Identifying functional flow linkages between stream alteration and biological stream condition indices across California

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RP led the preparation of this manuscript, data analysis, coding, and project design. KI contributed to data analysis and coding. RP, ES, KI, RM, SY, RL contributed to the conceptualization and project design. All authors contributed to writing this manuscript.

Keywords

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Abstract

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Large state or regional environmental flow programs, such as the one based on the California Environmental Flows Framework (CEFF), rely on broadly applicable relationships between flow and ecology to inform management decisions. California, despite having high flow and bioassessment data density, has not established relationships between specific elements of the annual hydrograph and biological stream condition. To address this, we spatially and temporally linked USGS gage stations and biological assessment sites in California to identify suitable site pairs for comparisons of streamflow alteration with biological condition at a statewide scale. Flows were assessed using a set of functional flow metrics which provide a comprehensive way to compare alteration and seasonal variation in streamflow across different locations. Biological response was evaluated using the California Stream Condition Index (CSCI) and Algal Stream Condition Index (ASCI), which quantify biological conditions by translating benthic invertebrate or algal resources with watershed-scale environmental data into an overall measure of stream health. These indices provide a consistent statewide standard for interpreting bioassessment data and, thus, a means of quantitatively comparing stream conditions throughout the state. The results indicate that indices of biological stream condition were most closely associated with flow alteration in timing metrics such as fall pulse timing, dry-season timing, and wet season timing. Magnitude metrics such as dry-season baseflow, wet season baseflow, and the fall pulse magnitude were also important drivers of variation, and a metric of seasonality was strongly tied to biological stream conditions, particularly in snowmelt streams. Development of flow criteria under CEFF should consider that alteration to any of these seasonal flow components (e.g., dry-season baseflow, fall pulse flow, wet-season baseflow, spring recession flow) may be important in restructuring biological communities.

Contribution to the field

Large state or regional environmental flow programs rely on broadly applicable relationships between flow and ecology to inform management decisions. California, USA, despite having high flow and bioassessment data density, has not established relationships between specific elements of the annual hydrograph and biological stream condition. We spatially and temporally linked river flow stations and biological assessment sites in California to identify suitable site pairs for comparisons of streamflow alteration with stream health based on biological indices of benthic invertebrates and algae at a statewide and stream class scale. These indices provide a consistent statewide standard for interpreting bioassessment data and, thus, a means of quantitatively comparing stream conditions throughout the state. The results indicate that stream health indices were most closely associated with flow alteration via timing metrics such as seasonality, fall pulse timing, dry-season timing, and wet season timing. Development of ecological flows should consider that alteration to any of these seasonal flow components may be important in restructuring biological communities, and flow management can be implemented using this approach to further identify linkages between flow and biological stream condition.

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Abstract

Large state or regional environmental flow programs, such as the one based on the California Environmental Flows Framework (CEFF), rely on broadly applicable relationships between flow and ecology to inform management decisions. California, despite having high flow and bioassessment data density, has not established relationships between specific elements of the annual hydrograph and biological stream condition. To address this, we spatially and temporally linked USGS gage stations and biological assessment sites in California to identify suitable site pairs for comparisons of streamflow alteration with biological condition at a statewide scale. Flows were assessed using a set of functional flow metrics which provide a comprehensive way to compare alteration and seasonal variation in streamflow across different locations. Biological response was evaluated using the California Stream Condition Index (CSCI) and Algal Stream Condition Index (ASCI), which quantify biological conditions by translating benthic invertebrate or algal resources with watershed-scale environmental data into an overall measure of stream health. These indices provide a consistent statewide standard for interpreting bioassessment data and, thus, a means of quantitatively comparing stream conditions throughout the state. The results indicate that indices of biological stream condition were most closely associated with flow alteration in timing metrics such as fall pulse timing, dry-season timing, and wet season timing. Magnitude metrics such as dry-season baseflow, wet season baseflow, and the fall pulse magnitude were also important drivers of variation, and a metric of seasonality was strongly tied to biological stream conditions, particularly in snowmelt streams. Development of flow criteria under CEFF should consider that alteration to any of these seasonal flow components (e.g., dry-season baseflow, fall pulse flow, wet-season baseflow, spring recession flow) may be important in restructuring biological communities.

1 Introduction

Flow alteration is a pervasive and significant issue globally and in California (Poff et al., 2007; Grantham et al., 2014). Over 95% of California's gaged streams have altered flow (Zimmerman et al., 2017), and hydrologic alteration of flow by dams, diversions and urbanization can impact both seasonal and inter-annual flow variability. These flow modifications can impact population connectivity and gene flow, biodiversity, as well as ecological processes (Dudgeon et al., 2006; Yarnell et al., 2010; Carlisle et al., 2011; Peek et al., 2021). While the causes and related impacts of flow alteration are well documented (Poff et al., 2007), significant gaps exist in linking flow management with ecological responses to track current stream conditions, evaluate restoration efficacy, and provide future flow recommendations (Poff and Zimmerman, 2010).

A critical component of developing ecological flow needs for management is to identify relationships between specific flow metrics (that represent distinct elements of the annual hydrograph) and measures of biological stream conditions at broad spatial scales. Biological indicators have been widely used for assessing stream conditions, and benthic invertebrates and algae have been successfully used as indicators of stream health in a wide range of studies across the USA (Stevenson and Smol, 2003; Lawrence et al., 2010; Stevenson et al., 2010; Lunde et al., 2013; Stevenson, 2014; Mazor et al., 2016; Steel et al., 2018). Notably, these bioindicators have been extensively used to quantify biological impairment associated with shifts in the environment. For instance, hydrologic alteration or impairment has been shown to strongly influence aquatic benthic invertebrate communities (Poff et al., 2007; Rehn, 2009), and benthic invertebrates have more recently been used to link metrics of hydrologic variability to biological response (Poff and Zimmerman, 2010; Steel et al., 2018). The direct relationship between algae and flow has been reported as limited (Kirkwood et al., 2009; Miller et al., 2009; Schneider et al., 2016), with some exceptions involving algal blooms in large rivers (Cheng et al., 2019; Xia et al., 2020) and directly following a flood (Schneider et al., 2016). However, impacts of flow alteration on water quality (Nilsson and Renöfält, 2008) can also indirectly influence the composition of algal communities (Allan, 2004; Lange et al., 2016), thus these indicators provide a way to assess current conditions in multiple ways.

A major challenge to linking specific flow metrics with biological stream conditions is pairing data spatially and temporally and disentangling complex interactions among various flow components. While several monitoring datasets exist across broad spatial and temporal scales, identifying ways to coalesce and synthesize these data in a cogent manner remains difficult. Synthesis of existing monitoring datasets into a single scale or outcome is an important step for providing context to comparing sites, prioritize management actions, and improve monitoring and evaluation of restoration actions. While unified assessment tools have been developed (see Mazor et al., 2016; Beck et al., 2019b; Theroux et al., 2020), it remains difficult to integrate biological and flow metrics across a highly managed and heterogeneous landscape such as California.

There are several key datasets that provide data suitable for evaluating links between functional flows and stream health via biological indicators, though each is collected independently, thus sites are not often nested or designed to work in parallel. For biological and biophysical data, the Surface Water Ambient Monitoring Program (SWAMP) is tasked with assessing surface water quality throughout California. The program coordinates water quality monitoring across the state and collects data to support water resource management by the State Water Boards. For example, the data collected by SWAMP's probabilistic Perennial Stream Assessment survey is used to characterize in-stream biological conditions and make estimates about the extent of healthy streams in different regions of the state. These data include several biological indicators, including benthic invertebrates, benthic algae, and measures of physical habitat integrity. In addition, the US Geological Survey (USGS)

National Water Information System (NWIS) is a comprehensive and distributed application that provides a wide range of water data, including daily stream flows from over 28,000 stations across the United States. However, identifying how these datasets may integrate effectively remains an important first step towards a more unified development of ecological flow needs in freshwater systems.

California is well suited to test methods for identifying patterns in biological stream conditions associated with flow alteration because of its diversity of climate, geology, hydrology, and land use impacts. To better describe and quantify the different components of a seasonal hydrograph, a functional flow approach provides a standardized hydrologic method to evaluate and compare the role of flows in a stream ecosystem (Yarnell et al., 2020). Twenty-four functional flow metrics (FFM) were developed for California by Yarnell et al (2015, 2020) and comprise five main flow components (fall pulse flow, wet-season baseflow, peak flow, spring recession flow, and dry-season baseflow) of a flow regime, with individual metrics describing the magnitude, timing, frequency, duration and rate of change of each functional component (Appendix Table S1). They are not directly linked to individual/specific organisms/groups, but are associated to specific biological and ecosystem processes (Yarnell et al., 2020). Calculated from existing flow data, functional flow metrics provide a comprehensive way to compare alteration and seasonal variation in streamflow across different locations.

Standardized bioassessment indices such as the California Stream Condition Index (CSCI) and the Algal Stream Condition Index (ASCI) are quantitative measures of stream condition which can be used across broad spatial scales (Mazor et al., 2016; Theroux et al., 2020). Leveraging these statewide datasets in conjunction with recent methods for quantifying hydrologic variability at the stream segment scale across California (Stein et al.; Yarnell et al., 2020), provides a unique opportunity to assess biological response to hydrologic alteration in California. ASCI and CSCI are predictive multimetric indices developed for California streams (Mazor et al., 2016; Theroux et al., 2020) and comprise many stream and landscape components that describe biological sensitivities or tolerances to disturbance. The indices allow for the evaluation of biotic response without specificity to one individual metric (e.g., taxa richness), enabling coverage of a broader range of characteristics and stressors associated with individual watersheds. These indices are intended to aid stream management and decision making (e.g., condition assessment, prioritization and flow target development; see (Stein et al., 2017; Mazor et al., 2018; Beck et al., 2019a) and have been integrated into unified assessments of stream health (Beck et al., 2019b). With low regional bias and consideration of natural variation, ASCI and CSCI can distinguish between reference and biologically degraded sites, can be applied at multiple scales, and are appropriate to apply to the diverse landscapes of California (Mazor et al., 2018).

Identifying and understanding functional flow linkages between biological responses and specific elements of the flow regime are crucial for implementing a functional flow approach. Identifying which metrics or elements of a flow regime have the greatest impact on benthic invertebrate and algal communities for monitoring and management of stream health provides a quantitative method to build on documented relationships between flow and functional processes in riverine systems (Yarnell et al., 2015). Functional flow metrics provide a method to quantify these linkages—for example the hyporheic zone is linked with wet season baseflow, the fall pulse flow helps flush nutrients downstream, and the spring recession can export nutrients from floodplain to channel—as different hydrologic elements can support different biogeochemical and ecosystem functions (Yarnell et al., 2015).

A significant gap in our understanding and implementation of environmental flows is determination of how certain flow components link to biological stream conditions. For assessment, monitoring, and recovery purposes, it is important to determine and evaluate such linkages. Identifying key parameters that are comparable and measurable (i.e., FFM, CSCI, ASCI) is important to assess restoration efficacy and track environmental change in managed freshwater systems, particularly as demand for freshwater increases. Despite this importance, few studies have examined these linkages at broad spatial scales. As such, our objectives were to: (i) identify functional flow-biological condition metrics that explain the greatest variation in statewide and regional data, and (ii) assess relationship trends between functional flow metrics and biological condition. This research has important implications for environmental flow management, particularly where practitioners seek to link biological response to functional flow components.

2 Materials and Methods

2.1 General Approach

To assess relationships between streamflow condition and stream health, all ASCI and CSCI sites were spatially and temporally paired with proximal USGS gages across California. Using these paired sites, we calculated functional flow metrics for the 24 metrics defined by Yarnell et al. (2020), using a minimum of 10 years of continuous flow data at each selected USGS gage site. In some cases, ASCI and CSCI sites were associated with more than one USGS gage. We calculated a metric of hydrologic alteration using a normalized difference between the observed median value and predicted median value of each metric. Statistical models were then developed to identify which of the functional flow metrics were most closely associated with biological index scores, and the directionality of those relationships.

2.2 Pairing of Biological Stream Condition (CSCI & ASCI) sites with USGS gage sites

We identified all bioassessment sites (n=2,935) in the SWAMP dataset with available ASCI and CSCI scores from data sampled between 1994-2018 during late spring and summer months (May to September, when sampling typically occurs). To pair bioassessment sites with USGS gage sites, we filtered locations to include only bioassessment sites occurring in the same HUC12 catchment as USGS gages with at least 10 years of contiguous daily flow data (Figure 1). We filtered bioassessment sites from the previous step to include only sites on the same National Hydrography Dataset (NHD) mainstem stream or river as the USGS gage (in the same HUC12 watershed)—provided each site was within 10 km downstream of the gage—using the *nhdplusTools*, *dplyr*, and *sf* packages in R version 4.1.1 (Blodgett, 2018; Pebesma, 2018; Wickham et al., 2018, 2019; R Core Team, 2021). Using this list of biological-gage site pairs, we removed sites that did not contain flow data after 1994 to ensure temporal overlap with the biological assessment sampling events (i.e., all ASCI and CSCI data was collected and calculated after 1994). Data from final site pairs were used in all subsequent analyses. For BMI sampling events and resulting ASCI or CSCI scores that occurred in the same water year at the same location, we calculated the median value of these replicate scores to use in the statistical modeling.

2.3 Calculating Delta Hydrology using Functional Flow Metrics

Once the selected ASCI and CSCI sites were paired with proximal USGS sites, we calculated functional flow metrics (Grantham et al.) over the longest contiguous period of record for each USGS gage using the using the Functional Flows Calculator API client package in R (version 0.9.7.2)[1], which uses hydrologic feature detection algorithms developed by Patterson et al. (2020) and the Python functional flows calculator[2]. We calculated a normalized metric based on the departure from the predicted reference flow (difference between the observed functional flow metric and the predicted functional flow metric) associated with the stream segment at the USGS gage (see Grantham et al. this issue for additional details on how predicted reference-based functional flow metrics were modeled). This measure of delta hydrology was calculated as:

$$(50\ percentile\ Observed\ FFM - 50th\ percentile\ Predicted\ FFM)\ /\ 50th\ percentile\ Predicted\ FFM$$

In some cases, the functional flow metric value for a single water year at a gage could not be calculated, resulting in an 'NA' value. This could occur for several reasons, such as the data record was incomplete, or the annual hydrograph was extremely different compared with the predicted reference condition. These instances would lack a seasonal flow pattern which the flow calculator needs to derive subsequent metrics (see Grantham et al., this issue). If more than 70% of the annual values for a metric across the period of record at a gage were NA, then the flow alteration for that metric at that gage was not included in the dataset. One additional metric, seasonality, was calculated for each gage using the same period of record, based on Colwell's metrics which measure the seasonal predictability of environmental phenomena (Colwell, 1974). These metrics are defined in terms of Predictability (P), Constancy (C), and Contingency (M)—where M means temporal variability, or seasonality, and P is the reliable recurrence of seasonal patterns across multiple cycles. Importantly, Colwell's P is maximized when environmental phenomenon is constant throughout the year, if the seasonal fluctuation is consistent across all years, or a combination of both (Tonkin et al., 2017). Following Tonkin et al. (2017), we used calculated seasonality as Colwell's M/P, as it can be applied in a wide range of ecological studies (Tonkin et al., 2017; Radecki-Pawlik et al., 2020; Peek et al., 2021), and provides a measure (ranging from 0 to 1, with 1 being highly seasonal) of how the environment varies within a single year, which in this case was based on daily flow values from each gage selected for analysis.

[1] https://github.com/ceff-tech/ffc_api_client

[2] https://github.com/NoellePatterson/ffc-readme

2.4 Statistical Analysis of Stream Condition Indices vs. Functional Flow Metrics

To determine which functional flow metrics had the strongest association with streamflow alteration, we modeled estimates of delta hydrology (departure from the predicted reference flow) for each functional flow metric against biological condition scores (i.e., ASCI and CSCI) using boosted regression tree analysis, following methods from Steel et al. (2018).

Each model was run with CSCI or ASCI as the response, and the delta hydrology statistic for each FFM as well as seasonality as the covariates. Boosted regression trees, a method from the decision tree family of statistics, are well suited for large and complex ecological datasets; they do not assume normality nor linear relationships between predictor and response variables, they ignore non-informative predictor variables, and they can accept predictors that are numeric, categorical, or binary (Elith et al., 2008; Brown et al., 2012). Boosted regression trees are also unaffected by outliers and effectively handle both missing data and collinearity between predictors (De'ath, 2007; Dormann et al., 2013). Importantly, such methods are becoming more common in ecological analyses and have been shown to outperform many traditional statistical methods such as linear regression, generalized linear models, and generalized additive models (Guisan et al., 2007). Boosted regression tree models were run with grid iteration and tuning across parameters (shrinkage [0.001–0.005], interaction depth [3–5], number of minimum observations in a node [3–10], and bag fraction [0.75–0.8]) in model validation, following guidelines from Elith et al. (2008). To assess the relative influence of each functional flow metric in the model, we used the mean-square error method (Ridgeway, 2015).

The most influential functional flow metrics were further examined by plotting the delta hydrology metric values against biological condition scores. To better understand regional patterns and assess relationships across different scales, we also analyzed ASCI and CSCI scores and delta hydrology for FFM across three stream classifications—snowmelt, rain, and mixed (combination of rain, snow, or groundwater)—based on Patterson et al (2020) and (Lane et al., 2017) at a regional scale in California. Thus, each model was run using only sites associated with one of these stream classes.

3 Results

3.1 Pairing of biological stream condition sites with USGS gage sites

We mapped a total of 2,935 unique locations with CSCI values, 2,320 unique locations with ASCI values, and 736 USGS gage sites (Figure 2-3) across California. Despite a relatively large pool of sites to work with, after filtering and pairing, we identified 233 ASCI and 231 CSCI sites associated with 222 USGS gages across the state. Thus, approximately 10% of the total bioindicator sites exist in close spatial proximity (<10 river kilometers) to USGS gage sites with long-term flow data (>10 years). Eight metrics were dropped (Appendix Table S1) from the functional flow metric calculations, thus, for every site pair, data included a single bioindicator score, and 16 flow alteration metric scores, one for each of the remaining functional flow metrics. The functional flow calculator returned a wide range of values that indicate the broad array of regional hydrologic conditions across California, including a small percentage (< 2) of extreme outliers that occurred in the 98th percentile or greater of all data (Figure 4).

3.2 Statistical Analysis for Statewide Site Pair Dataset

Boosted regression tree models with delta hydrology and seasonality metrics explained 46% of the deviance in CSCI data, with a cross-validation correlation of 0.678 (se = 0.019) and 31% in ASCI with a cross-validation correlation of 0.552 (se = 0.041). Of the 16 functional flow metrics included in the model, eight had relative importance values greater than 5%, and Colwell's seasonality metric was consistently one of the top three variables in all models (Figure 5, Table 1). The two most influential functional flow metrics in the statewide model were fall pulse timing (CSCI=13.6, ASCI=12.3% relative influence) and seasonality (CSCI=15.5%, ASCI=7.6%) (Figure 5). Dry season timing was one of the most important variables in the CSCI model, but it was not influential in the ASCI model (Table 1). Three of the top metrics for CSCI related to timing (fall pulse timing, Coldwell's seasonality, and dry-season timing), while the remaining significant metrics were associated with flow magnitudes (wet-season baseflow and fall pulse magnitude) (Table 1, Figure 5). For ASCI, the top metrics were also primarily associated with timing (fall pulse timing, Colwell's seasonality, wet season timing, and spring timing), while other influential metrics were largely associated with flow magnitude (dry-season baseflow, wet-season baseflow, and fall pulse magnitude). When comparing both ASCI and CSCI cumulatively, the strongest metrics were fall-pulse timing and Colwell's seasonality, followed by dry-season baseflow and wet-season timing. Interestingly, the smallest difference in relative importance occurred in the fall pulse magnitude metric (Figure 5, Table 1).

Normalized delta hydrology (departure from reference value) for three of the top functional flow metrics was plotted against the ASCI and CSCI scores, grouped by the degree of stream alteration based on thresholds defined by Mazor et al. (2016) and Theroux et al. (2020). Values that fall below zero indicate flow values that are earlier (timing) or decreased (magnitude) from the expected reference condition (Figure 6). Based on the delta hydrology, fall pulse timing occurred earlier than the expected reference condition across all flow alteration threshold categories—though the lowest values typically corresponded with the most altered category—for both ASCI and CSCI. For magnitude metrics, the pattern was more distinct in the fall pulse magnitude metric for ASCI, which showed all but the "Likely intact" scores were reduced from the expected reference condition, and for CSCI, all the "very likely altered" and "likely altered" categories had distributions that were reduced compared to the expected reference conditions (Figure 6). Interestingly, for Colwell's measure of seasonality, there was a consistent positive trend towards higher CSCI and ASCI scores with more predictable and consistent seasonality (recurring intra-annual patterns of temporal variability, e.g., summer low flow periods and winter floods occurring each year) (Figure 7).

3.3 Statistical Analysis by Stream Class

Using the paired sites, we split sites based on stream class (Patterson et al., 2020), which were predominantly in stream segments classified as Rain (Snowmelt: ASCI=37, CSCI=55; Mixed: ASCI=88, CSCI=83; and Rain: ASCI=231, CSCI=226). Note, ASCI and CSCI sites paired with multiple proximal USGS gages, thus sample sizes differ from the total number of unique stations (Figure 2-3). Stream class models of delta hydrology showed seasonality, fall pulse, dry season, and wet season flow components were consistently important in all regional models, while spring recession flow was important primarily in the rain and mixed stream class models (Table 1, Figure 8). The only regional model that included a peak flow component was the ASCI-snowmelt model. Here, the 10-year flood magnitude had the highest relative influence score for ASCI, but seasonality and fall pulse metrics were stronger drivers of delta hydrology in CSCI (Table 1). The fall pulse timing was the most dominant metric for CSCI in the rain model and ASCI in the model of mixed stream class sites, while the most important metric in the snowmelt model for CSCI was Colwell's seasonality (Table 1, Figure 9).

Several metrics with the highest relative influences in the regional stream class models were further examined by plotting the delta hydrology values for each functional flow metric against the paired bioindicator scores by the thresholds identified in each bioassessment index. Figure 9 shows the highly variable nature of the large dataset, which is to be expected given the inherent wide diversity of climate and topography across California. However, trends in the data indicate potential underlying relationships that should be explored further. These data indicate that as seasonality increases, stream condition (ASCI or CSCI) index also increases, though this pattern is most pronounced in the mixed and snowmelt stream classes (Figure 9A). For fall pulse timing, the rain stream class had the greatest number of sites and the clearest pattern, indicating all sites had earlier than the expected reference condition across all flow alteration categories—though the lowest values corresponded with the most altered category—for both ASCI and CSCI. In the mixed stream class and snowmelt stream class, this pattern was less prevalent.

4 Discussion

Linking flow and bioassessment data sheds light on which relationships are important to consider when establishing flow criteria and our results indicate that a functional flows approach is well suited to improve streamflow management in California (Tonkin et al., 2017, 2021). Alteration to seasonal flow components (e.g., spring recession or fall pulse flow) are closely related to stream health and may be important in restructuring biological communities. Specifically, metrics associated with flow timing (including seasonality) were the most influential in linking functional flow metrics to stream condition. Interestingly, while seasonality was the dominant predictor of delta hydrology for CSCI, it was the fourth most informative metric in ASCI, indicating at large spatial scales (e.g., California), there may be differences in sensitivity to seasonal flow changes between invertebrate and algal communities, and that CSCI based on benthic macroinvertebrates may be a more informative index in determining flow alteration-stream condition linkages.

4.1 Timing metrics had the strongest link to biological condition

In both statewide and regional models, timing metrics were the most important, often comprising three or more of the top five metrics. Of the timing metrics, fall pulse timing was the most influential in describing biological changes in the statewide CSCI and ASCI models. Fall pulse timing is strongly correlated with the first fall precipitation event following the dry season baseflow period, occurring between 1st October and 15th December (Patterson et al., 2020). Typically, fall pulse flows begin in November (Ahearn et al., 2004), but may vary widely (Patterson et al., 2020). Fall flushing flows and the timing of such are important in determining the biological condition of streams. For instance, the fall pulse flow is known to provide organic matter and nutrients subsidies to streams from adjacent riparian habitats and, thus, enhance food resources and detrital carbon for foraging invertebrates (Ahearn et al., 2004; Blanckaert et al., 2013). Fall pulse flows are also known to increase invertebrate habitat availability and heterogeneity (Blanckaert et al., 2013; Naman et al., 2016) and reconnect invertebrate communities and population gene flow through dispersal (Townsend and Hildrew, 1976; Mackay, 1992), providing a vital food resource for resident fishes and other higher order consumers. Thus, fall pulse flow timing may be a key factor in re-establishing food web and community connectivity (Elliott, 1973; Nislow et al., 1998; Romaniszyn et al., 2007). During the dry season low flow period, it is common for invertebrates to use the hyporheic zone as a refuge from potentially unsuitable environmental conditions (e.g., temperature) (Wood et al., 2010; Stubbington, 2012) For instance, fall pulse flows are known to reconnect streams with their hyporheic zone and, as a result, decrease water temperature (Yarnell et al., 2020). Invertebrates also use changes in water temperature (generally associated with season shifts) as a cue for fall or winter emergence (Ward and Stanford, 1982) the timing of which may help synchronize life history events or behavioral adaptations, ultimately increasing reproductive success (Lytle, 2001; Lytle and Poff, 2004).

Similar to CSCI, fall pulse timing also explained ASCI variability in the statewide model, much of which was driven by mixed rain and snowmelt streams. Fall pulse timing influence was less influential in snowmelt dominated streams, yet still notable. During the dry season low flow period, filamentous algal mats typically become more prevalent and are associated with increases in stream temperature, reduced streamflow velocity, and nutrient enrichment (McIntire, 1966; Poff et al., 1990; Suren et al., 2003). Changes in stream velocity associated with the arrival of the fall pulse flow may scour and effectively remove algal mats, while improving habitat for different algal assemblages or species ultimately flushing organic material downstream. In mixed rain and snow dominated streams, although fall pulse timing was mostly early, a clear improvement of ASCI condition was shown as values approached reference timing (Figure 9B).

Dry season baseflow was an important metric for ASCI in rain dominated streams, showing flows both above and below reference condition impacting algal condition (Table 1, Figure 6), which agrees with (Irving et al.) (this issue). There is a greater distribution of flows below the reference condition in the very likely altered class of ASCI versus the other classes. Dry season baseflow is the low flow period of the water year, which begins after the spring recession has stabilized (Patterson et al., 2020). These low flows support algal growth and primary producers by maintaining water temperature and dissolved oxygen (Appendix Table S1, (Yarnell et al., 2020). Low flows can increase algal biomass and cover (Biggs, 1985; Biggs et al., 2005; Schneider and Petrin, 2017), and due to lower velocities and water temperature, algal communities change from a diatom dominated assemblage to a filamentous algae dominated system (Dewson et al., 2007).

4.2 Seasonality and Climate Change

Cumulatively, timing was the dominant component linking biological stream condition with flow, which is an important factor for invertebrates that have evolved in river systems with consistent hydrologic seasonality and predictability. Timing metrics such as wet season timing, dry season timing, spring timing, and seasonality were all influential in the statewide and regional models. Wet season timing relates to the time of the water year when flows are consistently elevated from dry season low flows driven by rain or snow melt (Patterson et al., 2020), while dry-season timing denotes the time of the water year when flows consistently reach baseflow, following the spring recession (Patterson et al 2020). While California's Mediterranean climate integrates a significant amount of interannual variation (Persad et al., 2020), flow regulation has altered patterns of hydrologic seasonality and predictability in many watersheds (Kupferberg et al., 2012; Peek et al., 2021). These patterns are exacerbated by climate change, which research indicates earlier peak flow and snowmelt timing will continue to occur (Kapnick and Hall, 2010), as well as increased volatility and decreased seasonal predictability via more extreme wet and dry events and swings between these extremes (Swain et al., 2018; Persad et al., 2020). Therefore, environmental flow recommendations should consider the ecological flow needs of these communities at scales appropriate to future conditions. Stream health and biological conditions may not improve if existing communities are mismatched to current environmental conditions (Botero et al., 2015). Thus, efforts should focus on river reaches where flow management may provide opportunities to more closely mimic local reference conditions or consider which functional flow component will be the highest priority given management goals.

There are many potential factors that cannot be accounted for within modeling frameworks focused solely on the impacts of flow modification. Interactions with stream temperature, ecological dynamics associated with population density and predation, as well as water chemistry and nutrient loads can all play important roles in influencing biological stream condition (Nilsson and Renöfält, 2008; Miller et al., 2009; Lange et al., 2016; Schneider et al., 2016). However, the benefit of linking biological indices like CSCI or ASCI with flow is the ability to quantify and assess stream conditions across broad spatial areas, often with very different underlying geography, geology, and watersheds. These indices are designed to be regionally stable and are standardized so they can be compared across large spatial scales (Mazor et al., 2016). This also means it is important to use caution when interpreting regional models for ecological meaning because CSCI and ASCI produce locally relevant reference expectations. For example, landscape heterogeneity and local seasonality could be a strong driver of variation in the data comparisons of models from the same stream class because these sites may occur in very different geographic regions of California. Future modeling approaches at finer scales may benefit from more specific models that can account for important local variables or use individual functional feeding groups or taxa. Nonetheless, identifying key functional flow metrics that can be evaluated more deeply regarding potential thresholds or discrete trends in alteration will help inform the development of ecological flow criteria. This approach can be used to narrow down and identify specific flow metrics that may be most relevant for management by distilling disparate datasets into more useful and discrete information that can be used to aid decision making.

5 Conclusion

Future analyses may leverage this information and approach to focus on more discrete flow-stream condition linkages, with particular attention to temporal lags associated with drought impacts or the sensitivity of biological metrics. More specific hydrologically sensitive biological metrics (e.g., more distinct functional feeding groups in benthic invertebrate data, hydrologically sensitive taxonomic groups, etc.) may provide additional detail for assessment of the impacts of flow alteration on a given stream reach. Furthermore, this approach provides a method to assess these metrics through time, so adaptive approaches to flow management can be implemented, monitored, and revised based on important linkages between flow and biological stream condition.

This analysis highlights that despite the information-rich spatial datasets that span much of California, there remains a significant gap in leveraging and layering these datasets in an effective manner. Pairing biological and flow sites spatiotemporally was challenging, and sites were limited across all stream classes, but particularly in snowmelt dominated systems. When data from biological or hydrological time series are limited, alternative approaches can be implemented using modeled streamflow or modeled stream condition indices to predict whether or not flow alteration deviates from reference expectations (Irving et al.; Stein et al., 2017; Mazor et al., 2018; Maloney et al., 2021). Furthermore, ongoing monitoring may benefit from more discrete and targeted sampling to link biological data more accurately with surface flow data. Nonetheless, this current approach provides a novel integration of disparate spatiotemporal datasets and indicates broad relationships can be identified between functional flow metrics and indices of biological stream condition.

6 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

7 Author Contributions

RP led the preparation of this manuscript, data analysis, coding, and project design. KI contributed to data analysis and coding. RP, ES, KI, RM, SY, RL contributed to the conceptualization and project design. All authors contributed to writing this manuscript.

8 Contribution to the Field

Large state or regional environmental flow programs rely on broadly applicable relationships between flow and ecology to inform management decisions. California, USA, despite having high flow and bioassessment data density, has not established relationships between specific elements of the annual hydrograph and biological stream condition. We spatially and temporally linked river flow stations and biological assessment sites in California to identify suitable site pairs for comparisons of streamflow alteration with stream health based on biological indices of benthic invertebrates and algae at a statewide and stream class scale. These indices provide a consistent statewide standard for interpreting bioassessment data and, thus, a means of quantitatively comparing stream conditions throughout the state. The results indicate that stream health indices were most closely associated with flow alteration via timing metrics such as seasonality, fall pulse timing, dry-season timing, and wet season timing. Development of ecological flows should consider that alteration to any of these seasonal flow components may be important in restructuring biological communities, and flow management can be implemented using this approach to further identify linkages between flow and biological stream condition.

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13 Tables

Table 1. Mean relative influence values for functional flow metrics included in all CA and each of the three stream class-based models that assessed flow alteration in relation to ASCI & CSCI scores. Metrics and relative influence values in gray boxes and bolded were most influential (> 5%).

	All CA		Rain		Mixed		Snowmelt	
Flow Metric Name	**CSCI**	**ASCI**	**CSCI**	**ASCI**	**CSCI**	**ASCI**	**CSCI**	**ASCI**
Fall pulse timing	**13.6**	**12.3**	**20.2**	3.6	2.6	**35.7**	**8.6**	**10.4**
Fall pulse magnitude	**6.4**	**6.9**	**6.3**	4.9	2.7	**8.1**	**10**	**5.9**
Wet-season timing	**5.1**	**13.8**	2.8	**17.6**	3.6	**6.5**	2.1	**11.6**
Wet-season baseflow	**5.8**	**5**	**6.6**	4.4	1.1	4.6	1.1	**5.8**
Wet-season duration	4.4	2.7	4.4	3.4	**9.7**	**8.1**	**5.1**	2.5
Wet-season median flow	2.2	3.7	2.7	**5.7**	3.2	0.7	**8.2**	1.9
10-year flood magnitude	3.8	3.1	3.5	2.7	**5.3**	3.3	3.4	**16.7**
2-year flood magnitude	4.8	2.8	**5.2**	2.3	3.6	3.1	4.1	2.5
5-year flood magnitude	3	1.4	3.4	1.1	3.3	1.2	3.6	0.9
Spring timing	4.4	4.1	**8**	**6.8**	**9.1**	1.5	1.7	**8.4**
Spring duration	3.8	4	3.5	2.2	**8**	**7.3**	2.7	2.4
Spring recession magnitude	3.8	**6.5**	2.8	**5.8**	3	**6.7**	**7.6**	1.5
Dry-season high baseflow	2.7	5	3	**5.8**	**9**	1	1.2	**9.7**
Dry-season baseflow	**5.9**	**15.8**	**6.5**	**16.4**	4.7	3.2	**7.4**	2.8
Dry-season timing	**9.7**	1.2	**5.1**	1.1	**11.4**	2.7	**5**	2.6
Dry-season duration	**5.2**	4	**6.2**	3.5	**5.7**	4	**8**	1.4
Colwell's M/P	**15.5**	**7.6**	**9.8**	**12.7**	**14.2**	2.1	**20.3**	**13**

14 Figures

Figure 1. Flow diagram of steps used to pair biological stream condition sites and USGS gage locations.

Figure 2. Map of all sampling sites (A) possible CSCI sites and ASCI sites, (B) the potential gages (n=2097) for the final site pairs, and (C) all unique CSCI, ASCI, and USGS gages sites with >10 years of flow data. Note, some ASCI and CSCI sites paired with more than one gage site.

Figure 3. Map of selected biological sampling sites for unique ASCI (circles) and CSCI (diamond) data overlaying stream classifications adapted from Patterson et al. 2020.

Figure 4. Boxplot of delta hydrology of functional flow metrics used in the analysis across all gages for ASCI and CSCI. The solid pink line in the background indicates no difference between the observed 50th percentile and the predicted reference 50th percentile metric value. Values to the left of the line are reduced or early, values to the right are inflated or late, relative to the expected reference value. Extreme outliers (>98 percentile) have been removed from the boxplot.

Figure 5. Relative importance of functional flow metrics in boosted regression tree models assessing flow alteration relative to ASCI and CSCI scores for paired sites statewide. Relative influence values were calculated using a mean-square error (MSE) approach, which determines those variables with the largest average reduction in MSE. Functional flow metrics are described in Appendix Table S1.

Figure 6. Top FFM (normalized as Delta Hydrology) values vs binned ASCI and CSCI values (based on thresholds from Mazor et al., 2016 and Theroux et al., 2020) for all CA site pairs. The red zero line delineates departure from expected reference flow metric, values < 0 are reduced or early, values > 0 are inflated or late, relative to the expected reference value. Notches indicate an approximate 95% confidence interval to compare medians, thus if notches of two boxplots do not overlap this suggests the medians are significantly different (see McGill et al., 1978).

Figure 7. Colwell's seasonality versus binned ASCI and CSCI values (based on thresholds from Mazor et al., 2016 and Theroux et al., 2020) for all CA site pairs. Notches indicate an approximate 95% confidence interval to compare medians, thus if notches of two boxplots do not overlap this suggests the medians are significantly different (see McGill et al., 1978).

Figure 8. Relative importance of functional flow metrics in boosted regression tree models assessing flow alteration relative to ASCI and CSCI scores by stream classification (Patterson et al., 2020). Relative influence values were calculated using a mean-square error (MSE) approach, which determines those variables with the largest average reduction in MSE. Functional flow metrics are described in Table 1.

Figure 9A. Colwell's seasonality versus binned ASCI and CSCI values (based on thresholds from Mazor et al., 2016 and Theroux et al., 2020) for all site pairs by stream class. Notches indicate an approximate 95% confidence interval to compare medians, thus if notches of two boxplots do not overlap this suggests the medians are significantly different (see McGill et al., 1978).

Figure 9B. Fall pulse timing (normalized as Delta Hydrology) values vs binned ASCI and CSCI values (based on thresholds from Mazor et al., 2016 and Theroux et al., 2020) for all site pairs by stream class. The red zero line delineates departure from expected reference flow metric, values < 0 are reduced or early, values > 0 are inflated or late, relative to the expected reference value.

Figure 1.TIFF

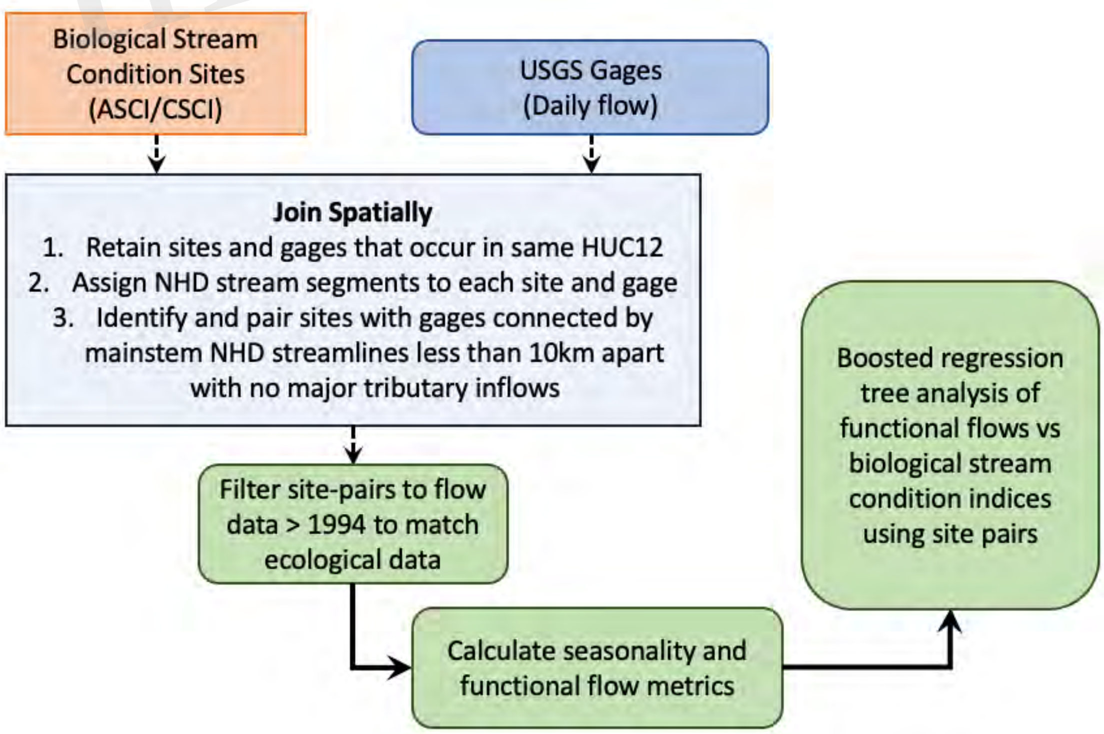

Figure 2.TIFF

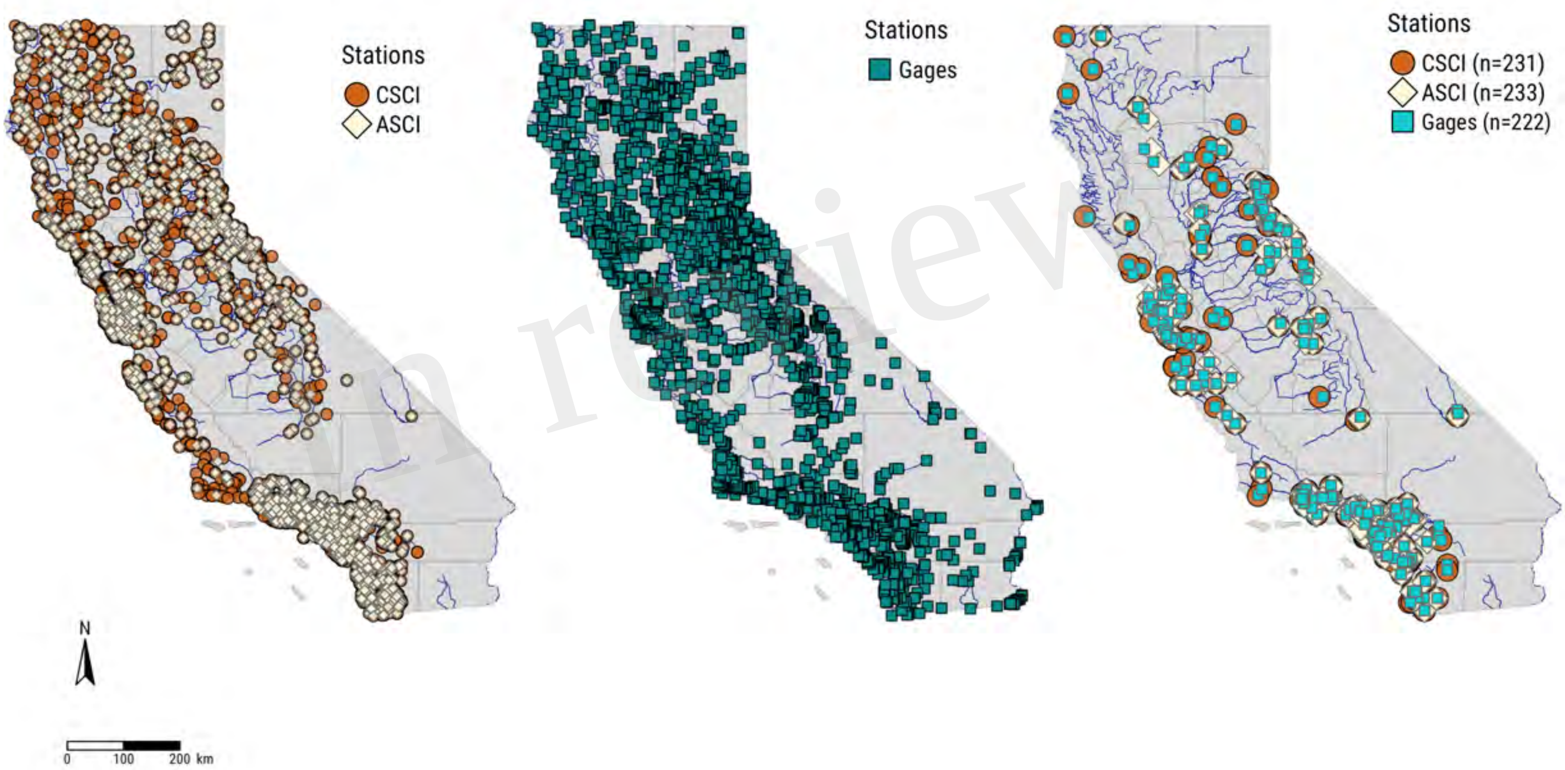

Figure 3.TIFF

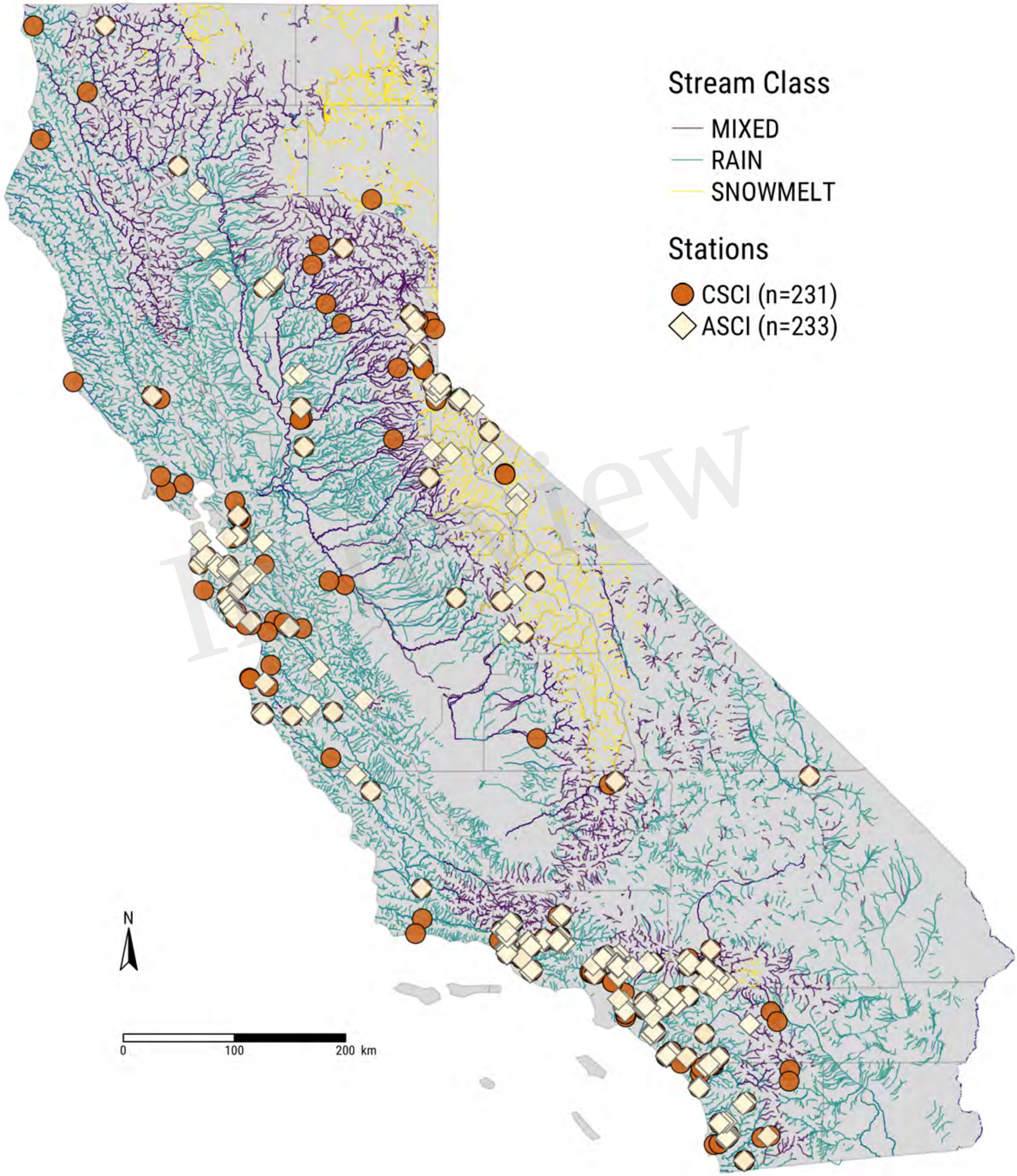

Figure 4.TIFF

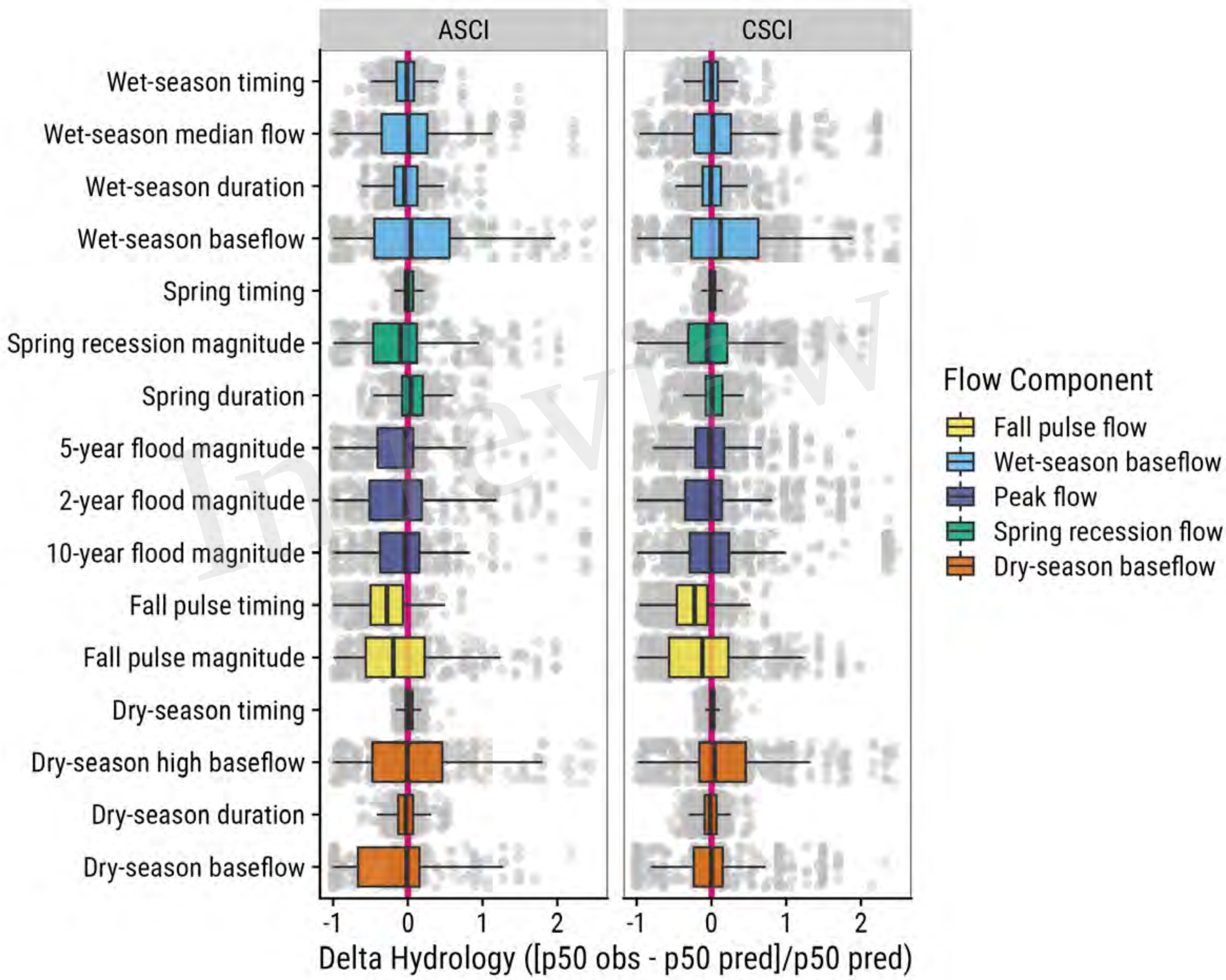

Figure 5.TIFF

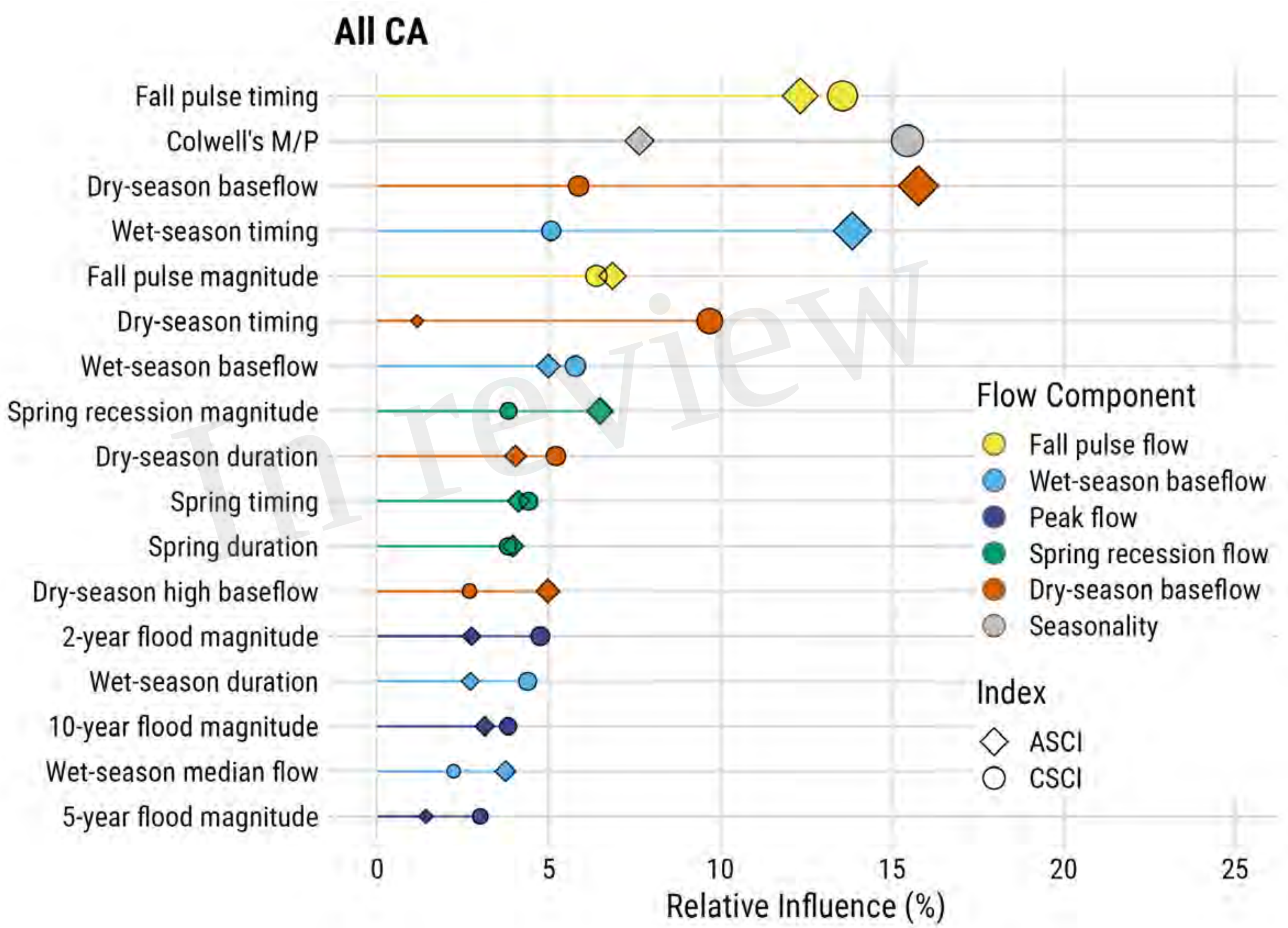

Figure 6.TIFF

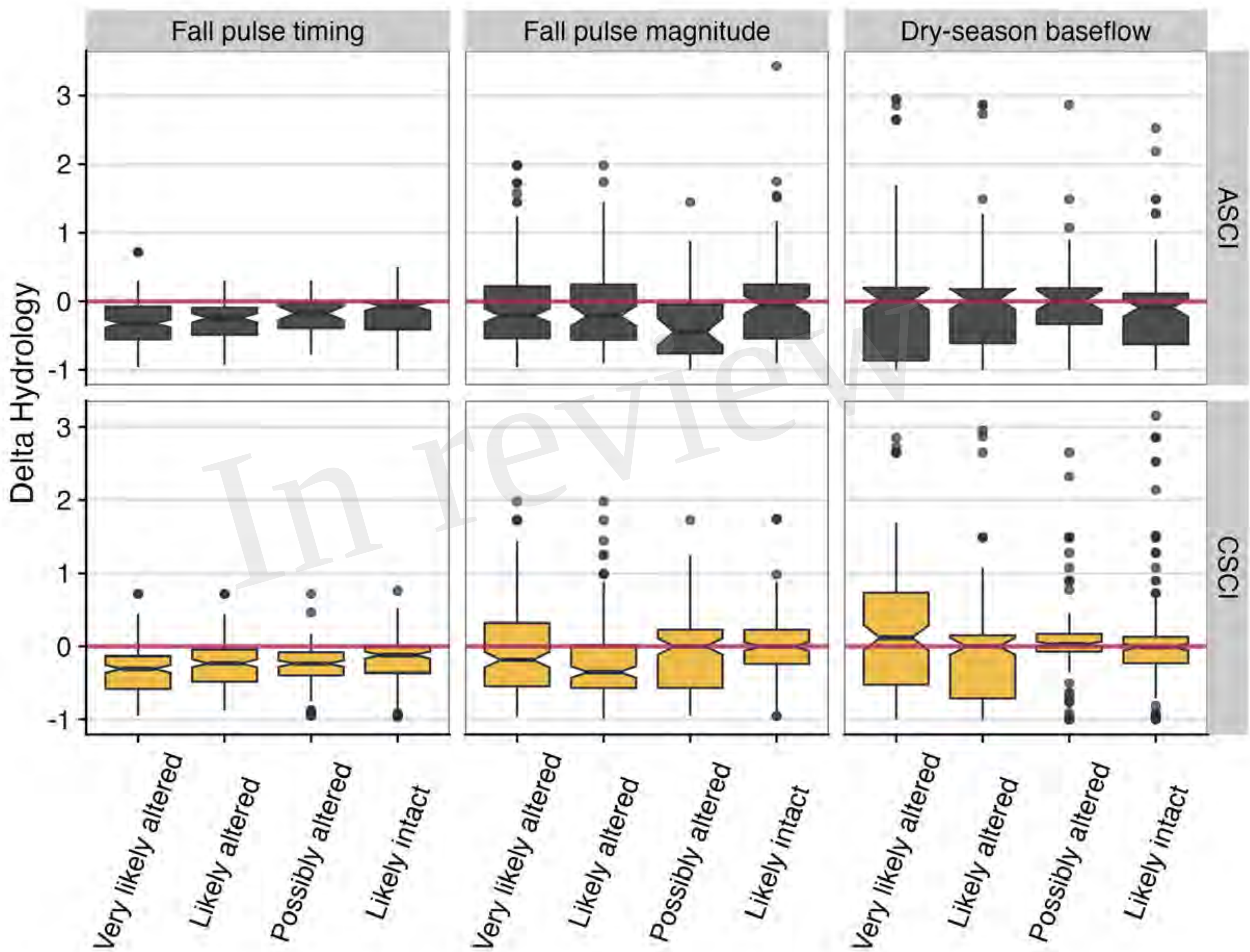

Figure 7.TIFF

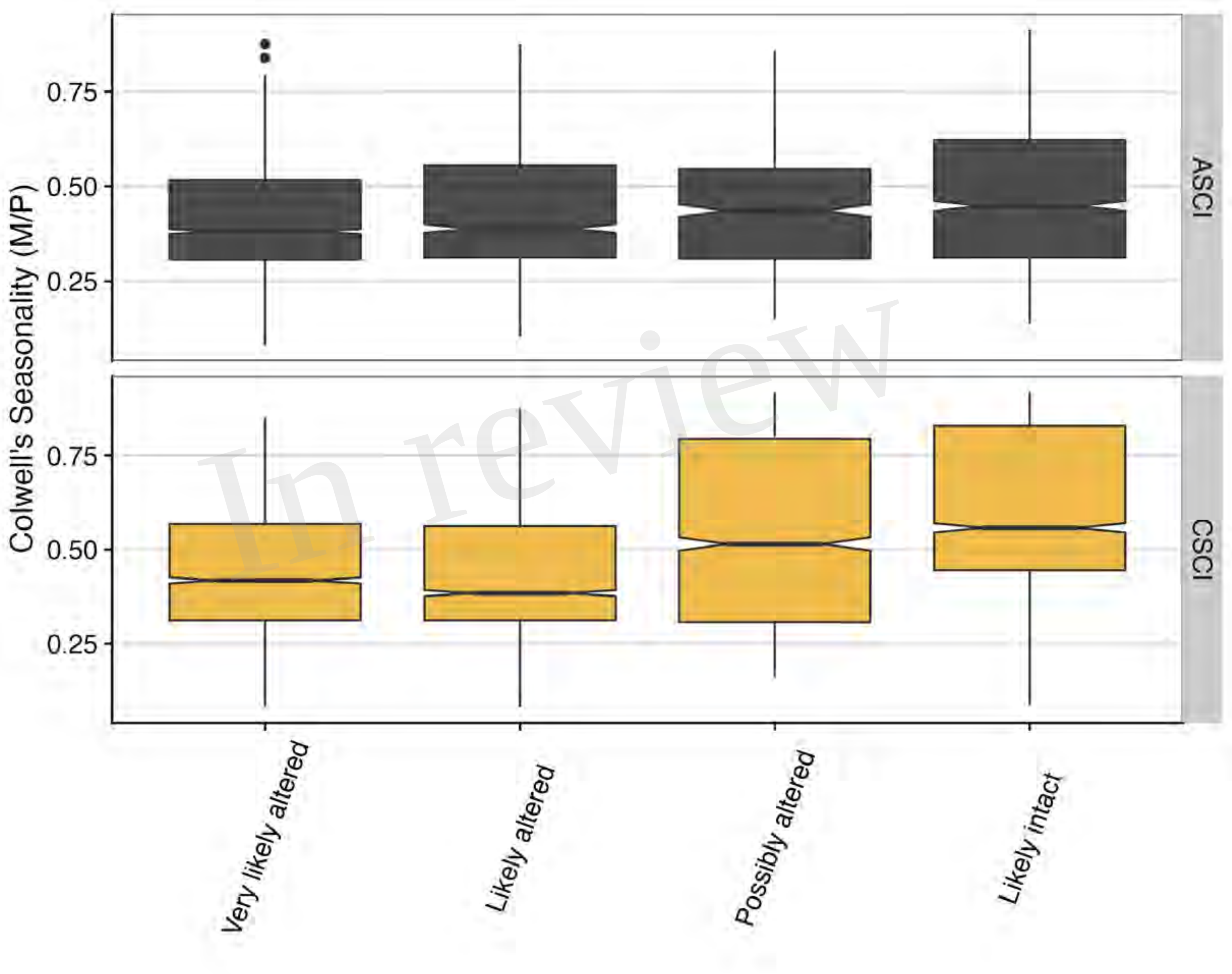

Figure 8.JPEG

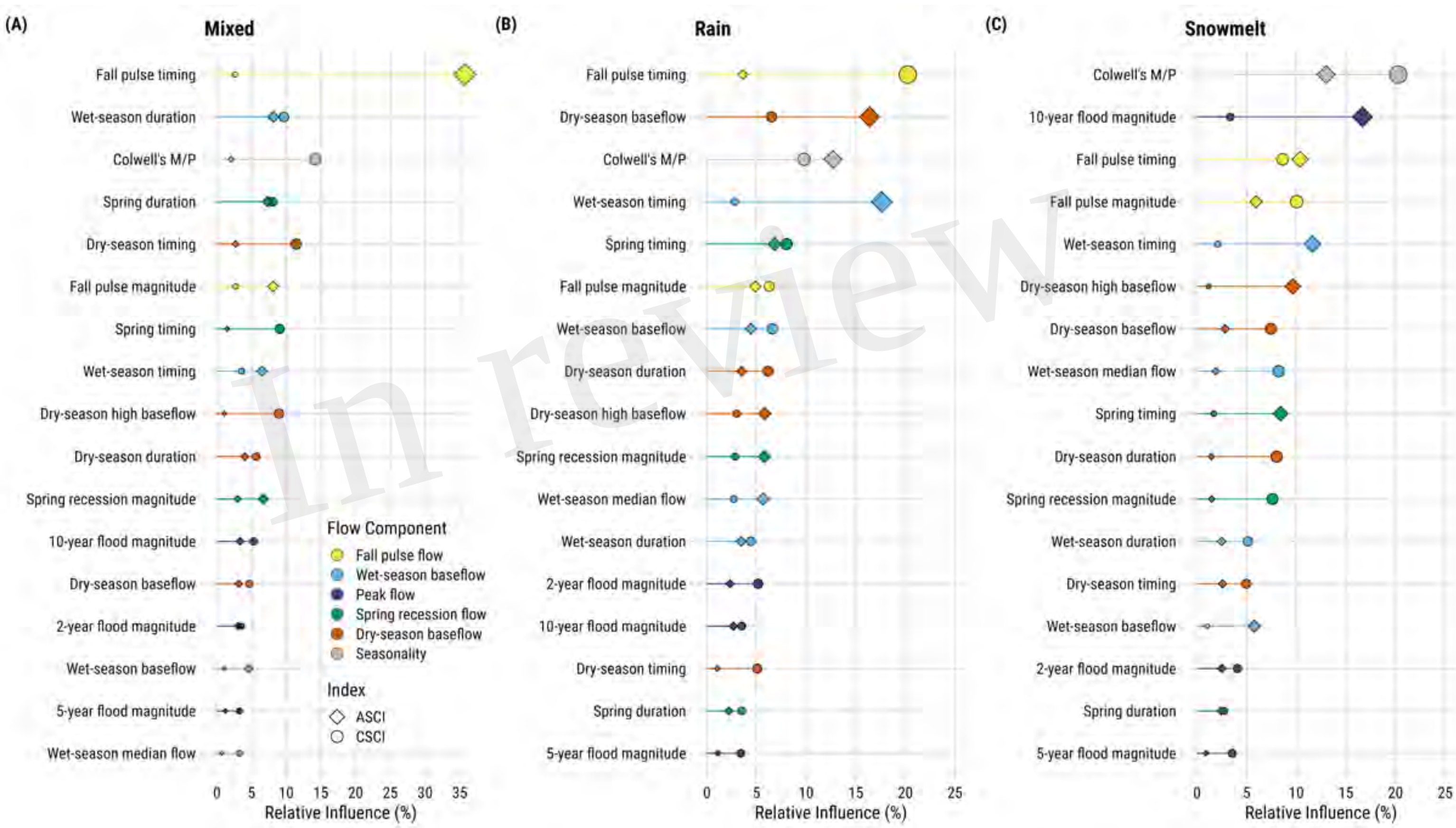

Figure 9.TIFF

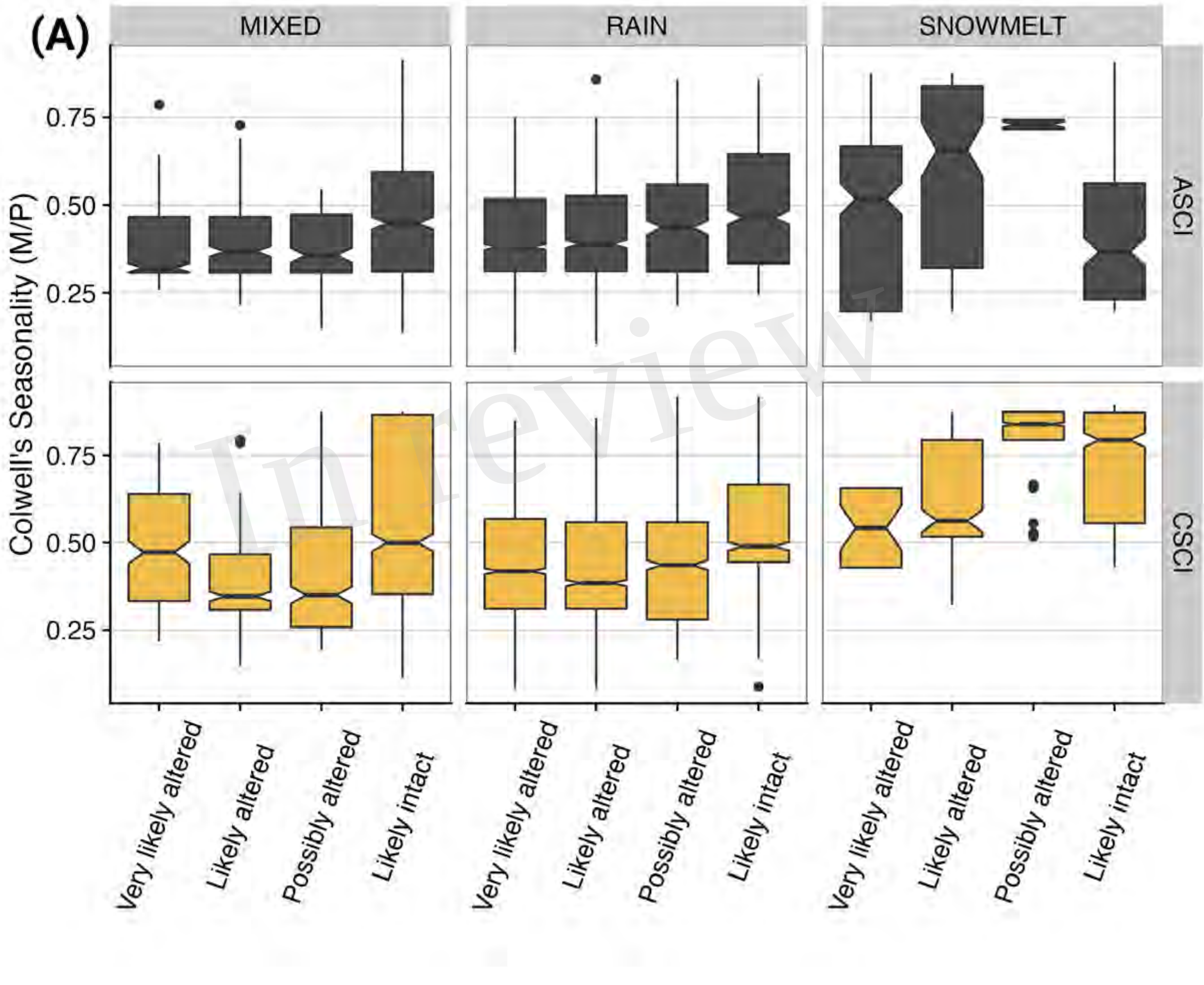

Figure 10.TIFF