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Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment

Daren M Carlisle^{1*}, David M Wolock², and Michael R Meador¹

Human impacts on watershed hydrology are widespread in the US, but the prevalence and severity of streamflow alteration and its potential ecological consequences have not been quantified on a national scale. We assessed streamflow alteration at 2888 streamflow monitoring sites throughout the conterminous US. The magnitudes of mean annual (1980–2007) minimum and maximum streamflows were found to have been altered in 86% of assessed streams. The occurrence, type, and severity of streamflow alteration differed markedly between arid and wet climates. Biological assessments conducted on a subset of these streams showed that, relative to eight chemical and physical covariates, diminished flow magnitudes were the primary predictors of biological integrity for fish and macroinvertebrate communities. In addition, the likelihood of biological impairment doubled with increasing severity of diminished streamflows. Among streams with diminished flow magnitudes, increasingly common fish and macroinvertebrate taxa possessed traits characteristic of lake or pond habitats, including a preference for fine-grained substrates and slow-moving currents, as well as the ability to temporarily leave the aquatic environment.

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Human influence on watershed hydrology is extensive and may be a primary cause of ecological impairment in river and stream ecosystems. In the US, natural streamflow regimes are influenced by dams and diversion structures (Graf 1999; Poff *et al.* 2007), land uses that alter runoff to stream channels, groundwater withdrawals from contributing aquifers, and interbasin water transfers (Jackson *et al.* 2001). Because the natural timing, magnitude, and frequency of streamflows dictate the evolutionary adaptations of many river biota (Bunn and Arthington 2002) and control many physical and chemical processes (Poff *et al.* 2010), anthropogenic alterations of streamflows may have profound effects on ecosystem structure and function.

Major questions about streamflow alteration and its ecological consequences remain unresolved. First, although streamflow is continuously monitored at thousands of sites across the conterminous US, a basic accounting of the prevalence and severity of streamflow alteration is lacking because there has not been a systematic national assessment of these sites. Second, sound management requires an understanding of the relationship between ecological integrity and streamflow alteration, yet few quantitative relationships have been reported at spatial scales beyond specific stream segments (Poff *et al.* 2003; Arthington *et al.* 2006). A key hindrance to addressing these questions is the inconsistency with which streamflow alteration and various biological responses have been quantified (Poff and Zimmerman 2010).

Using standardized indicators, we assessed streamflow magnitudes and associated biological communities across the conterminous US. We focused on streamflow magnitudes because this dimension of the flow regime is frequently linked to ecological impairment (reviewed by Poff and Zimmerman 2010) and has clear implications for water management (Postel and Richter 2003). Our first objective was to assess whether observed magnitudes of annual minimum and maximum flows differed from reference (ie estimated least disturbed) conditions at 2888 streamflow monitoring sites. Our second objective was to determine whether the integrity of two aquatic communities (ie fish and macroinvertebrates) was associated with the type and severity of streamflow alteration at a subset (~250) of these sites. At each monitoring site, alterations – in either streamflow or biological communities – were quantified as the ratio of observed conditions to expected reference conditions. This approach provides an intuitive indicator of the degree to which a stream exhibits the hydrological and biological characteristics that should naturally occur; data can therefore be aggregated and interpreted across diverse regions because they are standardized by each site's natural potential.

■ Methods

We quantified streamflow alteration as the ratio of observed magnitudes to those expected under reference conditions. We first identified a set of 1059 streamflow monitoring sites with perennial flows and with reference-quality (ie least disturbed) basins across the conterminous US (Carlisle *et al.* 2010; Falcone *et al.* 2010). We

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developed random forest (Cutler *et al.* 2007) models that use 93 geospatial attributes (eg climate, topography, soils, geology) for a given watershed to predict its observed mean annual minimum (7-day moving average) flow and, separately, mean annual maximum (daily average) flow (Carlisle *et al.* 2010; WebPanel 1). These models were used to predict expected magnitudes at 2888 non-reference streamflow monitoring sites based on the geospatial attributes of their respective watersheds. We quantified streamflow alteration at each assessed site as the ratio of observed mean annual (1980–2007) minimum and maximum magnitudes to expected mean annual magnitudes. The ratio can be either < 1 or > 1 , indicating that observed magnitudes are either diminished or inflated, respectively, relative to their respective expected reference conditions. We summarized streamflow alteration across the US by tabulating the number of sites that were inflated (ie observed/expected [O/E] values $> 90\%$ of those from reference sites), diminished (ie O/E values $< 90\%$ of those from reference sites), or unaltered (ie O/E values within the above limits) (WebTable 1). In addition, the severity of streamflow alteration was summarized by tabulating the number of sites with O/E values within quartiles > 1 or < 1 .

Likewise, biological integrity was quantified as the ratio of observed community attributes to those expected under reference conditions (O/E value, *sensu* Hawkins 2006). Selected community-level attributes varied slightly because of inherent differences in aquatic communities. For macroinvertebrates nationwide and for fish in the eastern US, the O/E value was the fraction of the set of taxa (in most cases, genera or species) expected at a site that was actually observed there. Estimates of expected community attributes were generated from regional multivariate predictive models, which have previously been described and validated (Wright 2000; WebPanel 1). The O/E value of fish communities in the western US was derived from an index of biological integrity (ie based on observed attributes) normalized to expectations from regional reference sites (Meador *et al.* 2008). Our final definition of biological integrity was binary, in which the aquatic community at each site was considered “impaired” if its O/E value was less than that of 90% of reference sites within the same region, or “unimpaired” if its O/E value did not meet this condition (WebPanel 1).

Three hypotheses about the relationship between biological integrity and streamflow alteration were evaluated. First, we hypothesized that, relative to eight covariates, streamflow alteration would be a primary predictor of biological integrity (ie impaired versus unimpaired). These covariates included water temperature, specific conductance, pH, total nitrogen, total phosphorus, channel gradient, agricultural land cover, and urban land cover of the riparian buffer (WebPanel 1). We performed classification tree analysis (De’ath and Fabricius 2000) with all covariates and the O/E indices for minimum and maximum flow as predictors. Trees were grown to maximum size and then pruned to minimize tree complexity and classification error

based on K-fold cross-validation (where $K=10$ subsamples of the original observations; Venables and Ripley 2002). Our second hypothesis was that the likelihood of biological impairment would increase with the severity of streamflow alteration. For each community, the proportion of impaired sites was tabulated within categories of streamflow alteration severity, which were defined by quartiles of O/E either > 1 (ie inflated) or < 1 (ie diminished). The Kruskal-Wallis test was applied to determine whether covariates varied significantly among these same categories. Few of the sites with biological data experienced inflated maximum flows, so this dimension of streamflow alteration was not considered in our analysis. Our third hypothesis was that functional traits of macroinvertebrate and fish taxa would indicate the presence of altered streamflow magnitudes. Sites with diminished (minimum and maximum) and inflated (minimum only) magnitudes were identified based on the distribution of O/E values at reference sites as described above (WebTable 1). We used predictions of expected community composition to identify taxa at each site that (1) were expected but not observed (hereafter “decreaser taxa”) and (2) were observed but not expected (hereafter “increaser taxa”). In the absence of pre- and post-disturbance data, these designations approximate taxa that have been lost or gained as a result of all anthropogenic influences at each site (Knapp *et al.* 2005). We aggregated lists of decreaser and increaser taxa across sites within each class of streamflow alteration ($n=119, 84,$ and 110 for inflated minimum, diminished minimum, and diminished maximum, respectively) and evaluated (using Fisher’s exact test) whether the two sets of taxa differed in the frequencies of functional traits associated with hydrological attributes, including reproductive strategy, mode of mobility, and geomorphic habitat and substrate preferences (WebPanel 1).

■ Results

Streamflow magnitudes were altered in most (86%) of the assessed streams (Figure 1a and b). Minimum flows were the most frequently altered, being inflated or diminished in 74% of streams. Maximum flows were altered in 54% of streams and diminished in most cases. The type and severity of streamflow alteration were associated with climate (Figure 1b). In arid climates, minimum and maximum flows were severely diminished, being less than half of expected magnitudes in most ($\sim 70\%$) monitored streams. Maximum flow magnitudes in wet climates were also commonly diminished, being less than three-fourths of expected magnitudes in most ($> 60\%$) monitored streams. In contrast, minimum flows in wet climates were commonly inflated, being $> 25\%$ higher than expected magnitudes in about half of monitored sites.

Streamflow alteration was the primary predictor of biological integrity for both communities (Figure 2). Impaired fish communities (70% correct classification) were associated solely with streamflow alteration and prominent at sites (1) with diminished maximum or minimum flows or

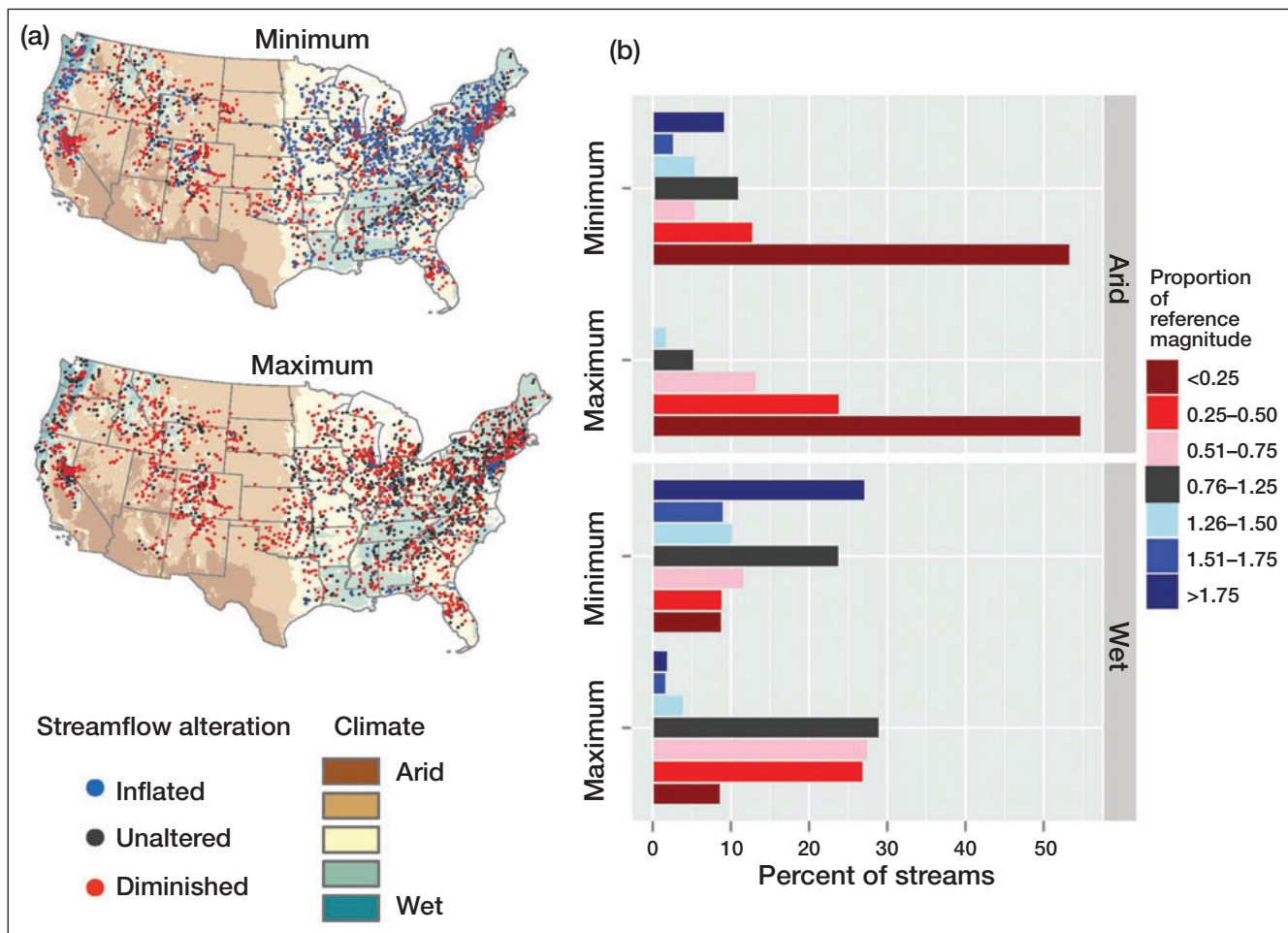


Figure 1. Alteration of minimum and maximum annual streamflow magnitudes, (a) at 2888 sites monitored from 1980–2007. “Inflated” condition indicates that observed average magnitudes exceeded expected reference magnitudes; “diminished” condition indicates that observed average magnitudes were less than expected reference magnitudes. (b) Severity of streamflow alteration, as a proportion of expected reference magnitude, within two classes of climatic conditions, defined by the difference between mean annual precipitation and potential evapotranspiration ($> 0 = \text{“Wet”}$, $< 0 = \text{“Arid”}$).

(2) with inflated minimum flows but unaltered maximum flows. Impaired macroinvertebrate communities (74% correct classification) were associated with diminished maximum flows, but this response was conditional on covariates such as stream gradient and land cover.

Biological impairment was associated with the severity of streamflow alteration (Figure 3). Increasing severity of diminished minimum and maximum flows was associated with a twofold increase in the likelihood that fish and macroinvertebrate communities were impaired. Two covariates (total phosphorus and specific conductance) were also associated with increased severity of diminished minimum and maximum flows, and sites in the highest severity classes were often diminished for both minimum and maximum flows. Severity of inflated minimum flow was less strongly associated with biological impairment than diminished streamflows, and appeared to be confounded with several covariates.

Differences between increaser and decreaser taxa suggested apparent shifts in functional traits of fish and macroinvertebrate taxa at sites with altered streamflows

(Table 1). Fish reproduction generally shifted from simple nesting to nest-guarding or broadcast-spawning strategies in streams with either form of flow alteration. In streams with diminished minimum or maximum flows, active swimmers replaced benthic-oriented and streamlined fish species, whereas macroinvertebrate taxa with the ability to temporarily leave the aquatic environment or move quickly within it (eg strong swimmers, fast crawlers) replaced taxa lacking these traits; moreover, pool (ie relatively slow currents)-loving macroinvertebrate taxa that prefer fine substrates replaced riffle (ie turbulent flowing)-loving macroinvertebrate taxa that prefer coarse substrates. In streams with inflated minimum flows, there was also an apparent increase in macroinvertebrate taxa that prefer erosional (ie relatively high current velocity) habitats.

Discussion

Understanding the relationship between biological integrity and streamflow alteration is critical if society is to make decisions about tradeoffs between human and

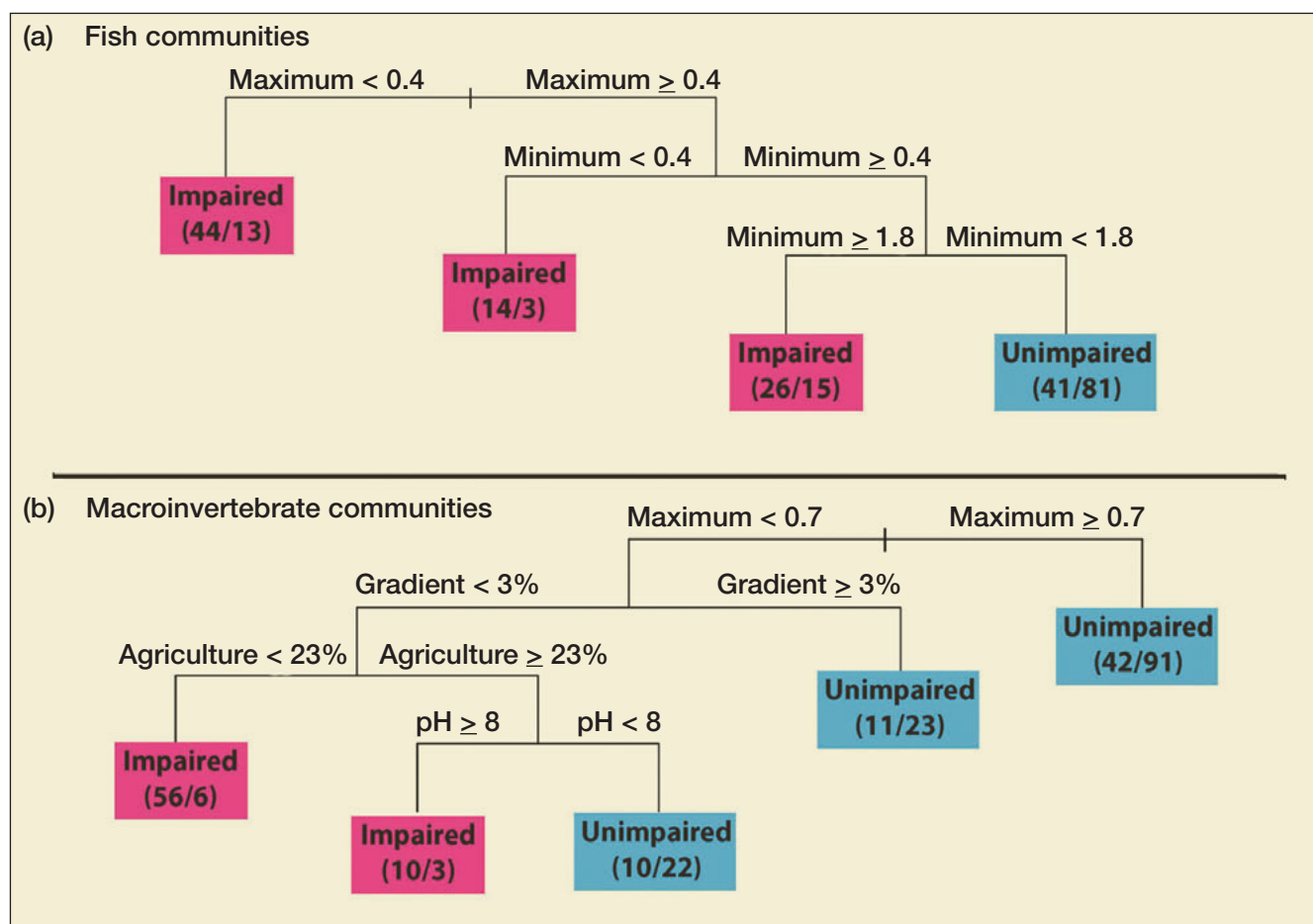


Figure 2. Classification trees predicting impairment of (a) fish and (b) macroinvertebrate communities at 237 and 274 stream sites, respectively, through measures of streamflow alteration and eight covariates. Each split in the tree is annotated with the values of the primary predictor that defines each branch; for example, fish communities were impaired at sites where observed magnitudes of maximum flows were < 0.4 of expected natural magnitudes. Streamflow alteration is expressed as the proportion of expected reference magnitude. Agriculture is expressed as percent of riparian area within a 100-m buffer. Predicted class (“Impaired/Unimpaired”) frequencies are given for each terminal node.

ecosystem requirements for water (Postel and Richter 2003). This assessment quantifies, for the first time at a multiregional scale, the severity of streamflow alteration in a large portion of the current streamflow monitoring network, as well as the integrity of associated biological communities. Our work is also distinct from previous large-scale studies (eg Konrad *et al.* 2008) in that we examined biological and hydrological characteristics in terms of their deviations from reference conditions, seeking to understand the potential ecological consequences of anthropogenic changes to the natural flow regime (*sensu* Poff *et al.* 2010). Our primary findings are that (1) most of the monitored streams experience altered flow magnitudes and (2) there is a strong association between diminished streamflow magnitudes and impaired biological communities across the conterminous US.

Given the central influence of the flow regime on stream ecosystems, our finding that anthropogenic changes in streamflow magnitudes are pervasive and severe suggests this factor may be a ubiquitous constraint on biological integrity. Previous studies have drawn simi-

lar conclusions using indirect measures (Graf 1999; Nilsson *et al.* 2005) or at sites with known temporal changes in streamflow alteration (Poff *et al.* 2007). Despite finding a high percentage of altered sites, we probably underestimated the occurrence and severity of streamflow alteration for two reasons. First, our measures of deviation from expected magnitudes are conservative relative to pristine conditions or conditions prior to European settlement, because estimates of expected streamflow magnitudes were derived from many reference sites (particularly in the midwestern US) influenced by some anthropogenic disturbance. Second, we limited our assessment to a single dimension of the natural flow regime – magnitudes – but the timing, duration, and rate of change are also ecologically important (Bunn and Arthington 2002; Mathews and Richter 2007). Had these dimensions been included, our estimate of the pervasiveness and severity of streamflow alteration would likely have increased.

Pronounced differences in streamflow alteration between arid and wet climates are partly due to distinc-

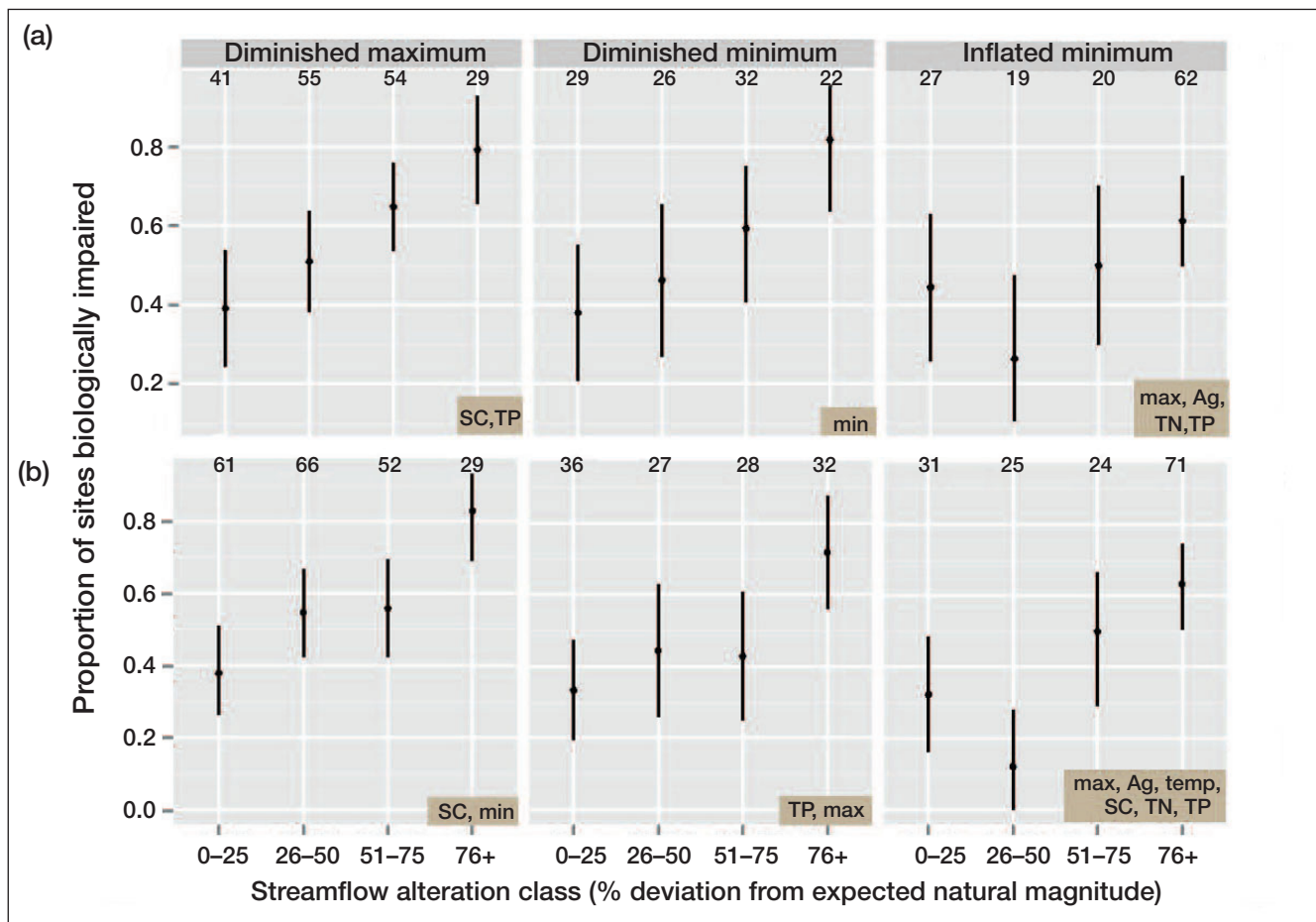


Figure 3. Proportion of sites with impaired (a) fish and (b) macroinvertebrate communities within classes of severity of streamflow alteration (expressed as percent deviation from expected natural magnitudes). “Diminished” indicates observed magnitudes less than expected natural magnitudes; “inflated” indicates observed magnitudes greater than expected natural magnitudes. Vertical black lines indicate 95% confidence intervals generated with bootstrapping. Values above each vertical line indicate the number of sites with each severity class. Inset boxes display covariates that differed significantly ($P < 0.05$) among severity classes, where SC = specific conductance, TP = total phosphorus, TN = total nitrogen, temp = water temperature, Ag = riparian agriculture land cover, max = maximum flow observed/expected (O/E), and min = minimum flow O/E.

tive management of watershed hydrology. The tendency for diminished flow magnitudes in arid climates is indicative of consumptive water uses causing net streamflow loss. The primary use of water in arid climates is for irrigated agriculture (Pimentel *et al.* 1997), but interbasin transfers and groundwater withdrawal for other uses also reduce streamflows (Jackson *et al.* 2001). Management of watershed hydrology in wet climates, in contrast, is often focused on flood control. This is most often achieved through small impoundments or large reservoirs that remove flood peaks and release the water later, during normally low flow periods; this management technique can result in inflated minimum flows and diminished maximum flows (Magilligan and Nislow 2005).

Streamflow alteration was the primary predictor of biological integrity, even after considering several covariates. Our set of anthropogenic covariates was not exhaustive, but some (eg riparian land cover) are potential surrogates for unmeasured factors, such as dissolved contaminants. Nevertheless, several covariates (eg nutrients and ripar-

ian land cover) that are recognized as influential to biological integrity were less important than streamflow alteration. Natural covariates were at least partially controlled for through the use of an O/E index for biological and streamflow measures, which predicts site-specific expectations based on natural factors such as climate and stream size (Hawkins 2006). Interactions of covariates and streamflow alteration in the macroinvertebrate model suggest that biological responses to diminished maximum flows depend on the environmental context. This phenomenon has not been explicitly studied, but may explain why a recent review (Poff and Zimmerman 2010) found that macroinvertebrate communities show a less consistent response to streamflow alteration than do fish communities.

The ecological importance of streamflow alteration is evident from our finding that the likelihood of biological impairment increased with the severity of diminished streamflow magnitudes. Some chemical covariates were also associated with increased severity of diminished

Table 1. Summary of trends in macroinvertebrate and fish traits at sites – with various forms of altered streamflow magnitudes – across the conterminous US

Trait	Community	Diminished minimum	Diminished maximum	Inflated minimum
Reproductive strategy	Fish	Nest guards replace simple nesters	Broadcast spawners replace simple nesters	Broadcast spawners replace simple nesters
Morphology/ locomotion	Fish	Active swimmers replace benthic and streamlined forms	Active swimmers replace benthics	None observed
	Macro-invertebrates	Active swimmers replace taxa with slow crawling rates	Active swimmers replace taxa with slow crawling rates	None observed
Exit ability	Macro-invertebrates	Increased taxa with exit ability	Increased taxa with exit ability	None observed
Geomorphic and substrate preference	Fish and macro-invertebrates	Pool taxa preferring fine-grained substrates replace riffle taxa preferring coarse substrates	Pool taxa preferring fine-grained substrates replace riffle taxa preferring coarse substrates	Increased taxa preferring riffles (macro-invertebrates only)

Notes: See WebPanel 1 for detailed statistical results.

streamflow magnitudes, so we cannot rule out their influence on biological communities – although elevated concentrations of chemicals would also be an expected result of reduced streamflow magnitudes (Bunn and Arthington 2002). We also cannot distinguish the relative influences of minimum and maximum flows, because both tended to be diminished in streams with the most severe streamflow alteration. Nevertheless, our findings demonstrate that, across divergent natural and anthropogenic settings, the likelihood of biological impairment grows with increased reductions of maximum and minimum streamflow magnitudes.

Finally, biological communities in streams with altered flow magnitudes appeared to lose and gain taxa with traits indicative of specific flow regimes. Streams with diminished flows showed increases in taxa with preferences for low water velocities and fine sediments (eg absence of flushing flows), and with the ability to escape periodic environmental bottlenecks – possibly to avoid desiccation. Streams with inflated minimum flows showed increases in macroinvertebrate taxa with preferences for turbulent currents – a likely result of sustained high flows. Fish species that were favored in all hydrologically altered streams possess reproductive strategies that require either a high level of parental care or no care at all, whereas species that build simple nests appeared to be lost from the system. Simple nests generally require water circulation to maintain egg viability and would therefore be sensitive to desiccation under diminished flows or scouring under inflated flow regimes. In contrast, nest-guarding species protect nests from predators and can behaviorally provide circulation when necessary. Alternatively, species that broadcast spawn compensate for harsh environmental conditions with high reproductive output. Although these

traits suggest a mechanistic link between biological impairment and altered streamflow magnitudes, some traits would be favored in any disturbed environment. Therefore, these traits are not themselves diagnostic of streamflow alteration, but are consistent with the hypothesis that altered streamflow magnitudes played a role in causing biological impairment.

Because the flow regime controls many physical, chemical, and biological processes, community responses to streamflow alteration are a product of direct and indirect pathways. We did not explore the mechanisms underlying the relationships between biological integrity and streamflow alteration, nor was the study design appropriate for evaluating

thresholds of streamflow alteration that are protective of biological communities. Nevertheless, our study provides a multiregional-scale perspective on the importance of natural streamflow regimes to the maintenance of aquatic communities and ecosystems, and provides water-resource managers with a much-needed perspective on the pervasiveness and severity of anthropogenic alteration of streamflow magnitudes. The degree to which streamflows are controlled in many river systems and the pervasiveness of streamflow alteration across the US suggest that a national priority of restoring natural streamflow magnitudes could be broadly implemented and would produce widespread and measurable ecological dividends (Postel and Richter 2003).

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WebPanel 1. Assessing streamflow alteration and biological integrity**Predicting expected streamflow magnitudes**

The procedure for predicting expected natural streamflow attributes is detailed elsewhere (Carlisle et al. 2010; Falcone et al. 2010), and briefly described here. Among ~7000 streamflow monitoring sites across the conterminous US, reference (ie least-disturbed) sites with perennial flow were selected through quantitative and qualitative criteria of human activity in the watersheds and local expert judgment. Minimum flow (annual minimum of the 7-day moving average of daily flow values) and maximum flow (annual maximum daily flow value) were averaged across all years of flow record available from 1950–2007 at reference sites (minimum of 20 years), and across at least 15 years of recent flow record (1980–2007) at assessed sites. Model performance was evaluated by computing the mean and standard deviation of the observed (O) to expected (E) ratio (from cross-validation) at reference sites. Predictive models exhibited 26–34% error, with relatively little bias (WebTable 1). Assessed sites were identified from stream gauges operated by the US Geological Survey (USGS) with at least 15 years of complete records (1980–2007) and whose watershed characteristics (eg terrain, soils, and climate) were within the multivariate distribution (sensu Bowman and Somers 2006) of those for reference sites. Drainage basins for the final set of 2888 assessed and 1059 reference sites included in this assessment encompass one-half of the total land area in the conterminous US and are typical of land use and water management across the country (WebTable 2).

Predicting expected biological communities

The details of model development and evaluation are documented elsewhere and briefly described here. The USGS National Water-Quality Assessment Program sampled macroinvertebrate (274 sites) and fish (237 sites) communities from 1993–2005 across the conterminous US where daily streamflow was also monitored. Field methods followed standard protocols and consistent quality assurance practices (Moulton et al. 2002) throughout the study period. Estimates of E were obtained from regional River Invertebrate Prediction and Classification System-type models (sensu Hawkins 2006) that predicted the probabilities of capturing at a site each taxon from the regional pool of native taxa. O for each site was calculated as the number of expected taxa that were actually collected in the sample. Separate predictive models for macroinvertebrates were developed with 338 reference sites in the eastern and central US (Carlisle and Meador 2007), 217 reference sites in the south-central US (Yuan et al. 2008), and 729 reference sites in the western US (Carlisle and Hawkins 2008). Predictive models for fish communities were developed with 266 reference sites in the eastern and central US (Meador and Carlisle 2009). Because fish communities in the western US are naturally species-poor, these sites were assessed with an index of biological integrity (IBI), which represents measures of community composition (eg proportion of exotic species) other than species richness. O for western fish was the observed value of the IBI calculated from the sample collected at each site (Meador et al. 2008), and E was estimated as the average IBI from reference sites within each ecoregion, which is conceptually similar to E derived from statisti-

cal models (Hawkins 2006). Thresholds for classifying communities as impaired were based on the uncertainty of each predictive model, as determined by the distribution of O/E values at reference sites within each modeled region. For this study, a consistent impairment threshold was applied across all sites for each community and was defined as the average of thresholds from each region (O/E < 0.80 for macroinvertebrates, O/E < 0.75 for fish).

Associations between streamflow alteration and biological condition

Because the lengths of antecedent (to biological sampling date) streamflow records varied among sites where biological communities were sampled, we evaluated whether streamflow indicators were influenced by the number of years used to compute O. For a set of 239 sites where 15 years of antecedent daily streamflow records existed, we found that O/E indicators for minimum and maximum flow computed with O averaged over 5, 10, or 15 years were highly correlated (Spearman rank > 0.90). We therefore used 5 years of antecedent streamflow records in order to maximize the number of sites where biology and hydrology were both assessed.

We compiled data for eight covariates in an attempt to evaluate whether these factors were confounded with streamflow alteration. Covariates were selected among available data to be broadly representative of natural and anthropogenic chemical and physical conditions at each site. Land-cover variables (percent of area within 100-m buffer of the stream network upstream of site) were included to represent the intensity of land use along the stream corridor. Details of sampling and calculation of covariates are given elsewhere (Carlisle et al. 2008). Spearman rank correlations between covariates and measures of streamflow alteration were generally weak (maximum |Spearman rho| = 0.57).

Trait analysis

Predictive models used to estimate expected community composition were used to identify taxa that were potentially lost (“increasers”) or gained (“decreasers”) in streams with altered streamflows. For each site with altered streamflow, taxa having a predicted probability occurrence > 0.50 (Carlisle and Hawkins 2008) but absent from the site were recorded as decreasers. Taxa having a predicted probability of occurrence < 0.50 but present at the site were recorded as increasers. In the western US, null models (Van Sickle et al. 2005) based on 158 reference sites for fish communities (Whittier et al. 2007) were used to predict the expected taxa at each site. All non-indigenous fish taxa were considered increasers in the western US. Lists of increaser and decreaser taxa were aggregated across all sites with each type of streamflow alteration, and those present in < 10% of sites were excluded. We analyzed select macroinvertebrate traits from Poff et al. (2006), enhanced with the database of Vieira et al. (2006), that we deemed would be responsive to hydrological characteristics or that were considered evolutionarily labile (Poff et al. 2006). We analyzed select fish species traits from Goldstein and Meador (2004). Fisher’s exact test was used to determine whether the frequencies of decreaser and increaser taxa were statistically different for each trait category. Statistical summaries are presented in WebTables 3 and 4.

WebPanel 1. Assessing streamflow alteration and biological integrity – continued**■ WebReferences**

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WebTable 1. Performance of models used to predict expected natural streamflow magnitudes for the conterminous US

Streamflow attribute	Mean O/E	SD	10th percentile	90th percentile
Minimum flow	1.00	0.26	0.71	1.26
Maximum flow	0.96	0.34	0.57	1.35

Notes: The 10th and 90th percentiles of observed/expected (predicted) values at reference sites were used as thresholds to classify streamflow alteration at assessed sites as diminished or inflated, respectively. SD = standard deviation.

WebTable 2. Characteristics of land- and water-use of river basins assessed in this study as compared with the entire conterminous US

Characteristic	Conterminous US	This study (percent of US)
Area (km ²)	8.08 × 10 ⁶	4.07 × 10 ⁶ (50%)
Total reservoir storage (acre ft)	1.38 × 10 ⁹	0.82 × 10 ⁹ (59%)
Agricultural land cover (%)	22	25
Urban land cover (%)	5	5

WebTable 3. Frequencies of functional trait states in fish taxa considered decreaseers (“dec”) or increaseers (“inc”) in streams with different types of streamflow alteration. *n* = number of taxa

Trait <i>n</i>	Diminished minimum	Inflated minimum	Diminished maximum
	dec, inc (22, 39)	dec, inc (18, 47)	dec, inc (17, 32)
Reproduction	<i>P</i> = 0.010	<i>P</i> = 0.011	<i>P</i> = 0.045
Bearer	0.00, 0.03	0.00, 0.02	0.00, 0.03
Complex nest	0.23, 0.50	0.39, 0.33	0.35, 0.41
Broadcast	0.36, 0.39	0.22, 0.56	0.23, 0.47
Simple nest	0.41, 0.08	0.39, 0.09	0.41, 0.09
Locomotion	<i>P</i> = 0.010	<i>P</i> = 0.278	<i>P</i> = 0.019
Accelerate	0.04, 0.16	0.05, 0.09	0.00, 0.12
Creeper	0.18, 0.32	0.22, 0.33	0.23, 0.31
Cruiser	0.41, 0.24	0.33, 0.41	0.35, 0.37
Hugger	0.32, 0.05	0.28, 0.06	0.29, 0.00
Maneuver	0.04, 0.24	0.11, 0.11	0.12, 0.19
Habitat preference	<i>P</i> = 0.034	<i>P</i> = 0.096	<i>P</i> = 0.024
Riffle/run	0.18, 0.03	0.28, 0.06	0.23, 0.00
Pool	0.04, 0.23	0.28, 0.25	0.18, 0.25
Backwater	0.00, 0.03	0.00, 0.02	0.00, 0.03
Variable	0.77, 0.72	0.44, 0.66	0.59, 0.72
Substrate preference	<i>P</i> = 0.492	<i>P</i> = 0.059	<i>P</i> = 0.028
Coarse	0.04, 0.03	0.22, 0.04	0.18, 0.03
Gravel	0.09, 0.03	0.00, 0.04	0.00, 0.00
Fines	0.04, 0.13	0.05, 0.23	0.00, 0.22
Vegetation	0.00, 0.00	0.00, 0.00	0.00, 0.00
Variable	0.81, 0.82	0.72, 0.68	0.82, 0.75

Notes: First row for each trait reports the *P* value from Fisher's exact test. Bold entries indicate *P* values <0.05. For each trait state, paired cells report the proportion of taxa possessing that trait for increaseers and decreaseers.

WebTable 4. Frequencies of functional trait states in macroinvertebrate taxa considered decreaseers (“dec”) or increaseers (“inc”) in streams with different types of streamflow alteration. *n* = number of taxa.

Trait <i>n</i>	Diminished minimum	Inflated minimum	Diminished maximum
	dec, inc (22, 31)	dec, inc (23, 33)	dec, inc (27, 29)
Exit ability	<i>P</i> = 0.161	<i>P</i> = 0.776	<i>P</i> = 0.008
Absent	0.68, 0.45	0.70, 0.64	0.74, 0.38
Present	0.32, 0.55	0.30, 0.36	0.26, 0.62
Desiccation resistance	<i>P</i> = 1.00	<i>P</i> = 1.00	<i>P</i> = 1.00
Absent	0.77, 0.81	0.78, 0.75	0.81, 0.82
Present	0.23, 0.19	0.22, 0.25	0.19, 0.18
Crawling rate	<i>P</i> = 0.025	<i>P</i> = 0.512	<i>P</i> = 0.036
Very low	0.45, 0.64	0.48, 0.42	0.44, 0.66
Low	0.45, 0.13	0.43, 0.36	0.41, 0.10
High	0.09, 0.22	0.09, 0.21	0.15, 0.24
Swimming ability	<i>P</i> = 0.804	<i>P</i> = 0.912	<i>P</i> = 0.646
None	0.77, 0.74	0.74, 0.67	0.70, 0.72
Weak	0.14, 0.10	0.17, 0.18	0.19, 0.10
Strong	0.09, 0.16	0.09, 0.15	0.11, 0.18
Flow preference	<i>P</i> = 0.018	<i>P</i> = 0.040	<i>P</i> = 0.002
Depositional	0.09, 0.29	0.17, 0.15	0.11, 0.28
Erosional	0.50, 0.61	0.48, 0.76	0.48, 0.69
Either	0.41, 0.10	0.35, 0.09	0.41, 0.03
Habit	<i>P</i> = 0.162	<i>P</i> = 0.912	<i>P</i> = 0.014
Burrower	0.27, 0.52	0.26, 0.33	0.22, 0.59
Sprawler	0.04, 0.06	0.13, 0.09	0.07, 0.03
Clinger	0.55, 0.26	0.48, 0.42	0.55, 0.21
Swimmer	0.14, 0.16	0.13, 0.15	0.15, 0.17

Notes: First row for each trait reports the *P* value from Fisher's exact test. Bold entries indicate *P* values <0.05. For each trait state, paired cells report the proportion of taxa possessing that trait for increaseers and decreaseers.