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Drought and Human Pressures Contribute to Persistent Changes in Freshwater Invertebrate Communities

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ABSTRACT

1. Freshwater ecosystems are threatened by increasing climate extremes including drought, which interacts with human pressures to drive biodiversity loss across spatial scales. River communities are considered resilient to droughts, but this characterization is based on short-term, small-scale studies. Moreover, drought resilience is increasingly compromised by human pressures.
2. We used an unprecedented long-term, large-scale dataset spanning 359 perennial and near-perennial river sites in south England sampled over 8–30 years to characterize ecological responses to multiple droughts and interacting human pressures, during a period of improving water quality. We determined how drought characteristics (including duration, magnitude, frequency, and spatial extent) and human pressures (including flow alteration and water quality) interact to influence aquatic invertebrate community resistance and resilience to droughts, including identification of persistent shifts in community composition.
3. Although communities recovered on average within 1.5 years after 83% of droughts, those at 47% of sites experienced ≥1 long-term, drought-related compositional shift, challenging the paradigm of their resilience. Persistent shifts increased with drought duration and decreased with drought frequency, while anthropogenic flow reductions and lower oxygen concentrations altered community resistance and resilience to drought. Communities also experienced temporal drift (i.e., gradual compositional change) concurrent with improvements in water quality, and shifts were similarly frequent in drought and non-drought periods.
4. Pollution-sensitive taxa often characterized communities following drought, indicating that these disturbance events can reset communities, allowing sensitive taxa to benefit from improved water quality. Our results also confirm the key effect of drought severity and frequency on long-term community responses and the impacts of water abstraction and pollution on these responses.
5. As drought severity increases in many global regions, our results could inform management actions that mitigate the ecological impacts of droughts in rivers exposed to multiple pressures.

1 | Introduction

River ecosystems and their biodiversity are shaped by the flow regime, including the duration, magnitude and frequency of high, low and zero flows, in particular during droughts and floods (Poff et al. 1997). Droughts can cause local- to regional-scale environmental change in river networks, including reduced flows, altered water temperatures and habitat fragmentation (Van Loon 2015), which collectively cause freshwater biodiversity to decline (Stubbington et al. 2024). Biological community responses reflect

the capacity of their constituent species to tolerate drought-induced environmental changes (i.e., resistance) and to recover thereafter (i.e., resilience; Donohue et al. 2016; Hillebrand et al. 2018). Drought characteristics such as duration, magnitude, frequency, timing, rate of onset and termination, and spatial extent collectively determine community responses, affecting species survival during drought and their subsequent capacity to recover (Aspin et al. 2018; Sarremejane, Stubbington, et al. 2021; Stubbington et al. 2024). However, community responses to drought characteristics are often limited to site-specific case studies, hindering understanding of the ecological consequences of these climate extremes across spatial and temporal scales.

Drought may cause abrupt changes in species abundance and diversity (Aspin, Hart, et al. 2019), typically including declines in taxonomic richness and increased regional extinction risk during widespread drought (Sarremejane, Stubbington, et al. 2021). Such changes could lead to tipping points: persistent shifts in community structure and function (Bêche et al. 2009; Bogan and Lytle 2011). However, unlike terrestrial ecosystems—in which drought can cause such shifts—rivers are conceptualized as disturbance-prone systems that experience few such shifts in response to drought or other extreme events (Capon et al. 2015). Accordingly, research suggests that riverine communities typically recover within 1–3 years post-drought—but such studies routinely lack pre- and/or post-drought data, potentially leaving shifts undetected (Stubbington et al. 2024). As such, community shifts may be unexpectedly common in river ecosystems, but their detection requires time series encompassing multiple droughts and inter-drought recovery periods.

Human pressures can alter the ecological effects of drought (Fournier and Magoulick 2022), potentially increasing the risk of river communities passing tipping points. For example, abstraction of surface water and groundwater may further reduce river flows during climatic drought, exacerbating biodiversity loss (Finn et al. 2009; Vaughn et al. 2015; Sarremejane et al. 2024). Responses to droughts driven by climate and by human activities including abstraction (i.e., anthropogenic drought; AghaKouchak et al. 2015) are difficult to disentangle, leaving their interacting effects poorly characterized. In addition, organic and inorganic nutrient pollution and associated oxygen depletion may exacerbate drought impacts, in particular in warm, slow-flowing waters (Fournier and Magoulick 2022). The environmental context in which drought unfolds, including catchment land use, instream habitat characteristics such as sediment composition (Vadher et al. 2017) and network position (Jacquet et al. 2022; Sarremejane et al. 2024), may also influence ecological responses.

Our aim was to determine how drought characteristics, human pressures including flow alteration and water quality, and environmental context interact to influence resistance and resilience to drought in river ecosystems, including identification of conditions associated with persistent shifts in community composition. We used long-term (1990–2022) data from 359 groundwater-dominated river sites in England (Figure 1A) describing river flow, human pressures, environmental context and freshwater invertebrate communities—which are abundant, diverse and responsive to environmental variability—to assess responses to drought and interacting pressures at local to regional scales. We used site-specific modelled hydrological data, including actual and naturalized (i.e., with and without

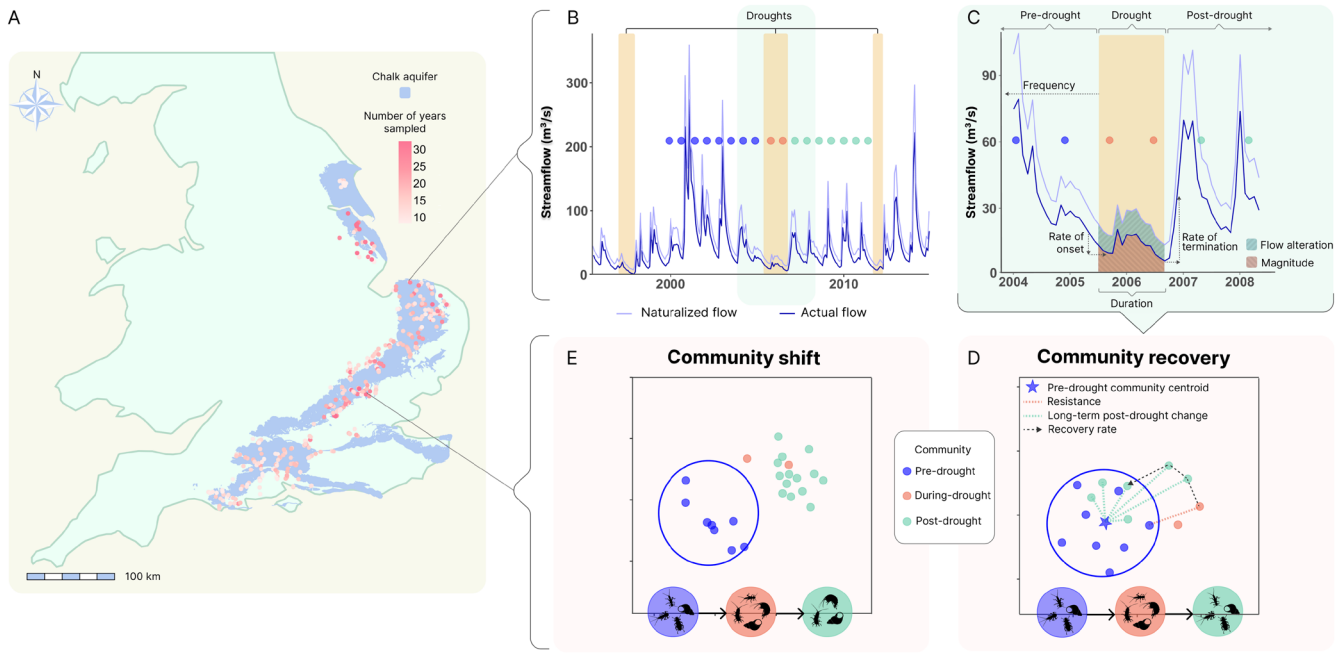

FIGURE 1 | (A) Study site locations (dots) in England. Illustration of (B) site-specific identification of drought periods; (C) calculation of drought characteristics; and use of pre-drought, drought-period and post-drought community samples to (D) determine resistance and resilience to drought and (E) to identify shifts in a multidimensional space representing each community's taxonomic composition. In (D), the distance from the last pre-drought community to the last community sampled during drought represents resistance, the mean length of the dotted green lines represents long-term post-drought compositional change, and the distance (dotted black line) for post-drought communities to return to within the 95th percentile distances (blue circle) of pre-drought communities divided by the recovery time (number of months between the last drought period and the first recovered community) represents the recovery rate.

the effects of abstraction and augmentation) flows to identify and characterize droughts and to assess the impacts of anthropogenic flow alteration on their characteristics (Figure 1B–C). We assessed community resistance and resilience using metrics characterizing during- and post-drought compositional changes (Figure 1D). We classified communities that did not return to their pre-drought composition as 'shifted' (Figure 1E). We then modelled the contribution of drought characteristics, human pressures and environmental context to community resistance, resilience and persistent shifts.

2 | Material and Methods

2.1 | Study Area and Invertebrate Data

Our study encompassed England's perennial and near-perennial chalk rivers: groundwater-dominated ecosystems that support high invertebrate biodiversity and abundance. We analysed invertebrate samples collected by the Environment Agency using the 3-min kick-sampling method (Murray-Bligh and Griffiths 2022) in spring (March–May) and autumn (September–December) 1990–2022. We considered an initial set of 427 sites for which samples were collected in ≥ 8 years, to ensure enough pre- and post-drought temporal replication. Invertebrates were identified to family and abundance recorded as log10 classes (i.e., 1, 2–9) then converted to the class median (Vaughan and Gotelli 2019).

2.2 | Drought Characteristics and Human Pressures

We summarized drought characteristics and anthropogenic flow alteration using hydrological variables calculated using monthly mean discharge data and groundwater models paired with surface-water recharge/runoff models (Soley et al. 2012). These models simulate river-catchment-specific actual and naturalized discharge using geology, topography, land use, precipitation, evapotranspiration, groundwater levels, river discharge, and surface water and groundwater abstraction data for 100-m reaches covering most chalk rivers for river-specific periods between 1960 and 2022.

We calculated reach-specific actual and naturalized monthly Q90 (i.e., the discharge exceeded 90% of the time) for the period 1970–2010. Reach-specific drought periods were defined as ≥ 3-month periods in which discharge was below its monthly Q90. Shorter periods were excluded to avoid analysing shorter periods of low-flow conditions. We defined the termination of a drought as the month preceding ≥ 6 consecutive months with discharge above the Q90. To quantify drought magnitude, we calculated flow percentage anomalies (Parry et al. 2016) as:

$$100\left(\left(\frac{\text{discharge}}{\text{mean monthly long}-\text{term discharge}}\right)-1\right)$$

For each reach containing an invertebrate sampling site, we calculated the duration, magnitude, timing and rate of onset, timing and rate of termination, and spatial extent of each drought and the frequency of previous droughts in the 5, 10 and 15 years preceeding drought onset (Table S1). We calculated metrics to characterize anthropogenic alteration of flow before and during drought (Table S1). We calculated post-drought changes in flow magnitude as the difference between the mean flow percentage anomaly post- and pre-drought. Sites with > 25% of months with zero discharge (i.e., seasonally intermittent and other non-perennial sites) and abnormal hydrographs (e.g., including negative discharge; $n = 68$) produced unreliable drought periods and were excluded, focusing the study on perennial and near-perennial sites.

We used Environment Agency data collected in 1990–2022 to quantify four water quality indicators: nitrate, ammonia, orthophosphate and dissolved oxygen (DO) concentrations ($mg \cdot L^{-1}$). We calculated the site-specific 1990–2022 mean for each indicator (210 ± 188 samples per site).

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 (Sarremejane et al. 2024). For each catchment, we calculated the mean % agricultural (including pasture and crops) and urban land cover (i.e., the dominant land covers in England) between 1990 and 2015.

We used site-specific modelled monthly mean water temperatures based on spot measurements collected by the Environment Agency from 891 sites between 1960 and 2022. We calculated site-specific monthly water temperature anomalies as the difference between each temperature record and its site-specific 1960–2022 monthly mean, then calculated the mean anomaly for each site-specific drought period. We calculated site-specific mean long-term water temperatures as the 1960–2022 mean.

We used three variables to describe site-specific environmental context. The distance of the invertebrate sampling site from the river source was used to represent network position and stream size. We used visual estimates of sediment grain-size composition made during invertebrate sampling visits to calculate the % fine sediment (sum of sand, silt and clay), which describes riverbed sedimentation.

Each invertebrate sampling site was paired with its closest hydrological, water quality and temperature site. We excluded sites located > 2.5 km from water quality or temperature sites and > 500 m from a hydrological model reach. Such distances have enabled characterization of invertebrate responses to environmental conditions in similar studies (Durance and Ormerod 2009; Vaughan and Gotelli 2019). We also excluded sites with < 30 water quality records and those at which wastewater effluent was released between invertebrate and water quality sampling sites. Of the 427 invertebrate sites, 359 had reliable hydrological data and 220 had water quality and temperature data available.

2.3 | Drought-Specific Biological Response Metrics

For each drought, we identified site-specific invertebrate samples collected before, during (including the 3 months following drought termination) and after each site-specific drought period (Figure 1). We calculated metrics to assess community

resistance and resilience to each drought, separating communities sampled in spring (March–May) and autumn (September–December; hereafter, spring and autumn communities) to account for seasonal changes in composition (Murray-Bligh and Griffiths 2022).

To calculate resistance metrics, we selected droughts for which ≥1 community was sampled (1) in the 2 years before drought onset and (2) during the drought period. In total, 638 and 504 droughts at 324 and 278 sites met these criteria in spring and autumn, respectively. We calculated community resistance as the turnover in taxa composition between the last pre-drought community and the last drought-period community (Figure 1D), based on Bray-Curtis distances, with higher values indicating greater compositional change. We calculated the difference between the last pre-drought and the last drought-period values for family-level taxonomic richness, and Ephemeroptera, Plecoptera and Trichoptera (EPT; three insect orders sensitive to both drought and anthropogenic degradation Paisley et al. 2014; Chadd et al. 2017) richness and abundance.

To calculate resilience metrics, we analysed droughts with ≥4 pre- and ≥1 post-drought communities, each with the first sampled <2 years from the drought period. Pre-drought communities were used to estimate pre-drought variability in community composition, excluding any sampled >10 years before drought onset. In total, 371 and 388 droughts from 216 and 226 sites met these criteria in spring and autumn, respectively. For each site, we estimated drought-specific change in community composition by calculating the distance between each pre- and post-drought community and the centroid of the pre-drought communities based on principal coordinate axes derived from Bray-Curtis distances (Anderson et al. 2006). For each site-specific drought, we calculated the recovery time as the number of months from drought termination to the first recovered community, that is, the post-drought community for which the distance to the pre-drought centroid was below the 95th percentile of the pre-drought distances (Figure 1D). We calculated the recovery rate as the total length of the community trajectory between the last drought period or the first post-drought community and the recovered community divided by the number of months between them (Figure 1D). Using all communities with ≥5 post-drought samples and ≥5 years of post-drought data, we classified communities which did not return to within the pre-drought multidimensional space as 'shifted', because >95% of the communities that recovered did so within 5 years. For these recovering and shifting communities, we calculated the mean distance between the pre-drought community centroid and the post-drought communities within 10 years of drought onset, to quantify the extent of long-term post-drought compositional change (Figure 1D).

2.4 | Data Analysis

We identified collinear predictors representing drought characteristics, human pressures and environmental context using variation inflation factors (VIF) and sequentially removed variables with the highest VIF until all had a VIF <3, determining sets of modelled predictors (Table S2).

We used generalized additive models (GAM) to assess linear and non-linear responses of each resistance and resilience metric to predictors. For each metric, we built two sets of models including either drought characteristics or human-pressure and environmental context variables as predictors (Table S2). We built separate models because human-pressure and environmental context data were only available for 220 sites. Each GAM was compared to a GAM including site as a random intercept, and the model with the lowest Akaike information criterion, corrected for small sample sizes (AICc), was used. Each predictor was fitted with a smooth term and assumed a Gaussian distribution. Response variables were log transformed as necessary to meet model assumptions, and outliers were removed to improve the robustness of relationships. For each model, we compared all potential predictor combinations and used the lowest AICc to select the best-fitting final predictor set (Table S2).

We used generalized linear models (GLM) with a binomial distribution to identify the factors associated with community shifts. We modelled a binary response variable representing whether post-drought communities shifted or not, using each predictor included in resistance and resilience models (Table S2). We built two sets of models and selected the final predictor set as described above. We also used linear mixed effect models (LMM) to compare the family richness, EPT richness and EPT abundance of shifted and recovered communities between 5-year pre- and post-drought periods. Drought identity was used as a random intercept. We used a randomization procedure to compare the proportion of shifts in drought and non-drought periods and if the effect of drought duration on community change resulted from temporal drift (i.e., directional changes in community composition).

To identify taxa characterizing shifting and recovering communities pre- and post-drought, we ran indicator 'species' analysis (Dufrêne and Legendre 1997), using point-biserial coefficients (De Cáceres and Legendre 2009) and presence–absence community matrices. This analysis calculates an index of association for each taxon based on its occurrence in each group. Coefficients are constrained between 0 and 1, with higher values indicating stronger associations. The significance of each association was tested with 999 random permutations.

We used R software version 3.5.0 (R Core Team 2023) for all analyses, including the packages vegan (Oksanen et al. 2019) and ecotraj (De Cáceres et al. 2019) for resistance and resilience metric calculation, mgcv (Wood 2011) and MuMIn (Bartoń 2019) for model building and averaging, and usdm (Naimi et al. 2014) for VIF analyses.

3 | Results

We identified 1653 site-specific drought periods. Sites experienced a mean ± SD of 4.6 ± 1.5 periods of 13 ± 8-month durations, with 11% experiencing zero monthly discharge during ≥1 drought (Appendix S1). During national-scale events in 1991–1992, 1996–1997, and 2011–2012, >75% of sites experienced drought, as did >40% during regional-scale events in 2005–2006 and 2017–2019 (Figure S1). All sites were impacted by human pressures, with most catchments dominated by

agricultural land use and most rivers affected by anthropogenic flow reductions (Appendix S1).

3.1 | Characteristics and Factors Associated With Persistent Shifts in Community Composition

Persistent shifts in invertebrate community composition occurred after 17% of droughts (whereas 83% of communities recovered), and 47% of sites experienced ≥1 drought-related shift (Figure S2). Communities at >90% of sites experienced temporal drift and shifts were as frequent during drought and non-drought periods (Appendix S2). Both shifting and recovering communities had higher family richness (in autumn only), EPT richness and EPT abundance post-drought (LMM, $p < 0.031$; Table S3). Shifting communities had comparable family richness, EPT richness and EPT abundance to recovering communities, both before and after shifting (LMM, $p > 0.104$; Table S3). Interannual variation in composition was higher in recovered than shifted communities (Appendix S2). Shifting communities were characterized by higher pre-drought occurrences of leeches, beetles, true bugs and snails, which are typical of slow-flowing and poorer quality water (Table S4). Post-drought, shifted and recovered communities were characterized by taxa that prefer fast-flowing, well-oxygenated water such as caddisflies and mayflies (Table S4).

Compared to recovering communities, shifting autumn communities had experienced longer, human-extended and less frequent droughts (GLM, $p \leq 0.007$; Figure 2; Table S5). Spring communities shifted more often at sites experiencing droughts of lower magnitude, larger spatial scale, terminating later in the year and with lower post-drought than pre-drought flow magnitudes (GLM, $p \leq 0.036$; Figure S3; Table S5). Drought-associated shifts were more frequent at sites with human-impacted water quality, as indicated by higher ammonia concentrations (GLM, $p = 0.019$), and higher mean long-term water temperatures (GLM, $p < 0.001$; Figure S4; Table S5). However, these models explained relatively little variance (R^2: 0.04–0.14; Table S5).

3.2 | Effects of Drought Characteristics and Anthropogenic Flow Alteration on Resistance and Resilience

Community change between pre-drought and drought periods (i.e., resistance) was characterized by both gains and losses of EPT and other taxa, with contrasting responses between sites and seasons (Appendix S3). For the 83% of communities that recovered, the mean ± SD post-drought recovery time across both seasons was 19 ± 22 months and 99% of communities recovered within 129 months (i.e., 10.8 years).

Compositional turnover between pre-drought and drought periods increased with duration (GAM, $p < 0.001$) and magnitude ($p \leq 0.014$) for both spring and autumn communities, indicating greater compositional change during longer, drier droughts (Figure 3A,B; Table S6). Increasing pre-drought frequencies reduced turnover (GAM, $p \leq 0.002$; Figure 3C, Figure S5) in both seasons: communities changed less during a drought when exposed to more previous droughts. In autumn, turnover associated with drought was greater at sites at which anthropogenic water abstraction or augmentation altered drought magnitude compared to sites with near-natural flows ($p = 0.001$; Figure 3D; Table S6). Due to high variation in responses among droughts and sites, these models explained limited variance ($R^2 = 0.23–0.29$). EPT and other taxa losses were also more common at sites affected by abstraction (Appendix S3).

Community resilience, as recovery rates, was influenced by drought frequency, magnitude and post-drought changes in flow magnitude. Rates increased and decreased with increasing drought frequency in the preceding 5 (GAM, $p \leq 0.010$) and 15 ($p \leq 0.023$) years, respectively, suggesting that more frequent droughts in the recent past promoted resilience whereas they lowered resilience over longer periods (Figure 4A; Figure S6A–C; Table S7). Recovery rates increased with drought magnitude: communities recovered faster after higher magnitude droughts (GAM, $p < 0.001$; Figure 4B). In addition, recovery rates of spring communities decreased with increasing

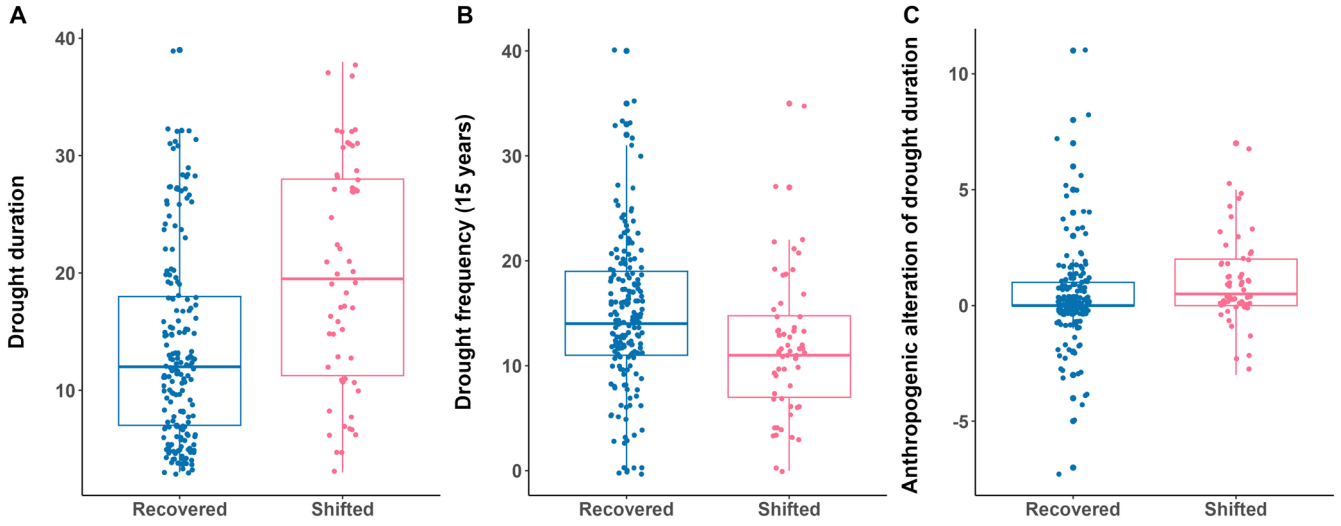

FIGURE 2 | Autumn communities that recovered or shifted in composition, in relation to drought duration (A), drought frequency in the preceding 15 years (B), and (C) anthropogenic alteration of duration. In each box, the horizontal line is the median, the box top and bottom indicate the first and third quartiles, and whiskers represent 95% confidence intervals.

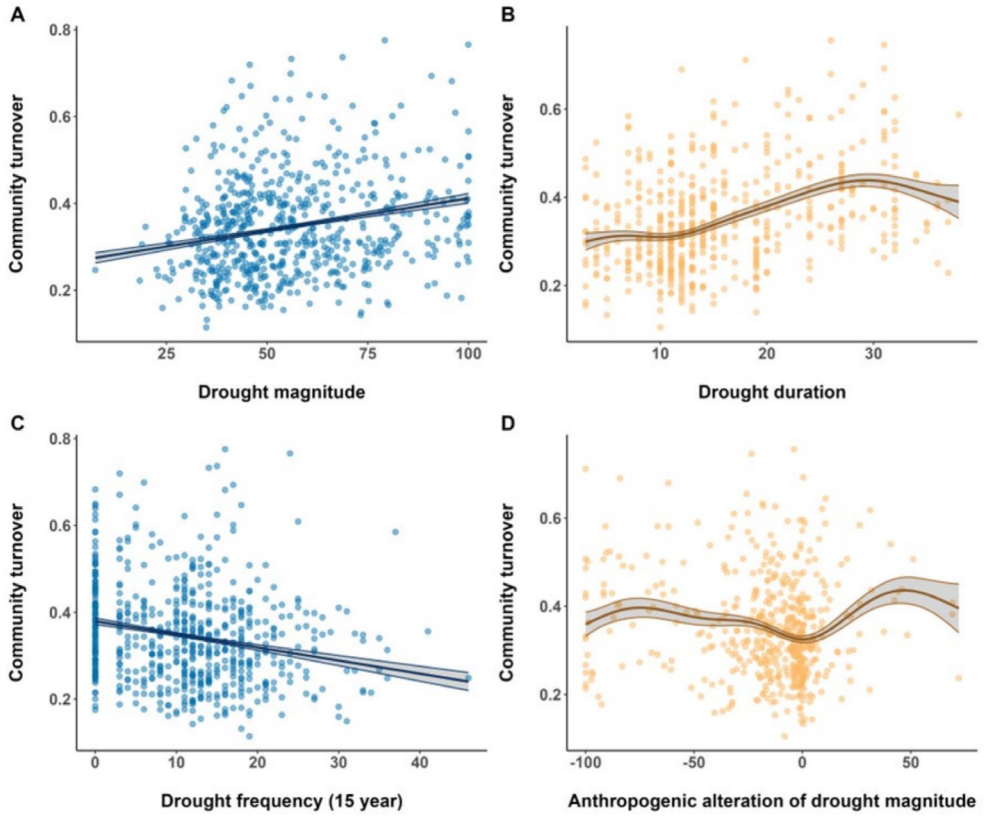

FIGURE 3 | Community resistance (as compositional turnover; higher values indicate lower resistance) in relation to drought magnitude (A), duration (B), frequency in the 15 preceding years (C) and anthropogenic alteration of magnitude (D) in spring (blue) and autumn (yellow). In D, negative, zero and positive values indicate below natural, natural and above natural flows, respectively. The lines and grey area represent the mean ± standard error of generalized additive model predictions.

post-drought changes in flow magnitude, indicating slower recovery when post-drought flows were higher (GAM, $p < 0.001$; Figure 4C). The explained variance in recovery rates was higher in autumn ($R^2 = 0.38$) than spring ($R^2 = 0.22$). Long-term change increased with drought duration and magnitude in both seasons ($p < 0.001$, $R^2 = 0.39$–0.44; Figure 4D,E; Figure S6K–L): communities moved further from their pre-drought composition as severity increased (Table S7). Change in autumn communities decreased as drought frequency in the preceding 15 years increased (GAM, $p = 0.030$; Figure 4F). Drought timing, rate of termination, spatial extent and anthropogenic alteration of duration also affected resilience as both recovery rates and long-term change, but relationships were inconsistent and often reflected few observations (Figure S6).

3.3 | Effects of Human Pressures and Environmental Context on Community Resistance and Resilience

DO, fine sediment and water temperatures influenced the resistance and resilience of invertebrate communities to drought (Tables S8 and S9). Community resistance, as turnover, and resilience, as long-term change, both decreased with increasing DO concentrations in both seasons (GAM, $p < 0.001$; Figure 5A,B, Figure S7): community composition at sites with lower DO changed more during drought periods and post-drought. Turnover and long-term change increased with the % fine sediment in autumn and spring, respectively (GAM, $p \leq 0.014$; Figure 5C,D). Temperature anomalies also influenced resilience, as represented by both long-term change and recovery rates, which decreased and increased, respectively, as temperatures rose above average (GAM, $p \leq 0.042$; Figure S7F–G). Human pressures explained less variance than drought characteristics, particularly for recovery rates ($R^2 = 0.01$–0.09) and were highest for long-term post-drought changes ($R^2 = 0.30$).

4 | Discussion

Using 8–30-year time series spanning 359 groundwater-dominated river sites, we assessed the ecological effects of droughts at unprecedented temporal and spatial scales. Although freshwater invertebrate communities recovered on average within 1.5 years, those at 47% of sites experienced ≥1 persistent, drought-related shift in taxonomic composition. Although patterns were weak, shifts were more common following longer, human-extended droughts, and at lower drought frequencies. However, shifts were as frequent during non-drought periods, and pollution-sensitive taxa often characterized shifted communities post-drought. Drought may have disrupted established communities dominated by competitive generalists, enabling sensitive taxa to colonize new niches (Leigh et al. 2019). Compositional change increased with drought duration and magnitude, demonstrating drought severity as a key determinant of ecological responses (Anderson et al. 2006; Aspin, Hart,

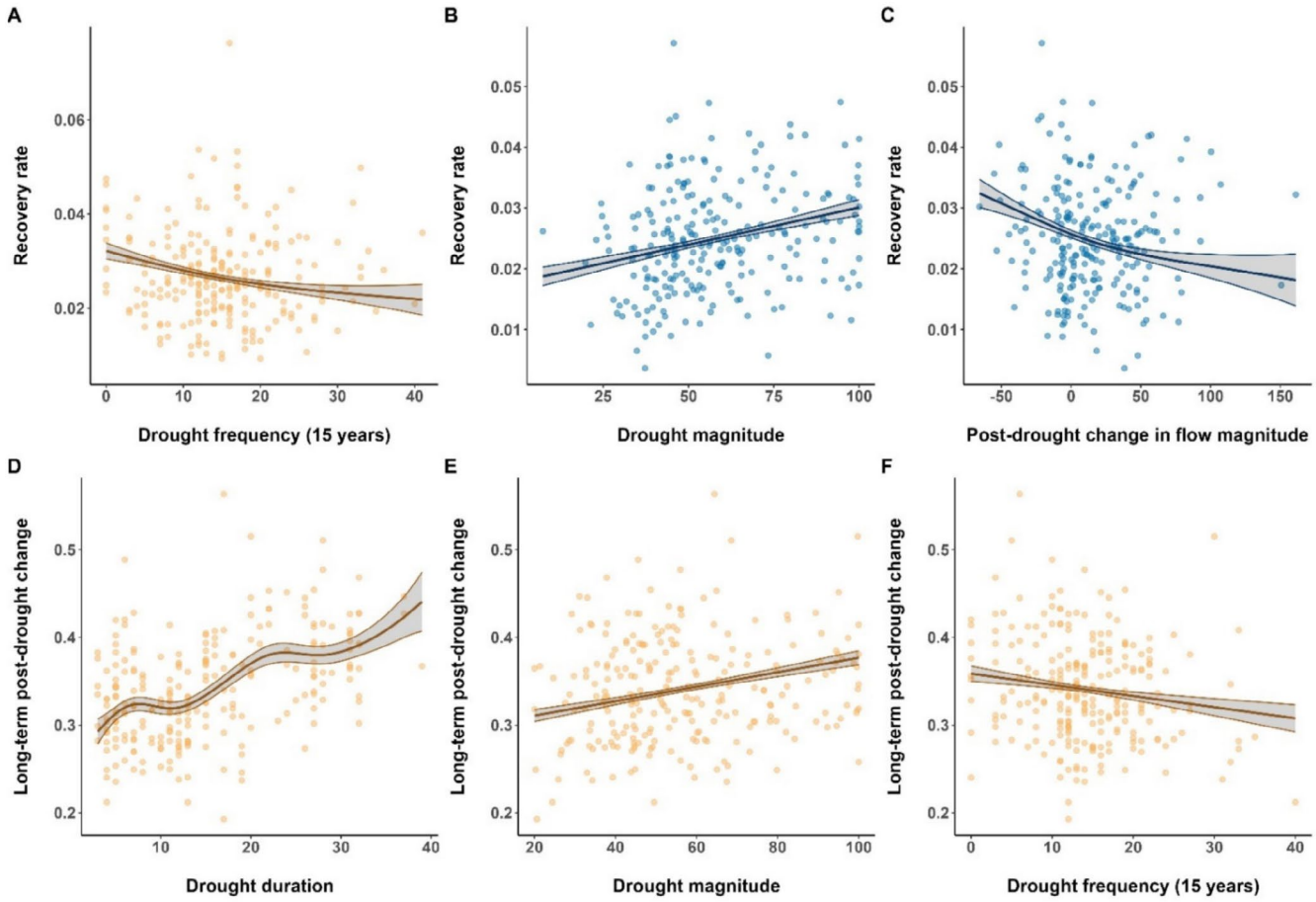

FIGURE 4 | Community resilience, as recovery rates (A–C) and long-term post-drought compositional change (D–F), in response to drought frequency in the preceding 15 years, magnitude, duration and post-drought change in flow magnitude in spring (blue) and autumn (yellow). The lines and grey areas represent the mean ± standard error of generalized additive model predictions.

et al. 2019). Human pressures including abstraction-related flow reduction and lower DO concentrations interacted with drought to alter community resistance and resilience. Challenging the widespread perception that groundwater-dominated rivers such as chalk streams are particularly stable river ecosystems (Sear et al. 1999), our results provide evidence that their communities are dynamic, with interactions between droughts and human influences associated with persistent changes in their species composition at large scales.

4.1 | Nearly Half of All Communities Experienced Persistent Shifts in Composition

While 83% of communities recovered from individual droughts within the 1–3 years typically reported by previous studies (Stubbington et al. 2024), those at 47% of sites experienced at least one persistent compositional shift during the 30-year study period. Although several drought characteristics influenced shift occurrence, shifts were as common in drought and non-drought periods.

Most communities also experienced gradual temporal drift in composition, which post-drought increases in the abundance and richness of sensitive 'EPT' taxa—in both shifted and recovered communities—suggest is largely attributable to improvements in water quality associated with measures taken to meet new legislative targets (Whelan et al. 2022; Pharaoh et al. 2023; Qu et al. 2023). Superimposed on these gradual changes, we observed sudden, persistent shifts associated with drought, which have rarely been recorded in river ecosystems (Daufresne et al. 2007; Bogan and Lytle 2011). Pre-drought indicators of shifting communities included taxa tolerant of pollution and slow flows, which were replaced by pollution-sensitive taxa post-drought. Drought may have eliminated pollution-tolerant but drought-sensitive taxa, creating low-competition ecological niches (Chase 2007; Barrett et al. 2021). Aerial dispersal may then have promoted rapid colonization by pollution-sensitive but drought-resilient EPT taxa from network-wide refuges, allowing them to establish populations in these niches (Sarremejane, Stubbington, et al. 2021; Fournier et al. 2023).

4.2 | Drought Severity and Frequency Are Associated With Community Resistance and Resilience

We confirm drought duration and magnitude (which collectively represent drought severity) as key factors influencing ecological responses (Sarremejane, Messager, and Datry 2021). Biological traits confer resistance to drought-related conditions such as low flows and drying, with community composition

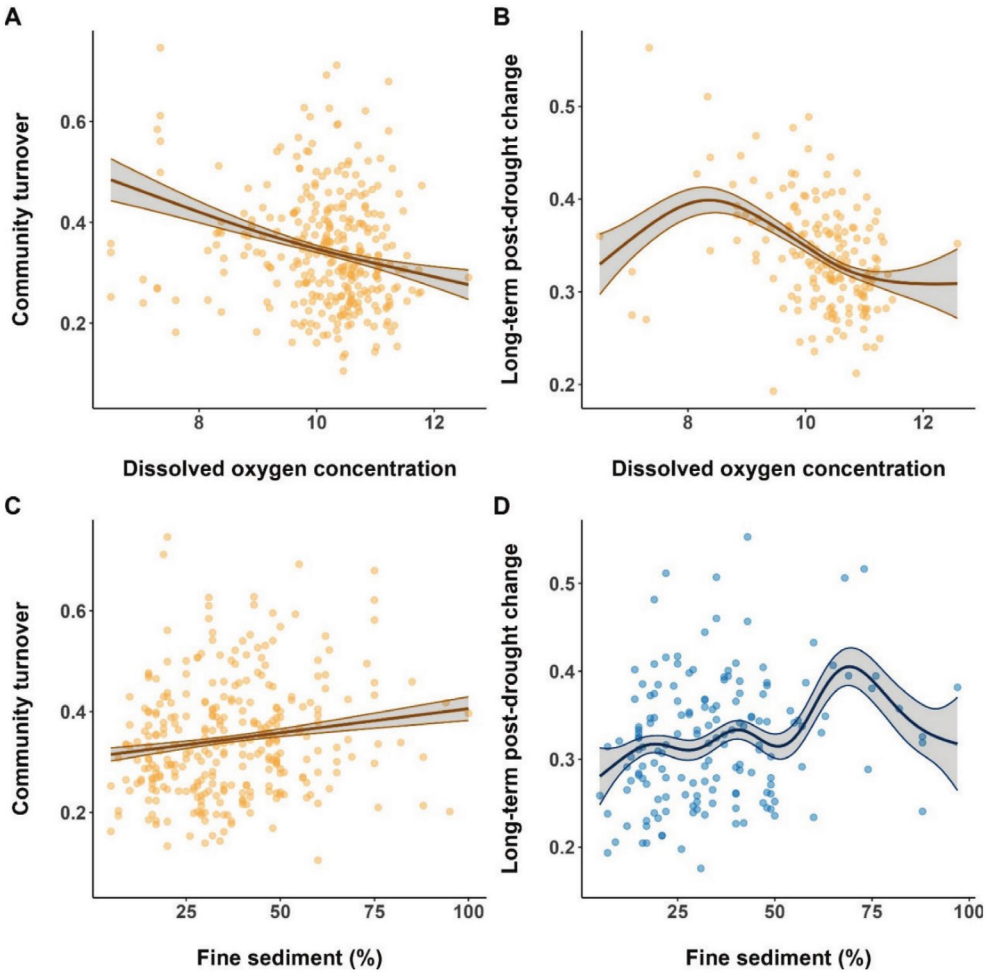

FIGURE 5 | Relationships between community resistance (as compositional turnover; A, C) and resilience (as long-term post-drought compositional change; B, D) and dissolved oxygen concentrations (A, B) and % fine sediment (B–D) for (A–C) autumn and (D) spring communities. The lines and grey area represent the mean ± standard error of generalized additive model predictions.

changing as drought unfolds and the tolerance thresholds of individual taxa and organisms are exceeded (Boulton 2003; Chadd et al. 2017). Longer, higher-magnitude droughts may thus drive stronger compositional changes (Aspin, Khamis, et al. 2019; Aspin, Hart, et al. 2019). We found contrasting site-specific responses to drought, characterized by both taxa gains and losses, suggesting that both colonization of drought-tolerant taxa such as slow-flow specialists and extirpation of drought-sensitive taxa (e.g., adapted to fast-flow) were associated with community changes during drought. Such community changes may have lasting consequences post-drought if extirpations and priority effects collectively enable new colonists to establish (Chase 2007; Barrett et al. 2021).

Compositional turnover between pre-drought and drought periods, and long-term post-drought compositional change, decreased with increasing long-term (15-year) drought frequency. Resistant taxa may dominate communities that experience more frequent disturbances (Leigh et al. 2016; Chalmandrier et al. 2025), which therefore change less when exposed to new events (Crabot et al. 2020). However, autumn communities recovered faster and shifted more often at lower drought frequencies, suggesting context-dependent effects of drought frequency on recovery rates. In particular, sites that experienced very few droughts (i.e., 0–3 drought months) during the 15 years prior to drought onset were further downstream (i.e., 7.5–45 km from the river source) and had relatively stable flows with no zero-flow events. Despite high turnover associated with drought, communities at these sites may have recovered quickly if their hydrological connectivity enabled post-drought colonization from nearby refuges (Stubbington et al. 2019; Sarremejane, Truchy, et al. 2021). Alternatively, shifts may have become more common as drought frequencies declined if communities were poorly adapted to drought conditions, or due to greater impacts of confounding factors such as water quality at these downstream sites.

We found evidence that site-specific hydrological variability altered the legacy effects of drought, with communities exposed to high variability more likely to support taxa with wide-ranging flow tolerances and able to recover rapidly post-drought (Scarsbrook 2002; Eveleens et al. 2019). For communities sampled in spring, both resilience metrics (long-term change and recovery rates) increased and shift frequencies decreased with increasing drought magnitude, indicating that communities were more variable but more resilient at higher magnitudes. High-magnitude droughts (> 80% reductions in flow) typically occurred at sites with high hydrological variability, with

84% experiencing zero-flow conditions—potentially including river drying. In addition, flow alteration typically exacerbated drought at these sites, reducing flow magnitudes by a median of 71%. Communities exposed to such flow variability may experience more diverse and unpredictable temporal changes in composition than those in stable flows and may thus be more able to track hydrological changes (Sarremejane et al. 2018) and less likely to experience long-term shifts (Huttunen et al. 2017). Water abstraction may accentuate such patterns if communities also track human-caused fluctuations between low and zero flows.

Spring community recovery was slower when flows increased to higher post-drought magnitudes. In England, the 2009–2012 drought terminated in spring with high-magnitude floods (Parry et al. 2016), potentially slowing community recovery by flushing drought survivors downstream and preventing colonists from establishing viable populations (Stubbington et al. 2009; Woodward et al. 2015). Our results thus highlight the potential ecological impacts of compound events such as drought–floods, which are projected to become increasingly common (Barendrecht et al. 2024; Hirabayashi et al. 2008).

4.3 | Human Pressures Influence Responses to Drought

Drought-associated community change increased with anthropogenic alteration of flow magnitude and decreased with DO concentrations, highlighting the greater vulnerability of human-impacted communities to drought (Fournier and Magoulick 2022; Sarremejane et al. 2024). The compositional turnover of autumn communities during drought increased with anthropogenic alteration of its magnitude, indicating greater compositional change at sites with human-altered flow (Sarremejane et al. 2024). Autumn communities exposed to human-extended droughts also shifted more, suggesting that anthropogenically prolonged low- or zero-flow conditions may push communities past tipping points, causing persistent shifts. Autumn communities may be more responsive to anthropogenic drought than spring communities if flow falls below the already low levels that chalk-river communities typically experience in this season (Dunbar et al. 2010). The decreasing community change with increasing DO concentrations indicates that good water quality may support community stability during drought and promote post-drought recovery (Sarremejane et al. 2024). Oxygen concentrations typically decrease as flows decline during drought, especially in human-altered systems polluted by organic-rich effluent (Mosley 2015). Management actions that mitigate such impacts on water quality could thus enhance ecological resilience to drought (Durance and Ormerod 2009).

5 | Conclusion

Increases in drought severity are projected in many global regions (Spinoni et al. 2018), including in temperate climates such as the UK (Parry et al. 2024). Our results provide insight into ecological responses to such future changes in hydrological conditions in rivers also exposed to multiple human pressures. Although invertebrate communities recovered quickly from most individual droughts, persistent compositional shifts occurred at almost half of the sites, likely driven by drought and interacting factors including water quality. Such community shifts could lead to wider changes in ecosystem functioning, in particular when key species, from producers to predators, are eliminated from food webs (Ledger et al. 2013; Vaughn et al. 2015; Aspin, Khamis, et al. 2019). Understanding how intensifying droughts may alter community composition and thus ecosystem functioning could inform management actions that protect biodiversity within functional ecosystems as they adapt to an increasingly extreme climate.

Author Contributions

Conceptualization: Romain Sarremejane, Judy England, Rachel Stubbington. Developing methods: Romain Sarremejane, Glenn Watts, Stuart Allen, Thomas Aspin. Conducting the research, data analysis, and preparation of figures and tables: Romain Sarremejane. Data interpretation, writing: Romain Sarremejane, Rachel Stubbington, Judy England, Glenn Watts, Stuart Allen, Thomas Aspin.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at: 10.6084/m9.figshare.32957840.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Hydrological metrics used to characterize drought and its anthropogenic alteration. F%A, flow percentage anomaly. **Table S2:** Predictors included in each model after selection, following exclusion of collinear predictors based on variation inflation factors. **Table S3:** Differences in family richness, EPT (Ephemeroptera, Plecoptera and Trichoptera) richness and EPT abundance and among shifting and recovering communities and pre- and post-drought periods and their interaction, based on linear mixed effect models. EPT abundance was log+1 transformed. Est. = model estimates. Bold indicates p values < 0.05. **Table S4:** Indicator taxa characterizing recovered and shifted communities pre- and post-drought for autumn and spring communities. **Table S5:** The effects of drought characteristics, environmental context and human pressures on community shifts based on the generalized linear models with the lowest AICc, assessing. **Table S6:** The effects of drought characteristics on community turnover in autumn and spring based on the generalized additive models with the lowest AICc. **Table S7:** The effects of drought characteristics on community resilience metrics based on the generalized additive models with the lowest AICc. **Table S8:** The effects of environmental context and human pressures on community resistance metrics based on generalized additive models with the lowest AICc. **Table S9:** The effects of environmental context and human pressures on community resilience metrics based on the generalized additive models with the lowest AICc. **Figure S1:** Percentage of sites in a drought period in each month between January 1990 and December 2020. **Figure S2:** Location of sites with communities that shifted at least once or always recovered during drought periods. **Figure S3:** Drought characteristics with significant differences between spring communities that shifted or recovered after drought. **Figure S4:** Differences in ammonia concentration and long-term water temperature among sites with communities that shifted or recovered after drought for autumn (A) and spring (B) communities. **Figure S5:** Response of community turnover to drought characteristics for autumn (yellow) and spring (blue) communities. **Figure S6:** Community resilience to drought, as indicated by (A–J) recovery rates and (K–N) long-term post-drought community change in relation to drought characteristics for spring (blue) and autumn (yellow) communities. **Figure S7:** Responses of (A–E) resistance and (F–K) resilience metrics to environmental context and human pressure variables for autumn (yellow) and spring (blue) communities. **Appendix S1:** Drought characteristics and human pressures. **Table S10:** Mean, standard deviation (SD) and data distribution, including minimum, median, maximum and 10th, 25th, 75th and 90th quantiles for each modelled drought characteristic, human pressure and environmental context variable. F%A, flow % anomaly. **Figure S8:** Pearson correlation coefficients between drought characteristics. Table S1 provides full characteristic names and descriptions. **Figure S9:** Pearson correlation coefficients between human pressure and environmental context variables. **Appendix S2:** Temporal drift and its impact on shifts. **Figure S10:** The variability of recovered and shifted, pre- and post-drought spring communities. **Figure S11:** Distribution of the proportion of shifts across 99 randomizations. **Appendix S3:** Effect of drought characteristics, environmental context and human pressures on changes in invertebrate richness, EPT richness and EPT abundance. **Table S11:** The effects of drought characteristics on family richness difference, EPT richness difference and EPT abundance difference in autumn and spring, based on the generalized additive models with the lowest AICc. **Table S12:** The effects of human pressure and environmental context variables on family richness difference, EPT richness difference and EPT abundance difference, based on the generalized additive models with the lowest AICc. Abbreviations

are defined in Table S5 title. Bold indicates p values < 0.05. Fig. indicates the corresponding panel of Figure S11. **Figure S12:** Responses of family richness (A–E, H–I), EPT richness (F, J) and EPT log+1 abundance differences (G, K–N) to drought characteristics for autumn (yellow) and spring (blue) communities. **Figure S13:** Responses of EPT abundance difference (A, B) and family richness difference (C–E) to human pressure and environmental context variables for autumn (yellow) and spring (blue) communities.