

RESEARCH ARTICLE

Human impacts mediate freshwater invertebrate community responses to and recovery from drought

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Abstract

1. Drought is an increasing risk to the biodiversity within rivers—ecosystems which are already impacted by human activities. However, the long-term spatially replicated studies needed to generate understanding of how anthropogenic stressors alter ecological responses to drought are lacking.
2. We studied aquatic invertebrate communities in 2500 samples collected from 179 sites on rivers emerging from England's chalk aquifer over three decades. We tested two sets of alternative hypotheses describing responses to and recovery from drought in interaction with human impacts affecting water quality, fine sediment, water temperature, channel morphology, flow and temporal change in land use. We summarized communities using taxa richness, an index indicating tolerance of anthropogenic degradation (average score per taxon, ASPT) and deviation from the average composition.
3. Responses to drought were altered by interactions with human impacts. Poor water quality exacerbated drought-driven reductions in taxa richness. Drought-driven deviations from the average community composition were reduced and enhanced at sites impacted by flow augmentation (e.g. effluent releases) and flow reduction (e.g. abstraction), respectively.
4. Human impacts altered post-drought recovery. Increases in richness were lower at sites impacted by water abstraction and higher at sites with augmented flows, in particular as recovery trajectories extended beyond 3 years. ASPT recovered faster at sites that gained woodland compared to urban land, due to their greater recovery potential, that is, their lower drought-driven minimum values and higher post-drought maximum values.
5. *Synthesis and applications.* We show that communities in river ecosystems exposed to human impacts—in particular poor water quality, altered flow volumes and land use change—are particularly vulnerable to drought. These results provide evidence that management actions taken to enhance water quality, regulate abstraction and restore riparian land use could promote ecological resilience to drought in groundwater-dominated rivers such as globally rare chalk streams and

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other rivers of the Anthropocene, as they adapt to a future characterized by increasing climatic extremity.

KEYWORDS

abstraction, anthropogenic impact, chalk stream, drought, macroinvertebrate, multiple stressors, resilience, resistance

1 | INTRODUCTION

Freshwater biodiversity is threatened by changes in the frequency and severity of droughts (Vicente-Serrano et al., 2022) and increases in water temperatures (Van Vliet et al., 2011). Such hydroclimatic changes co-occur with anthropogenic pressures including water abstraction, water pollution, altered channel morphology and land-use change, which interact to alter biological communities (Jackson et al., 2016). Experiments have assessed the interactive effects of drought and anthropogenic pressures on river communities (e.g. Fournier & Magoulick, 2022), but such experimental studies cannot capture the large-scale and long-term effects of extreme events. Conversely, large-scale time-series analyses have mainly focused on interactive responses to human impacts and trends in streamflow and temperature (e.g. Vaughan & Gotelli, 2019), omitting the effects of extreme events (but see Daufresne et al., 2007). Ecological responses to interacting drought and other pressures thus require large-scale, long-term characterization to understand past and future environmental change.

Anthropogenic stressors such as elevated water temperatures and nutrient concentrations typically have long-term effects on biological communities, whereas droughts are unpredictable disturbances which can elicit relatively short-term ecological responses (Harris et al., 2018). How communities exposed to anthropogenic stressors respond to and recover from droughts depends on the resistance and/or resilience of their constituent species and refuge quality and accessibility (Sarremejane, Stubbington, et al., 2021). Although limited resistance means that community composition changes during a drought, resilient taxa typically enable communities to return to their pre-disturbance composition within 1–3 years post-drought (Stubbington et al., 2024), although persistent compositional shifts can occur (Bogan & Lytle, 2011).

Communities exposed to human impacts may be less drought resistant if adaptations conferring tolerance to anthropogenic and drought-related stressors differ (Dunbar et al., 2010; Stubbington et al., 2022). For example, nutrient pollution may exacerbate drought effects if it promotes algal growth in warm, slow-flowing waters, altering communities at multiple trophic levels (Fournier & Magoulick, 2022). In addition, anthropogenic habitat modifications such as sedimentation and channel resectioning, which are extensive in agricultural and urban areas, can reduce habitat and refuge diversity and worsen the negative effects of low flows on

communities (Dunbar et al., 2010). Alternatively, human-impacted communities could be little altered by drought if they comprise stress-tolerant generalist taxa (Mykrä & Heino, 2017). Resilience may also be lower in human-impacted rivers if habitat alterations such as dams sever links between impacted reaches and refuges, slowing post-drought recolonization. Network position may also influence community responses to disturbance, with isolated headwater communities recovering more slowly than those in connected mainstems (Sarremejane, Truchy, et al., 2021). However, few studies have explored how droughts and anthropogenic stressors interact to determine post-drought community resilience (Stubbington et al., 2024).

Limited spatiotemporal replication often hinders the characterization of long-term community changes, which requires observations to encompass droughts and entire recovery trajectories. Limited stressor gradients may also prevent the identification of non-linear responses and potential thresholds beyond which interacting stressors have dramatic ecological effects (Mack et al., 2022). However, long-term biomonitoring data enable the characterization of drought effects across large spatial scales, including in rivers with diverse human-impact characteristics. Identifying stressor combinations that influence community responses to drought could inform management strategies that promote resilience in human-altered rivers.

We used long-term, large-scale invertebrate and environmental data from groundwater-dominated rivers to determine how human pressures—including water quality, fine sediment, channel morphology, land use change and flow alteration—modulate invertebrate community resistance and resilience to drought. We developed two sets of alternative hypotheses (H) to describe community responses to (H1–2) and recovery from (H3–4) drought. We hypothesized (H1) that responses to drought become stronger with increasing human impacts if stressor combinations have additive effects on organisms. Alternatively, drought-driven changes including taxonomic losses may become less pronounced (i.e. resistance may increase) as human impacts increase if co-adaptation to anthropogenic and drought-induced stress promotes resistance (H2). We also hypothesized (H3) that recovery rates increase with site-scale naturalness and connectivity, because such conditions promote refuge quality and accessibility. Alternatively, human-impacted communities may recover faster if they are dominated by a few resilient, generalist taxa (H4). Community trajectories may also be non-linear, for example, if drought has stronger effects at low and high human stressor intensities.

2 | MATERIALS AND METHODS

2.1 | Study area and invertebrate data

Our study encompasses rivers fed by England's chalk aquifers (Figure 1), which are characterized by hydrological and thermal stability. We extracted invertebrate samples collected from 2240 sites on these chalk rivers by the Environment Agency (EA) of England in 1990–2022. Samples were collected in spring (March–May) using the standard 3-min kick-sampling method (Murray-Bligh & Griffiths, 2022). Invertebrates were identified to family and abundance recorded as log10 classes (i.e. 1, 2–9 etc.) then converted to the class median (Vaughan & Gotelli, 2019). We selected sites that had been sampled for ≥ 7 years, to encompass drought and post-drought periods.

2.2 | Hydroclimatic and human-impact variables

We characterized drought and flow alteration using hydrological variables calculated at 10-day to monthly intervals from coupled groundwater (MODFLOW) and surface water recharge/runoff hydrological models (Rushton & Skinner, 2012; Soley et al., 2012). Model output included simulated actual and naturalized (i.e. with the effects of abstraction and augmentation removed) discharge for 100-m reaches of most chalk rivers, representing site-specific information from which we derived human-induced flow alteration metrics.

We calculated reach-specific flow anomalies as the difference between actual discharge and the long-term monthly mean discharge divided by the long-term monthly SD. Monthly mean $\pm$ SD discharge was calculated for the whole discharge time series

(1966–2013 $\pm$ 8 years) for each reach. For each 6-month period (moving by 1 month) from January 1989 to the most recent flow record, we calculated low-flow anomalies (LFA) as the 25th percentile (below which the lowest 25% of flows occur) of the anomalies, using the *hetoolkit* R package (Dunbar et al., 2023). Negative and positive anomalies indicate flows lower and higher than the long-term mean, respectively, and we considered LFA < -1 and > 1 as representing very low (drought) and very high flows. We matched each invertebrate sample with the LFA of the preceding summer (April–September) at the closest hydrological model reach. We calculated the time since drought (TSD) for each invertebrate sample as the number of days between sample collection and the most recent hydrological drought, defined as a 6-month period with an LFA below the 10th percentile of all 6-month anomalies at the reach (Harris et al., 2018; Van Loon, 2015).

We calculated 13 variables to characterize human impacts: flow alteration, water quality (five variables), geomorphological alteration, land-use change (four variables), fine sediment and water temperature anomalies.

We calculated the extent of flow alteration for each 6-month period as the ratio between the actual and naturalized Q75 (i.e. the discharge exceeded 75% of the time). Flow alteration values (FAV) < 1 and > 1 indicate actual flows lower and higher than natural, respectively. We interpret FAV of 0.95–1.05 as indicative of natural flows. We matched each invertebrate sample with the FAV of its closest hydrological model reach in the preceding summer.

We used EA data to quantify five water quality parameters: nitrate, ammonia, orthophosphate and dissolved oxygen (DO) concentrations (mg L^{-1}) and biological oxygen demand (BOD; mg DO L^{-1}). Parameters were measured too inconsistently to allow temporal matching with invertebrate sampling dates. We therefore calculated the mean of each parameter for 1990–2005 and 2006–2021 at each

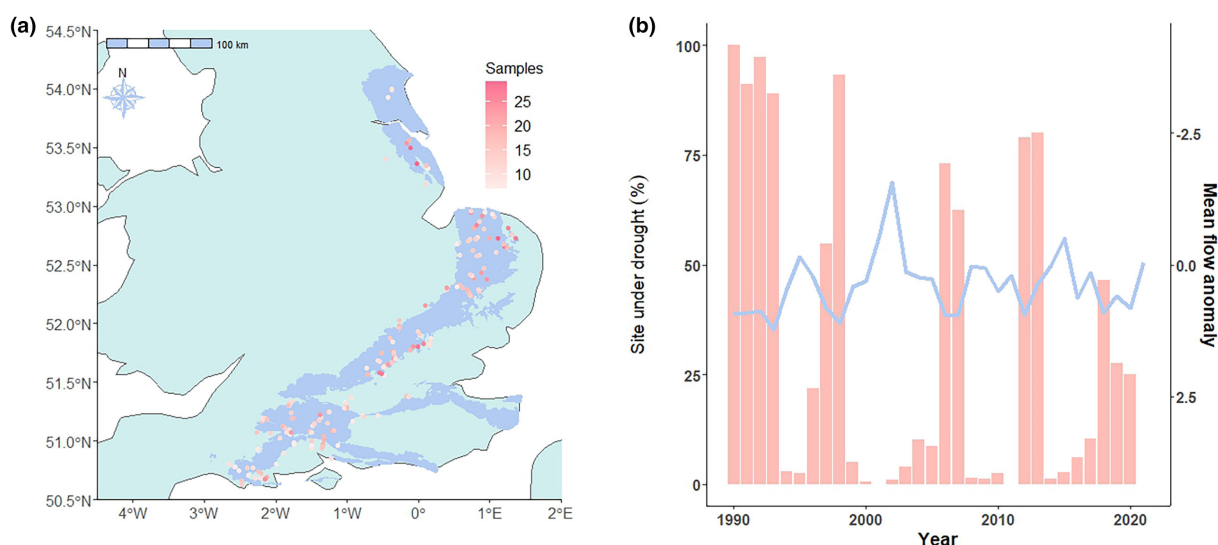


FIGURE 1 Site location and sampling frequency (a) and hydrological conditions across years (b). In (a), blue areas represent the chalk aquifer (source: British Geological Survey). In (b), bars represent the % of sites that experienced drought conditions < 1 year before invertebrate sampling and the line is the mean flow anomaly across all sites sampled in each year; the number of sites varied among years (Figure S1a).

site. We divided the data at 2005–2006 as the median date and to reflect changes in water quality following the introduction of EU water quality legislation (Whelan et al., 2022). Each invertebrate sample was matched with water quality values from the corresponding period.

We used the Channel Resectioning Index, derived from river channel morphology surveys (Naura et al., 2016), to assess morphological alteration. The index quantifies bank and channel modification by resectioning (e.g. straightening, channelization) for 500-m reaches of all rivers in England and ranges between 0 and 30, with higher values indicating greater modification.

We determined land cover in the catchment upstream of each invertebrate sampling site using ArcGIS Pro, a 50-m digital terrain model and a 1990–2015 land-cover change map (Rowland et al., 2020). For each catchment, we extracted the % woodland, cropland, pasture and urban land cover for 1990 and 2015. We calculated the % difference in each cover type between 2015 and 1990, to estimate change in pressures associated with land-use change. Negative and positive values indicate that % cover decreased or increased over time, respectively.

Sediment grain size composition was visually estimated at each site on each invertebrate sampling date. We calculated the % fine sediment as the sum of sand, silt and clay.

We used site-specific modelled monthly mean water temperatures based on direct measurements from 891 sites collected by the EA between 1960 and 2023. The model predicts water temperatures using land-cover information and air and water temperature measurements. We calculated site-specific monthly water temperature anomalies and their mean for each 6-month period between 1989 and 2023. Anomalies were calculated as the difference between each temperature record and its site-specific long-term (1960–2023) monthly mean, divided by its long-term SD. We matched each invertebrate sample with the mean water temperature anomaly of the most recent 6 months.

The distance of the invertebrate sampling site from the river source (defined following Murray-Bligh & Griffiths, 2022) was used to represent site connectivity and location within a river network.

2.3 | Final site selection

Each invertebrate sampling site was paired with its closest (straight-line) hydrological, water temperature, morphological alteration and water quality site using site geospatial coordinates and the R package *sf* (Pebesma, 2018). We excluded invertebrate sites located >500m from a hydrological site and >1km from water quality, morphological alteration or temperature sites, except for seven sites with water quality or temperature information <1.5km from the invertebrate site. These distances are within the range of similar studies (e.g. Durance & Ormerod, 2009). We also excluded sites with <50 water quality records, and those at which wastewater effluent was released between invertebrate and water quality sites. In total, 179 sites were retained ($n=2500$ invertebrate samples), representing the chalk aquifer except southeast England and the Kennet and Pang catchments, for which hydrological model simulations were

unavailable (Figure 1). A mean $\pm$ SD of 16 ± 6 invertebrate samples were collected per site (Figure 1) and 78 ± 36 sites were sampled per year. We analysed only four samples from 1990 and 4–13 from 2020 to 2021 due to missing hydroclimatic data (Figure S1a).

2.4 | Biological metrics

For each sample, we calculated four metrics to summarize invertebrate community responses. We measured taxa richness as the number of families. We calculated the abundance-weighted 'WHPT' average score per taxon (ASPT), a biomonitoring index that reflects responses to organic pollution and general environmental degradation (Paisley et al., 2014) and thus provides a general measure of invertebrate community health and broader ecosystem quality. Taxon scores range between -1.6 and 13 , with higher scores indicating greater sensitivity to degradation (Paisley et al., 2014). We also calculated the distance of each community from its site-specific centroid using abundance-based Bray–Curtis dissimilarities, to assess deviation from the long-term average composition (hereafter, community deviation; Sarremejane et al., 2020). We also calculated Hill–Shannon diversity (Appendix S1).

2.5 | Data analysis

We used Pearson correlation matrices and variance inflation factors (VIF) to assess multicollinearity among hydroclimatic and human-impact variables, and sequentially removed those with a VIF >3 (Zuur et al., 2010). We used Pearson correlations between each % land-use change and each 1990 land cover % to assess if land-use changes were correlated with initial land use. The % change in pasture was removed due to its collinearity with other variables and negative correlation with the % change in cropland (Pearson $r = -0.92$; Figure S2).

We used separate principal component analyses to create two axes (PC1, PC2) representing water quality (WQ) and two axes representing land-use (LU) change, thus rationalizing the modelled environmental parameters. WQ-PC1 was positively correlated with DO (0.47) and negatively correlated with ammonia (-0.58), BOD (-0.48) and phosphate (-0.44), with lower values indicating poorer water quality (Figure S3a). WQ-PC2 was positively correlated with nitrate (0.85). LU-PC1 was positively correlated with % urban change (0.69) and negatively correlated with % woodland change (-0.67), with higher values reflecting sites at which urban land and woodland increased and decreased, respectively. LU-PC2 was positively correlated with % cropland change (0.95), with higher values representing increases in cropland (Figure S3b).

We used linear mixed-effect models (LMM) to detect linear biological responses and interactions between hydrological and human-impact variables, and used hierarchical generalized additive models (HGAM; Pedersen et al., 2019) to detect non-linear relationships. For each biological response metric, we built two sets of LMM and HGAM, to assess interactive responses to human impacts and (i) LFA or (ii) TSD. Type i 'response' models assessed community responses

to recent flow conditions, addressing H1–H2. Type ii ‘recovery’ models assessed community change over time post-drought, addressing H3–H4. LMM and HGAM model selection procedures differed due to computational limitations.

Saturated LMM included each two-way interaction between LFA or TSD and FAV, water temperature anomalies, the Channel Resectioning Index, % fine sediment, WQ-PC1, WQ-PC2, LU-PC1, LU-PC2 and distance from source. Site was included as a random intercept and sample year as a predictor with a random slope, to account for temporal trends and unexplained spatiotemporal variability. We selected the most influential set of predictors using a model-averaging approach. As such, all predictor combinations were assessed but only parameters of models with corrected Akaike's information criteria (ΔAICc) <2 were selected and their estimates and confidence intervals averaged.

Saturated HGAM included tensor smooth interactions for the same predictors as LMM, smooth terms (main effects) for each environmental predictor and a random factor smooth interaction term producing a smooth across years for each site. To improve model fit and select the final set of parameters, we built subset models and sequentially removed non-significant parameters from the saturated model (but kept main effects when a tensor smooth interaction was significant) until all parameters were significant. AICc were compared to check the final model had a better fit (i.e. lower AICc) than the saturated and other subset models.

We used the AICc, adjusted R^2 and root-mean-square error (RMSE) to evaluate the fit of each final model. Each model RMSE was calculated on the data used to build it and standardized by dividing the RMSE by the range of the response variable. RMSE are reported as % of the range. We used a cross-validation procedure to compare linear and non-linear model prediction accuracy. To do so, for each response variable and response/recovery LMM and HGAM, we built 30 models using a random subset of 95% of the data and then calculated RMSE on the predictions for the remaining 5%. We assessed differences in model accuracy between each LMM/HGAM pair using an ANOVA on the 30 cross-validated RMSE. For each response variable and response/recovery model, we present results for the model with the lowest AICc.

FAV were $\log_{10}(x+1)$ -transformed in all models to reduce the influence of high values. TSD was log-transformed in LMM because community recovery usually follows a log response. All predictor variables were standardized so that each had a mean of 0 and a variance of 1.

No ethical approval was required for this research.

3 | RESULTS

3.1 | Hydroclimatic and anthropogenic conditions

More than 40% of sites experienced drought in the year preceding sample collection in 1989–1993, 1998–1999, 2006–2007, 2012–2013 and 2018 (Figure 1b). The mean low-flow anomaly (LFA) was

–0.32, and 16% and 5% of samples had anomalies <-1 and >1 , respectively (Figure S1b). Time since drought (TSD) varied between <1 year and 21 years, with 28% and 5% of samples collected <1 year and >10 years after drought, respectively (Figure S1c).

Human-induced flow alteration affected most sites: 50% and 15% of samples had flow alteration values (FAV) <0.95 (indicating abstraction) and >1.05 (indicating augmentation), respectively (Figure S1d). Water pollution affected most sites: 50% had nitrate, phosphate and ammonia concentrations and BOD >7.17 , >0.11 , >0.05 and $>1.42\text{ mg L}^{-1}$, respectively (Figure S1e–i). Most sites were dominated by cropland (median [range]: 54.0% [0%–98.0%]) and pasture (24.2% [1.4%–99.1%]) with zero to moderate woodland (7.3% [0%–31.9%]) and zero to high urban (3.5% [0%–98.1%]) cover in 1990. Most sites were in catchments that experienced small increases in urban land (median [range]: 1.4% [–1.3% to +22.2%]) and woodland (0.9% [–6.9% to +17.4%]) and major changes in cropland (0% [–39.4% to +45.4%]) associated with changes in pasture (–2.9% [–53.0% to +39.4%]; Figure S1j–m). Cropland, pasture and urban land-use changes had moderate positive correlations with the % pasture ($r=0.53$), cropland (0.45) and urban (0.45) land use in 1990, respectively (Figure S2).

All sites were morphologically altered (Figure S1n). Substrates comprised 0%–100% fine sediment, with 25% of samples having $>50\%$ fine sediment (Figure S1o). The mean distance from source was $20.1 \pm 14.5\text{ km}$ (Figure S1p). Water temperature anomalies were mostly positive (median = 0.39; Figure S1q), indicating temperatures above the 1960–2023 average.

3.2 | Linear and non-linear biological responses

Taxa richness varied between 4 and 48 (mean $\pm$ SD 25 ± 7) families per sample (Figure S4a) and was best predicted by non-linear models (HGAM). WHPT-ASPT varied between 2.4–7.1 (5.2 ± 0.8 ; Figure S4c) and was best predicted by LMM. Community deviation varied between 0.09 and 0.67 (0.27 ± 0.08 ; Figure S4d) and was best predicted by HGAM (Table 1).

3.3 | Responses to low-flow anomalies: Response models

Richness decreased with LFA (Figure S5a) and this relationship changed with water quality (WQ-PC1; Table S1). Richness increased with LFA at sites with poor water quality: poor quality caused greater declines during below-average flows (Figure 2a and Figure S6a; Table S1).

WHPT-ASPT increased with LFA (Figure S7a). An interaction between LFA and land-use change (LU-PC1) indicated that WHPT-ASPT was lower during below-average flows at sites in catchments which gained woodland compared to those which gained urban land (Figure 3 and Figure S8a; Table S2). The effects of LFA on WHPT-ASPT were lower at sites that had gained cropland and higher at sites

TABLE 1 Estimates comparing the top hierarchical generalized additive model (HGAM) and linear mixed-effect model (LMM) accuracies for response and recovery models. Root-mean-square error (RMSE) percentages indicate the normalized RMSE as % of the response variable range.

						ANOVA	
						F	p
		R ²	AICc	RMSE	RMSE (n = 30)		
Response (low-flow anomaly)							
Richness	LMM	0.593	14858.7	3.916 (8.9%)	4.419 ± 0.248	5.393	0.024
	HGAM	0.725	14794.7	3.535 (8.0%)	4.272 ± 0.241		
WHPT-ASPT	LMM	0.805	1908.6	0.279 (6.0%)	0.320 ± 0.028	1.022	0.316
	HGAM	0.874	1937.2	0.258 (5.5%)	0.313 ± 0.025		
Community deviation	LMM	0.368	-346.4	0.198 (10.1%)	0.217 ± 0.011	13.744	<0.001
	HGAM	0.547	-495.1	0.180 (9.1%)	0.206 ± 0.012		
Recovery (time since drought)							
Richness	LMM	0.597	14843.0	3.899 (8.9)	4.387 ± 0.250	4.056	0.049
	HGAM	0.726	14801.5	3.530 (8.0%)	4.259 ± 0.242		
WHPT-ASPT	LMM	0.807	1872.2	0.277 (5.9%)	0.314 ± 0.026	0.610	0.438
	HGAM	0.876	1924.8	0.255 (5.5%)	0.314 ± 0.025		
Community deviation	LMM	0.377	-377.2	0.196 (10.0%)	0.215 ± 0.011	9.985	0.003
	HGAM	0.548	-500.9	0.181 (9.2%)	0.206 ± 0.011		

Note: RMSE are reported as the mean ± SD of 30 cross-validation models. ANOVA statistics compare the RMSE of the 30 LMM and HGAM. Bold indicates the model with the lowest corrected Akaike's information criterion (AICc).

farther from the source, although confidence intervals overlapped slightly with 0 (Table S2).

Interactions between LFA and both flow alteration and land-use change influenced community deviation (Table S1). Whereas deviation decreased with LFA at FAV <1, it increased with LFA at FAV >1 (Figure 4a): communities at sites altered by abstraction deviated more during drought (i.e. LFA <-1.5), whereas communities at sites with higher than naturalized flows deviated more when low flows were above average (i.e. LFA >1.5; Figure 4a and Figure S9a). Community deviation also decreased and increased with LFA at sites with increased woodland and urban land (LU-PC1), respectively (Figure 4b; Table S1): during below-average low flows, communities deviated more at sites with increased woodland (Figure S9b).

3.4 | Change over time since drought: Recovery models

Richness and WHPT-ASPT increased, and community deviation decreased, with TSD (Figures S5, S7 and S10). Richness responses to TSD depended on flow alteration and land-use change (LU-PC2). Increases in richness with TSD were greater at sites with higher than naturalized discharge (i.e. FAV >1) and were subdued at sites with FAV <1 (Figure 2b). Although FAV had little effect on richness when TSD was <3 years, positive relationships (with lower richness predicted at sites with FAV <1) arose as TSD increased. Richness decreased with TSD where cropland decreased, but increased with TSD where cropland increased (Figure 2c).

WHPT-ASPT increased with TSD faster at sites in catchments that gained woodland, because WHPT-ASPT was lower just after drought at these sites (Figure S8; Table S2) and because post-drought maximum WHPT-ASPT values were lower at sites which gained urban land (Figure 3). Increases in WHPT-ASPT with TSD were also steeper at sites with poor water quality (WQ-PC1), because post-drought reductions in WHPT-ASPT were most pronounced at these sites (Figure S7d). WHPT-ASPT recovered faster from drought as distance from source increased (Figure 4 and Figure S8; Table S2).

Community deviation decreased slightly with TSD (Figure S10; Table S1), in particular where cropland increased. Community deviation also decreased more strongly with TSD when temperatures were above average, but effects were small (Figure 4).

4 | DISCUSSION

We demonstrate that human impacts alter aquatic invertebrate community responses to and recovery from drought in chalk streams: groundwater-fed rivers of considerable management interest due to their water resource provision, high biodiversity and global rarity. Land-use changes, water quality and anthropogenic flow alteration interacted with drought to determine the extent of community responses and post-drought recovery rates. We found support for hypothesis H1, that responses to drought are stronger in communities exposed to human impacts, in particular poor water quality and altered flows. We found little evidence to support hypothesis H2, that human-impacted communities are less responsive to drought because taxa co-tolerate multiple stressors. Supporting our hypothesis

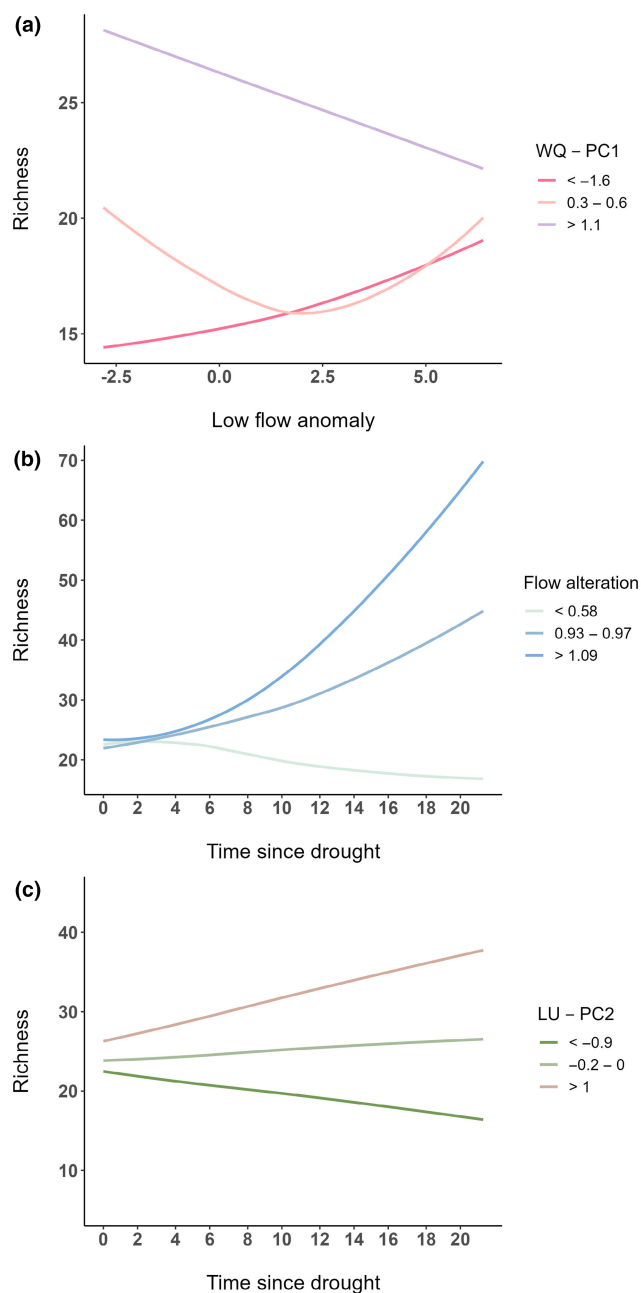


FIGURE 2 Invertebrate taxa richness response to interacting hydrological and human impact predictors, based on HGAM predictions: (a) low-flow anomalies and water quality (WQ-PC1); (b) time since drought (TSD, years) and flow alteration; and (c) TSD and cropland/pasture land-use changes (LU-PC2). Groupings for human impact predictors were defined as <10th percentile, between the 45 and 55th percentile and >90th percentile of the variable. Y-axis scales differ.

that resilience increases with site naturalness (H3), post-drought increases in taxa richness were slower at abstraction-impacted sites. However, communities recovered faster at sites with poor water quality, indicating the greater resilience of human-impacted communities—which comprise generalist, stress-tolerant taxa—compared to communities at relatively natural sites (H4). We detected non-linear responses of richness and changes in community composition,

highlighting the potential for interactions between drought and human impacts to drive community shifts. By identifying human influences that exacerbate the ecological impacts of drought, our results indicate priority management actions needed to support the resilience of river ecosystems facing climatic extremity.

4.1 | Responses to drought were stronger at human-impacted sites

Supporting H1, taxa richness was lower during drought at sites with poorer water quality. Poor water quality and drought may interact to exacerbate ecological impacts, if decreasing streamflow increases organic and inorganic nutrient concentrations and depletes DO availability (Mosley, 2015). In particular, phosphorus availability and warmer temperatures may promote algae growth in unshaded reaches, accentuating oxygen depletion and eliminating sensitive invertebrates such as large-bodied predators, with potential cascading effects (Ledger et al., 2013).

Communities deviated more from their average composition during drought at sites impacted by water abstraction. Both climatic drivers and water resource pressures can cause hydrological drought (Van Loon, 2015), and our results provide evidence of community responses to anthropogenic drought (i.e. water deficits caused directly by human activities; AghaKouchak et al., 2015). Climate-driven flow reductions typically increase gradually in severity, giving organisms time to respond, for example by moving into refuges (James et al., 2008). During such climatic droughts, even small abstraction-related streamflow declines may have particular potential to push instream habitats across thresholds, for example by interrupting connected flow, thus altering community composition (Boulton, 2003). Elimination of sensitive taxa may have driven communities further from their average composition.

WHPT-ASPT was lower during below-average flows, aligning with previous reports that such indices—which represent community responses to environmental degradation—also decrease with flow cessation and river drying (Stubington et al., 2022). During drought, declining flow velocities reduce turbulence and increase water residence times while falling water depths increase the influence of solar radiation and elevate water temperatures, reducing DO concentrations and increasing metabolic oxygen demand (Mosley, 2015; Verberk et al., 2016). As such, reflecting their oxygen requirements, taxa may be co-sensitive to drought and to human impacts including organic enrichment (Crabot et al., 2021).

Drought-driven community deviation and declines in community health (as represented by WHPT-ASPT) were greater at sites at which catchment-wide woodland increased compared to those at which urban land increased. Woodland is associated with lower human impact intensities, with riparian vegetation attenuating catchment-derived pollution and, via shading, moderating water temperatures and limiting algal growth, thus increasing invertebrate biodiversity (Harrison & Harris, 2002). Such communities have more taxa to lose during drought, potentially explaining greater deviations

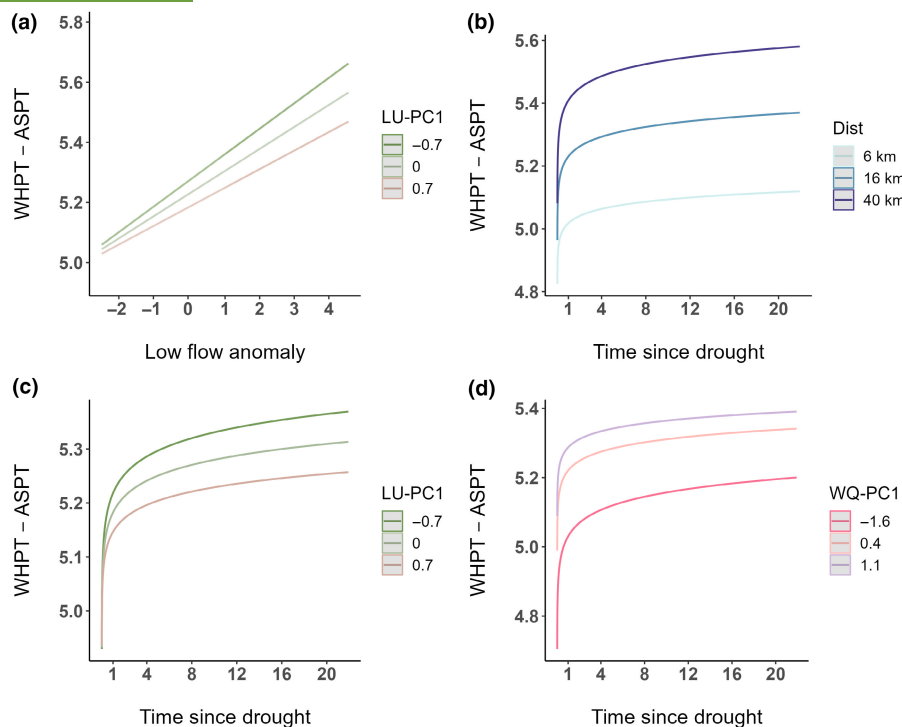


FIGURE 3 WHPT-ASPT response to low-flow anomalies in interaction with woodland and urban land-use change (LU-PC1; a), and to time since drought (TSD) in interaction with site distance from source (Dist; b), LU-PC1 (c) and water quality (WQ-PC1; d), based on LMM predictions. Relationships are logarithmic because TSD was log-transformed. Groupings are defined in Figure 2. Y-axis scales differ.

and declines. Equally, communities in urban rivers may tolerate low DO and elevated pollutant concentrations (Walsh et al., 2005), and thus be little altered by drought.

4.2 | Human impacts altered recovery after drought

As time since drought increased, gains in taxa richness, improvements in ecological quality (as indicated by WHPT-ASPT) and decreases in community deviation—all of which reflected post-drought recovery—differed depending on flow alteration and land-use change. Supporting our hypothesis that naturalness promotes resilience (H3), increases in richness were slower at abstraction-impacted sites, in particular as post-drought durations extended beyond 3 years. Anthropogenic drought may prevent complete recovery after climate-driven hydrological drought ends by limiting habitat availability for sensitive, rheophilic taxa (Bogan & Lytle, 2011). Equally, richness increased quickly after drought at sites with higher-than-natural discharge, perhaps because flow augmentation (e.g. by effluent) promoted connectivity between refuges and drought-impacted sites in river networks affected by widespread abstraction (Hamdhani et al., 2020), again supporting H3. These results indicate that the contributing effluent was of sufficient quality to support biodiverse communities (Vaughan & Gotelli, 2019; Whelan et al., 2022). The faster increases in WHPT-ASPT at sites in catchments that gained woodland rather than urban land also offer tentative support

for H3: Despite greater drought-driven reductions, greater naturalness may have accelerated population establishment by sensitive rheophilic taxa represented by high WHPT-ASPT scores.

Post-drought increases in WHPT-ASPT indicated that community recovery became faster as distance from the stream source increased, supporting the hypothesis that hydrological connectivity promotes resilience (H3). This suggests that populations of high-scoring, drought-sensitive taxa such as many Ephemeroptera, Plecoptera and Trichoptera—which, if eliminated by drought, recolonize primarily by dispersal of flying adults—recovered more quickly at better connected downstream sites than in isolated headwaters (Sarremejane, Truchy, et al., 2021).

We also found some support for our alternative recovery hypothesis (H4), that communities recover more quickly at human-impacted sites. First, although WHPT-ASPT indicated that community health was lower at sites with poorer water quality, the index increased faster post-drought at these sites. Communities in poor quality water may be dominated by taxa with resilience traits including multivoltinism, accelerating post-drought community recovery (Kuzmanovic et al., 2017).

Increases in richness and decreases in community deviation with time since drought were greater at sites in catchments in which cropland increased in conjunction with decreases in pasture, reflecting local changes in agricultural land use. Site-specific variability in farming practices prevents generalization about the relative impact intensities of cropland and pasture, and this result may or may not indicate the greater 'resilience' of cropland

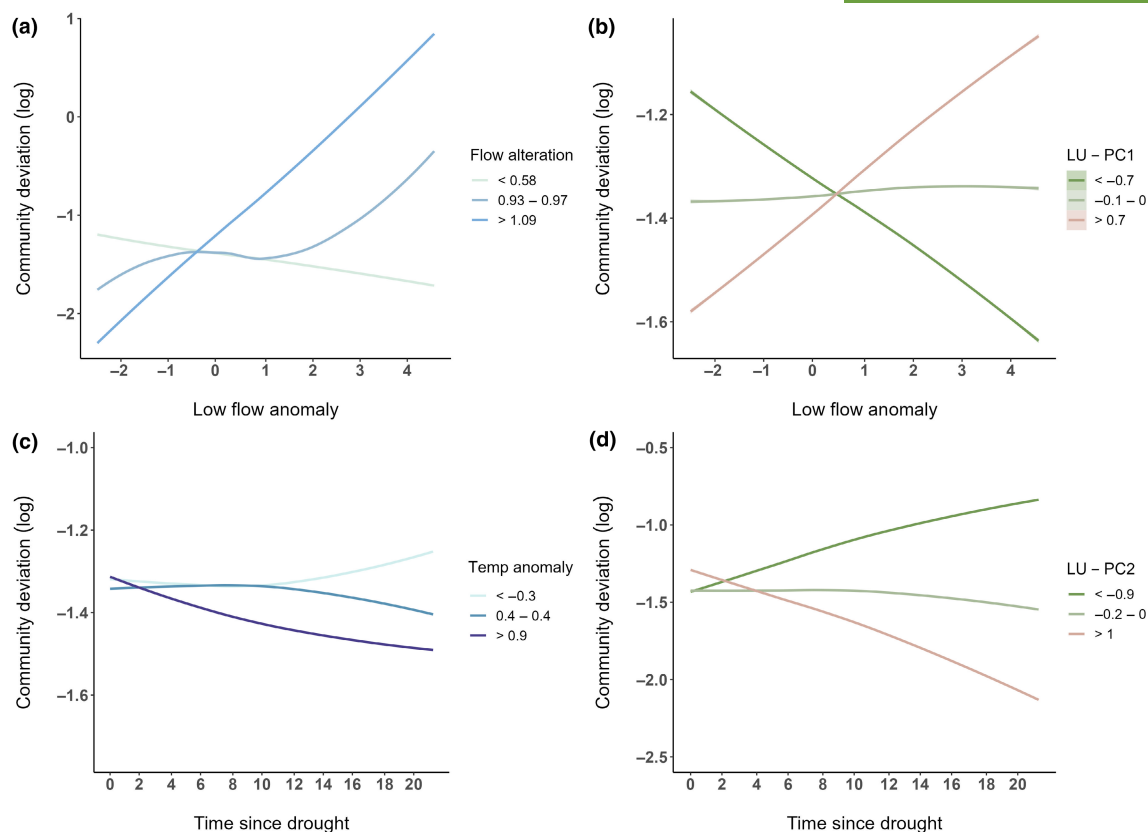


FIGURE 4 Community deviation from the average composition response to low-flow anomalies in interaction with temperature anomalies (a) and woodland/urban land-use change (LU-PC1; b), and change with time since drought in interaction with distance from source (c) and cropland/pasture land-use change (LU-PC2; d), based on HGAM predictions. Community deviation was log-transformed. Groupings are defined in Figure 2. Y-axis scales differ.

communities. The faster recovery of communities at impacted sites aligns with Holling's (1973) definition of engineering resilience, as measured by ecological stability and thus resistance to disturbance and rapid post-disturbance recovery. Rather than comprising more resilient taxa than those at relatively natural sites, communities in agricultural landscapes may recover faster because they are dominated by widespread generalists (Harrison & Harris, 2002; Mykrä & Heino, 2017) that can persist in poor quality habitats during drought (Boersma et al., 2014).

4.3 | Non-linear responses to drought and human impacts

Taxa richness and community deviation were better predicted by non-linear than linear models, evidencing non-linear responses to interacting drought and human impacts. In particular, the contrasting, water-quality-dependent responses of richness to drought suggest that poor water quality could severely compromise drought resistance, by reducing DO concentrations to below the requirements of even tolerant taxa. Interactions between 'pulsed' drivers such as drought (Harris et al., 2018) and long-term pressures such as water pollution may have particular potential to drive communities beyond

thresholds at which they shift to species-poor, non-functional states (Carrier-Belleau et al., 2022). Although considered rare in river ecosystems (but see Bogan & Lytle, 2011), community shifts to new stable states are an increasing risk due to interactions between intensifying climatic extremity and ongoing anthropogenic pressures (Daufresne et al., 2007).

5 | CONCLUSIONS

In groundwater-dominated rivers such as chalk streams, existing actions to manage water resources, including their quantity and quality, may be insufficient to ensure ecological stability before, during and after drought. By demonstrating that human impacts reduce community resistance and resilience to drought, our results have the potential to inform adaptation of current drought management strategies. First, our finding that anthropogenic flow reductions exacerbate drought-driven changes in community composition and compromise post-drought recovery highlights the need to protect flows during drought, for example by limiting abstraction or augmenting flows in over-abstracted reaches. Second, we found that poor water quality exacerbates drought-driven declines in taxa richness, suggesting that addressing diffuse pollution through measures

such as nature-based solutions and catchment sensitive farming, as well as ongoing regulation of point source discharges, could support ecological resistance and resilience to drought. In addition, natural drought management actions, such as adding large wood to headwater channels to store water and create drought refuges, could limit the interacting impacts of drought and human activities (Stubbington et al., 2024). More widely, tackling the human pressures that co-occur with drought could enable river ecosystems to adapt to increasing climatic extremity.

AUTHOR CONTRIBUTIONS

Romain Sarremejane, Rachel Stubbington and Judy England conceived the ideas and designed the methodology. Judy England, Mike Dunbar, Rosalind Brown and Marc Naura provided data and supported data analysis. Romain Sarremejane analysed the data and led manuscript writing with Rachel Stubbington. All authors contributed to drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.3r2280gr8> (Sarremejane et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Results from hierarchical generalized additive models for richness and community deviation, i.e. models with the lowest AICc, Effective degrees of freedom (edf), *F* values, *p* values and the transformation used on the response variable are reported.

Table S2. Results from linear mixed-effect models for Hill diversity and WHPT-ASPT.

Table S3. Estimates comparing the top hierarchical generalized additive model (HGAM) and linear mixed-effect model (LMM) accuracies for response and recovery models.

Figure S1. Data distribution (*n* = 2500) for sampling year (a) and each environmental variable, including hydrological (a–c), water quality (e–i), land-use change (j–m), fine sediment (n), morphological alteration (o), distance from the stream source (p) and water temperature (q).

Figure S2. Matrix of Pearson's correlation coefficients between % land use changes and % land use in 1990.

Figure S3. Principal component analyses (PCA) representing invertebrate samples (black points) in relation to variables representing water quality (6xgcgWQ; a) and change in land use (LU; b). BOD, biological oxygen demand; DO, dissolved oxygen.

Figure S4. Data distribution ($n=2500$): of the response variables used to represent invertebrate communities: family-level taxonomic richness (a), Hill-Shannon diversity (b), WHPT-APST (average score per taxon; a biomonitoring index indicative of community 'health') (c), and community deviation, that is, distance from the centroid representing the site-specific, long-term average composition (d).

Figure S5. Relationships between invertebrate family richness and hydroclimatic and human-impact variables selected in the top model.

Figure S6. The response of invertebrate community taxonomic richness to water quality (represented by axis 1 of a principal components analysis [PCA]: WQ-PC1; a), flow alteration (b) and land-use changes (represented by PCA axis 2: LU-PC2; c), depending on the low-flow anomaly (LFA) and time since drought (TSD).

Figure S7. Relationships between WHPT-ASPT (average score per taxon, a biomonitoring index) and hydroclimatic variables (a, b), human-impact variables (c–f), distance from the stream source (g) and year (h).

Figure S8. The responses of WHPT-ASPT (average score per taxon, a biomonitoring index) to land-use changes (LU-PC1; a, c), distance

from the stream source (b) and water quality (WQ-PC1; d) depending on the low-flow anomaly (LFA) and time since drought (TSD).

Figure S9. The response of community deviation (i.e. distance to site-specific community centroid) to flow alteration (a), land-use changes (represented by the first [LU-PC1] and second [LU-PC2] axes of a principal components analysis; b, d) and water temperature anomaly (c) depending on low-flow anomalies (LFA) and time since drought (TSD).

Figure S10. Relationships between community deviation (i.e. distance to site-specific community centroid) and time since drought (a), human-impact variables (b–e), distance from the stream source (f) and year (g).

Figure S11. Hill diversity response to the time since drought in interaction with land use changes (LU-PC1).

Appendix S1. Analyses and results for Hill-Shannon diversity.

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