basin-network.html>
- PRISM Climate Data* (PRISM Climate Group, 2020); <https://prism.oregonstate.edu/>
- Kendall, M. *Rank Correlation Methods* (Griffin, 2011).
- Singh, N. K. & Borrok, D. M. A Granger causality analysis of groundwater patterns over a half-century. *Sci. Rep.* **9**, 12828 (2019).
- Hamed, K. H. & Ramachandra Rao, A. A modified Mann-Kendall trend test for autocorrelated data. *J. Hydrol.* **204**, 182–196 (1998).
- Sen, P. K. Estimates of the regression coefficient based on Kendall's tau. *J. Am. Stat. Assoc.* **63**, 1379–1389 (1968).
- Biau, G. & Scornet, E. A random forest guided tour. *Test* **25**, 197–227 (2016).
- Singh, N. K., Emanuel, R. E., Nippen, F., McGlynn, B. L. & Miniati, C. F. The relative influence of storm and landscape characteristics on shallow groundwater responses in forested headwater catchments. *Water Resour. Res.* **54**, 9883–9900 (2018).

50. Falcone, J. A. *Geospatial Attributes of Gages for Evaluating Streamflow* (US Geological Survey, 2011).
51. Liaw, A. & Wiener, M. Classification and regression by randomForest. *R News* **2**, 18–22 (2002).
52. Friedman, J. H. Greedy function approximation: a gradient boosting machine. *Ann. Stat.* **29**, 1189–1232 (2001).

Acknowledgements

The research published in this paper was supported by the 'Lake Futures' project under the Global Water Futures program, funded by the Canada First Research Excellence Fund.

Author contributions

N.K.S. and N.B.B. conceptualized the project. N.K.S. designed the methodology. N.K.S. and N.B.B. conducted the investigation. N.K.S. and N.B.B. did the visualization. N.B.B. supervised. N.K.S. wrote the original draft. N.B.B. reviewed and edited the draft.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41893-022-00848-1>.

Correspondence and requests for materials should be addressed to Nitin K. Singh.

Peer review information *Nature Sustainability* thanks the anonymous reviewers for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s), under exclusive licence to Springer Nature Limited 2022

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection Data were collected by United States Geological Survey and Environment Canada

Data analysis Commonly used software such as Arc GIS and R were used for making figures

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Flow datasets are publicly available through United States Geological Survey (<https://waterdata.usgs.gov/nwis/rt>) and Environment Canada (<https://wateroffice.ec.gc.ca/>). Climate datasets are publicly available from Oregon state university (<https://prism.oregonstate.edu/explorer/>) ; Figures 1-3 are derived from raw data.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	n/a
Data exclusions	<i>Describe any data exclusions. If no data were excluded from the analyses, state so OR if data were excluded, describe the exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.</i>
Replication	<i>Describe the measures taken to verify the reproducibility of the experimental findings. If all attempts at replication were successful, confirm this OR if there are any findings that were not replicated or cannot be reproduced, note this and describe why.</i>
Randomization	<i>Describe how samples/organisms/participants were allocated into experimental groups. If allocation was not random, describe how covariates were controlled OR if this is not relevant to your study, explain why.</i>
Blinding	<i>Describe whether the investigators were blinded to group allocation during data collection and/or analysis. If blinding was not possible, describe why OR explain why blinding was not relevant to your study.</i>

Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	n/a
Research sample	<i>State the research sample (e.g. Harvard university undergraduates, villagers in rural India) and provide relevant demographic information (e.g. age, sex) and indicate whether the sample is representative. Provide a rationale for the study sample chosen. For studies involving existing datasets, please describe the dataset and source.</i>
Sampling strategy	<i>Describe the sampling procedure (e.g. random, snowball, stratified, convenience). Describe the statistical methods that were used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient. For qualitative data, please indicate whether data saturation was considered, and what criteria were used to decide that no further sampling was needed.</i>
Data collection	<i>Provide details about the data collection procedure, including the instruments or devices used to record the data (e.g. pen and paper, computer, eye tracker, video or audio equipment) whether anyone was present besides the participant(s) and the researcher, and whether the researcher was blind to experimental condition and/or the study hypothesis during data collection.</i>
Timing	<i>Indicate the start and stop dates of data collection. If there is a gap between collection periods, state the dates for each sample cohort.</i>
Data exclusions	<i>If no data were excluded from the analyses, state so OR if data were excluded, provide the exact number of exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.</i>
Non-participation	<i>State how many participants dropped out/declined participation and the reason(s) given OR provide response rate OR state that no participants dropped out/declined participation.</i>
Randomization	<i>If participants were not allocated into experimental groups, state so OR describe how participants were allocated to groups, and if allocation was not random, describe how covariates were controlled.</i>

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	n/a
Research sample	<i>Describe the research sample (e.g. a group of tagged <i>Passer domesticus</i>, all <i>Stenocereus thurberi</i> within Organ Pipe Cactus National Monument), and provide a rationale for the sample choice. When relevant, describe the organism taxa, source, sex, age range and</i>

any manipulations. State what population the sample is meant to represent when applicable. For studies involving existing datasets, describe the data and its source.

Sampling strategy

Note the sampling procedure. Describe the statistical methods that were used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient.

Data collection

Describe the data collection procedure, including who recorded the data and how.

Timing and spatial scale

Indicate the start and stop dates of data collection, noting the frequency and periodicity of sampling and providing a rationale for these choices. If there is a gap between collection periods, state the dates for each sample cohort. Specify the spatial scale from which the data are taken

Data exclusions

If no data were excluded from the analyses, state so OR if data were excluded, describe the exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.

Reproducibility

Describe the measures taken to verify the reproducibility of experimental findings. For each experiment, note whether any attempts to repeat the experiment failed OR state that all attempts to repeat the experiment were successful.

Randomization

Describe how samples/organisms/participants were allocated into groups. If allocation was not random, describe how covariates were controlled. If this is not relevant to your study, explain why.

Blinding

Describe the extent of blinding used during data acquisition and analysis. If blinding was not possible, describe why OR explain why blinding was not relevant to your study.

Did the study involve field work? Yes No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern

Methods

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging