DR. ROMAIN SARREMEJANE (Orcid ID : 0000-0002-4943-1173)

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Drought effects on invertebrate metapopulation dynamics and quasi-extinction risk in an intermittent river network

Romain Sarremejane[1,2*], Rachel Stubbington[3], Judy England[4], Catherine E. M. Sefton[5], Michael Eastman[5], Simon Parry[5] and Albert Ruhi[1]

ORCID: Romain Sarremejane 0000-0002-4943-1173, *, Rachel Stubbington 0000-0001-8475-5109, Judy England 0000-0001-5247-4812, Catherine E. M. Sefton 0000-0002-8157-0368, Albert Ruhi 0000-0003-4011-6457

[1]Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA 94720, USA

[2]INRAE, UR RiverLY, Centre de Lyon-Grenoble Auvergne-Rhône-Alpes, 5 rue de la Doua, 69100 Villeurbanne, France

[3]School of Science and Technology, Nottingham Trent University, Nottingham NG11 8NS, UK

[4]Environment Agency, Horizon House, Deanery Road, Bristol BS1 5AH, UK

[5]UK Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire OX10 8BB, UK

* Corresponding author: Romain Sarremejane, romain.sarremejane@gmail.com

Abstract

Ecological communities can remain stable in the face of disturbance if their constituent species have different resistance and resilience strategies. In turn, local stability scales up regionally if heterogeneous landscapes maintain spatial asynchrony across discrete populations—but not if large-scale stressors synchronize environmental conditions and biological responses. Here, we hypothesized that droughts could drastically decrease the stability of invertebrate metapopulations both by filtering out poorly adapted species locally, and by synchronizing their dynamics across a river network. We tested this hypothesis via multivariate autoregressive state-space (MARSS) models on spatially replicated, long-term data describing aquatic invertebrate communities and hydrological conditions in a set of temperate, lowland streams subject to seasonal and supraseasonal drying events. This quantitative approach allowed us to assess the influence of local (flow magnitude) and network-scale (hydrological connectivity) drivers on invertebrate long-term trajectories, and to simulate near-future responses to a range of drought scenarios. We found that fluctuations in species abundances were heterogeneous across communities and driven by a combination of hydrological and stochastic drivers. Among metapopulations, increasing extent of dry reaches reduced the abundance of functional groups with low resistance or resilience capacities (i.e., ability to persist in situ or recolonize from elsewhere, respectively). Our simulations revealed that metapopulation quasi-extinction risk for taxa vulnerable to drought increased exponentially as flowing habitats contracted within the river network, whereas the risk for taxa with resistance and resilience traits remained stable. Our results suggest that drought can be a synchronizing agent in riverscapes, potentially leading to regional quasi-extinction of species with lower resistance and resilience abilities. Better recognition of drought-driven synchronization may increase realism in species extinction forecasts as hydroclimatic extremes continue to intensify worldwide.

Keywords: Drought, ecological resilience, flow intermittence, functional traits, Moran effect, spatial synchrony, time-series modelling

1. Introduction

Organism abundances commonly fluctuate over time due to changes in environmental conditions, dispersal, and biotic interactions (Arnoldi, Loreau, & Haegeman, 2019; Pimm, 1984). Despite such local temporal variability, populations and communities often remain stable at the regional scale (Wang, Lamy, Hallett, & Loreau, 2019; Wilcox et al., 2017). Whereas local community stability is controlled by the stability of local populations and their compensatory dynamics, regional stability emerges from spatial asynchrony among populations connected by dispersal (i.e., metapopulations; Hammond, Loreau, de Mazancourt, & Kolasa, 2020; Larsen et al. 2021; Wang et al., 2019). Understanding how environmental change may erode local stability, and the scaling of local stability to higher levels of biological organization, has become a pressing research need (Erős et al., 2020; Patrick et al., 2021; Petsch, 2016; Walter et al., 2017).

Population-level responses to large-scale disturbance and stress can be spatially heterogenous if local habitat conditions or connectivity vary across a landscape (Patrick et al., 2021). In such cases, large-scale environmental controls may be locally attenuated or exacerbated, allowing for a diversity of biological responses depending on local conditions (Bunnell et al., 2010; Cayuela et al., 2020; Hansen et al., 2019). Such diverse responses are key to preserving asynchronous dynamics and ecological rescue, i.e., the capacity of colonists from thriving populations to repopulate impacted ones through dispersal (Brown & Kodric-Brown, 1977; Hammond et al., 2020). Nevertheless, spatially coordinated environmental fluctuations have the potential to synchronize metapopulation dynamics across large scales, a phenomenon known as the 'Moran effect' (Moran, 1953). This pattern has been observed in groups as diverse as mammals (Hansen et al., 2013; Moran, 1953), insects (Hanski & Woiwod, 1993; Oliver et al., 2015), and bacteria (Moustakas, Evans, Daliakopoulos, & Markonis, 2018). Quantifying changes in biological stability in response to extreme environmental conditions thus requires understanding of whether spatially coordinated stress may synchronize biological responses and drive populations towards extinction (Heino, Kaitala, Ranta, & Lindström, 1997).

The severity of extreme events such as droughts, heatwaves, and floods can be quantified by their magnitude, frequency, duration and spatial extent (Sousa, 1984; Thibault & Brown, 2008). Whereas disturbance magnitude, frequency, and duration control niche filtering and thus the amplitude of community-scale changes (Crabot, Heino, Launay, & Datry, 2020), spatial extent influences regional processes such as spatial synchrony and dispersal among populations (Keitt, 2008). At the community level, species may respond asynchronously to disturbance due to niche differentiation and variation in resistance abilities (i.e., their capacity to tolerate a disturbance in situ). Such differences often allow individual species to thrive and decline at different times (Wang & Loreau, 2016). Whereas resistance mechanisms typically operate at local scales, resilience mechanisms involve recolonization from both local and regional refuges (Chester & Robson, 2011). Thus, resilience mechanisms may be particularly vulnerable to changes in habitat connectivity and the spatial extent of stress or disturbance (Zelnik, Arnoldi, & Loreau, 2018).

Hydrology is a key driver of stream ecosystem structure (Poff et al., 1997), often controlling the dynamics of physical habitats, populations, and communities across spatial scales (Palmer & Ruhi, 2019). Organismal responses to hydrological variation operate mostly through a range of species-specific life-history, morphological, and behavioural adaptations (Lytle & Poff, 2004; Poff et al., 1997), but also via neutral processes related to organism dispersal, colonization, extinction, and speciation (Dong et al., 2017; Saito et al., 2021). Low flows, and in particular stream drying, often lead to population declines and drastic changes in community composition (Bêche, Connors, Resh, & Merenlender, 2009; Lake, 2003), especially in rivers that rarely dry (Hill et al., 2019). Whereas hydrological drought (here defined as a supraseasonal deficit in surface water; Tallaksen & Van Lanen, 2004) is an extreme disturbance, seasonal flow cessation and drying are common and less consequential in intermittent rivers (Datry, Bonada, & Boulton, 2018). Flow intermittence contracts and fragments aquatic habitats, creating a mosaic of flowing, non-flowing, and dry patches (Larned, Datry, Arscott, & Tockner, 2010). Such dynamism may impose a strong filter on local communities, while also reducing network-scale dispersal (Chester, Miller, Valenzuela, Wickson, & Robson, 2015; Jaeger, Olden, & Pelland, 2014), and thus the ability of resilient taxa to recolonize after a disturbance.

Communities regularly exposed to hydrological extremes can be stable if they are mainly composed of resistant and resilient strategists (Scarsbrook, 2002). In streams, resistance to drying is conferred by traits such as aerial respiration, the capacity to burrow into humid sediments, and desiccation-tolerant dormant stages—the last of which can be conceptualized as ‘dispersal through time’ (Buoro & Carlson, 2014). In contrast, resilience is enhanced by high dispersal and reproductive capacities, which facilitate recolonization when water returns (Aspin et al., 2019; Bogan et al., 2017). Climate-driven droughts are predicted to increase in extent, magnitude, and duration across the globe (Prudhomme et al., 2014; Spinoni, Vogt, Naumann, Barbosa, & Dosio, 2018). Severe droughts could drastically increase regional extinction risk by compromising local species persistence and by synchronizing their responses. Analysis of long-term, spatially replicated data capturing extreme droughts across riverscapes may enable quantification of this emergent risk.

Here, we explored the role of drought as a synchronizing driver of freshwater invertebrate communities using a 13-year biological and hydrological dataset from 20 river sites in southern England. This time series included two multi-year droughts, allowing us to assess community and metapopulation responses to supra-seasonal (i.e., "unpredictable") variation in hydrology. Using detailed trait information, we defined functional groups of taxa with contrasting resistance and resilience strategies to elucidate the functional basis of responses to hydrological variability. We also estimated local and regional probabilities of populations reaching critical decline thresholds (i.e., quasi-extinction risk; Holmes, Sabo, Viscido, & Fagan, 2007) under a range of drought scenarios. We hypothesized that: (H1) community responses to local and regional hydrology may vary as a function of the resistance and resilience strategies of their constituent taxa (Figure 1a–b); (H2) drought may induce spatially coordinated (i.e., synchronous) population declines for less resilient and resistant taxa, whereas more resilient and resistant strategists may show spatially heterogeneous responses because they can exploit a variety of environments across the river network (Figure 1c); and (H3) drought severity may heighten quasi-extinction risk of drought-vulnerable taxa by decreasing their abundance simultaneously across the river network (Figure 1c).

2. Methods

2.1. Study area

The study area includes seven temperate-climate headwater streams in the Colne and Lee river catchments in southern England, UK, each draining a 35–175 km^2 catchment (Figure 2). Both catchments have comparable land use, topography and geology. These groundwater-fed streams flow over a highly porous chalk-dominated bedrock, and have a combination of perennial reaches, near-perennial reaches that only dry during extreme droughts, and intermittent reaches that experience seasonal drying. The networks typically expand and contract seasonally, and predominantly comprise contiguous flowing reaches. The spatial extent and timing of the dry phase varies interannually depending on antecedent precipitation and groundwater levels (Sefton, Parry, England, & Angell, 2019). The study area experienced severe droughts in 2005–2006 and 2011–2012, which increased the extent of no-flow (ponded and dry) conditions in the streams (Sarremejane, England et al., 2020). Catchments are dominated by arable, pastoral, and urban land uses, and all 20 sites have moderate to high water quality, with drying being the main abiotic stressor (Sarremejane, Stubbington, Dunbar, Westwood, & England, 2019). The sites were selected to represent the intermittence regimes and other habitat conditions within each network. The mean Euclidean distance between sites is 23 km [min–max: 0.4–60] and the two main river catchments flow into the Thames 62 km (network distance) from one another.

2.2. Hydrological data and metrics

To describe local hydrological conditions, we used daily mean discharge from eight gauging stations spanning all streams (Figures 2 and S1). Site-specific daily discharge was estimated using linear regressions between spot-gauging records taken at or <1 km from the sampling site and daily discharge data from the nearest gauging station (Gordon, McMahon, Finlayson, Gippel, & Nathan, 2004; Sarremejane et al., 2019; Table S1). In addition, monthly observations of flowing, ponded, and dry hydrological states were collected in 18–32 reaches per stream from 2004 to 2018 to describe regional hydrological conditions, with dry and ponded states constituting no-flow conditions (Sefton et al., 2019).

We calculated two hydrological metrics to represent local and regional hydrological conditions, respectively: mean daily discharge (*LocalFlow*, in $m^3 s^{-1}$) and the spatial extent of flowing reaches across all seven streams (*RegFlow*, as the % network flowing) for each six-month period (September–February and March–August) between 2005 and 2017. LocalFlow describes the magnitude of hydrological changes locally, and RegFlow captures temporal variation in network hydrological connectivity (i.e., the % of the network fragmented by no-flow conditions). Droughts were characterized by extreme low flows and extended drying across the river network. Finally, we used site-specific monthly hydrological state observations to classify each site according to its long-term flow permanence regime, measured as the percentage of months the site was flowing (*Flow%*). Sites with Flow% of <90%, 90–99%, and 100% were classified as having intermittent, near-perennial, and perennial flow permanence regimes, respectively, based on natural thresholds in the Flow% distribution (Sarremejane, England et al., 2020).

2.3. Aquatic invertebrate sampling

Invertebrates were collected at 20 sites across six of the streams, each spring (March–May) and autumn (September–November) between autumn 2005 and spring 2017 (i.e., 25 samples per site). Samples were collected using a 3-min kick/sweep technique with a pond net (mesh size = 1 mm) supplemented by a 1-min hand search, including all habitats in proportion to their occurrence (ISO, 2012). Most invertebrates (i.e., 81% of individuals) were identified to species or genus, and the rest to family. All individuals were counted. Drying prevented sampling of some sites in some years, leading to 5.6% of ‘dry samples’, for which all abundances were set as ‘true’ zeros. Samples missing for other, logistic reasons (2.7%) were set as missing data (‘NA’).

2.4. Invertebrate functional groups

To classify taxa according to their documented ability to tolerate drying via resistance and/or resilience mechanisms, we used nine traits (subdivided in 23 categories; Table S2) relating to life cycles, morphology, physiology, and behaviour, sourced from Tachet et al. (2010) and Sarremejane, Cid et al. (2020). We used a fuzzy-coding approach to assign traits to taxa at the genus level, with affinities standardized as the percentage affinity for each category within a trait. For taxa identified to family, we assigned a mean value based on all genera in the family (following Bêche, Mcelravy, & Resh, 2006). To characterize resistance strategies, we focused on traits describing *resistance forms* (e.g., dormant stages), *aerial respiration* (i.e., spiracles), and *interstitial space use* (Tachet et al., 2010; Table S2). To represent resilience strategies, we used *life cycle duration*, *number of reproductive cycles per year*, *adult life span*, *wing size* (for winged insects only), and *life-long fecundity* (Table S2).

We then used these resistance and resilience traits to identify functional groups of taxa, because species often share similar suites of traits. To this end, we calculated among-taxa functional dissimilarity using the Gower distance, which is suitable for categorical and fuzzy-coded traits (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009). We then used hierarchical cluster analysis with Ward's method based on the Gower distance matrix to identify clusters of taxa with similar trait profiles (see e.g., Aspin et al., 2019). The optimal number of clusters (here, resistance and resilience functional groups) was visually assessed by plotting the total within-cluster sum of squares against the number of clusters (Figure S2). We thus identified four resistance and four resilience groups (Figure S2). We used indicator species analysis to identify the trait categories indicative of each cluster (De Cáceres & Legendre, 2009). This method provides an index of association, here, the point-biserial coefficient (r_{pb}), for each trait category within the *a priori* defined groups (De Cáceres & Legendre, 2009). R_{pb} values were constrained between 0 and 1, with higher values indicating higher occurrence of taxa within the trait category within a given group. The statistical significance of such associations was tested via 999 random permutations.

2.5. Estimating invertebrate responses to drought

We used a time-series modelling approach based on multivariate autoregressive state-space (MARSS) models (Holmes, Ward, & Wills, 2012) to assess the effects of antecedent hydrological conditions (including drying during droughts) on fluctuations in invertebrate abundance, and to estimate future responses under a range of simulated drought scenarios (section 2.6). To fulfil the requirements of the time-series analyses described below, we first filtered the invertebrate dataset to retain 'frequent' taxa occurring in >50% of the 25 seasonal samples at a minimum of one site. The 59 retained frequent taxa were then modelled using *community models* (section 2.5.2). The taxonomic richness of frequent taxa per site ranged between 4 and 41: mean 18.6 ± SD: 9.0 (Table S3). We also defined 'widespread' taxa as those occurring in >50% of all samples and sites, excluding taxa identified to family. We used the eight identified widespread taxa to explore metapopulation dynamics with *metapopulation models* (section 2.5.3; Table S3).

To assess metapopulation synchrony in the observed data, we measured spatial synchrony (i.e., correlation) for abundances of functional groups and widespread taxa across all sites over the study period. We calculated synchrony for rolling six-year periods (i.e., 12 time steps) for each functional group and widespread taxon as the mean Pearson correlation between site-specific abundance and the total abundance at all other sites (as in Gross et al., 2014). We obtained 95% confidence intervals via empirical bootstrap. Synchrony varies between -1 and 1, with positive values not overlapping with zero indicating significant synchrony (i.e., spatially-coordinated fluctuations).

2.5.1. MARSS model general specifications

MARSS is a state-space version of the more commonly used multivariate autoregressive (MAR) models. MAR models rely on patterns of temporal autocorrelation and have been used extensively in ecological research to examine the effects of environmental variation on community trajectories as well as spatial structure in sets of populations (Hampton et al., 2013; Ruhi, Dong, McDaniel, Batzer, & Sabo, 2018; Ward et al., 2010). MARSS models include a state process representing 'true' fluctuations in the data (Equation 1), as well as an observation process that accounts for measurement error (Equation 2). This state-space structure is beneficial because observation error is prevalent in long-term datasets, and can change inferences about a process (e.g., Knape & de Valpine, 2012).

A MARSS model in log-space can be written as:

$$\boldsymbol{x}_t = \boldsymbol{B}x_{t-1} + \boldsymbol{C}c_{t-1} + \boldsymbol{w}_t\,, where\ \boldsymbol{w}_t \sim MVN(0,\boldsymbol{Q})\ \#(1)$$

$$\boldsymbol{y}_t = \boldsymbol{Z}x_t + \boldsymbol{v}_t\,, where\ \boldsymbol{v}_t \sim MVN(0,\boldsymbol{R})\ \#(2)$$

where taxon abundances enter the model as $\boldsymbol{y}_t$ in Equation 2, and $\boldsymbol{R}$ is the observation error covariance matrix. The effects of covariates c on the population state $\boldsymbol{x}_t$ are assessed via the $\boldsymbol{C}$ matrix (see Table S4 for complete model specifications). In our case, this matrix captured the effects of hydrological variables on the abundance of each taxon.

2.5.2. MARSS community models

To test H1, we built a set of MARSS models for each site to assess the effects of local and regional hydrological conditions on the populations within each community. In these models, the abundance of each frequent taxon at a site was a separate response (or state), but was modelled simultaneously. We fitted different model structures by constraining the covariate matrix $\boldsymbol{C}$ in alternative ways, and by including different sets of covariates c that reflected the potential effects of local (LocalFlow) and/or regional (RegFlow) hydrological variation in the six months preceding sampling of each biological community. Specifically, we compared: (1) a *stochastic* model in which no covariate (no $\boldsymbol{C}$ matrix) was included, assuming no hydrological effects; (2) a *local-hydrology* model in which only the local hydrological driver was included; (3) a *regional-hydrology* model in which only the regional hydrological driver was included; and (4) a *multiscale-hydrology* model in which both local and regional hydrological drivers were allowed to influence responses (see Table S4).

We then modified these taxon-specific models (models 2–4; Table S4) to generate functional-group models (models 5–7; Table S4) by constraining the $\boldsymbol{C}$ matrix so that taxa in the same resilience or resistance group were 'forced' to share responses to hydrology (as in Ruhi, Holmes, Rinne, & Sabo, 2015). The functional-group models tested the prediction that responses to drought are similar among invertebrate taxa with comparable trait profiles.

2.5.3. MARSS metapopulation models

To test H2, we used a similar approach to the MARSS community models, but including sets of populations across sites instead of sets of taxa at single sites. We fitted one MARSS metapopulation model for each of the eight functional groups and the eight widespread taxa (Table S4), using RegFlow in the six months preceding biological sampling as a covariate. To calculate site-specific functional group abundances, we summed abundances of all taxa within each resistance and resilience group in all samples from each site. For each functional group and widespread taxon, we used site-specific abundances across the 20 sites as response variables, and compared support for three models representing different ways in which hydrological connectivity influences metapopulations: (i) a *stochastic* model in which RegFlow was not included as a covariate, assuming no hydrological effects on metapopulations; (ii) a *site-specific* model in which RegFlow was allowed to influence populations within each site independently, representing site-specific hydrological effects; and (iii) a *flow-group* model in which RegFlow was 'forced' to have the same effect for all sites in a given flow permanence group (i.e., intermittent, near-perennial or perennial, Table S4). This latter structure tested whether invertebrate responses to hydrological connectivity varied among sites with contrasting flow permanence regimes.

To verify the effects of widespread taxa within functional groups on model results, we performed a leave-one-out sensitivity analysis in which metapopulation models were built with widespread taxa sequentially removed from their respective functional groups (Appendix 1).

To assess the effects of hydrology on population synchrony, we built models in which covariance and variance (in ***Q,*** Equation 1) were estimated from the data (models iv–v; Table S4). We compared stochastic models (i.e., without a hydrological covariate) to flow-group models including RegFlow as a covariate, and we measured covariance standardized by the variance (i.e., covariance/variance, or correlation) across functional groups and widespread taxa. We interpreted lower covariance/variance values in the flow-group model compared to the stochastic model as a significant effect of RegFlow on synchrony: 'unexplained' covariance in the stochastic model was captured by the hydrological variable when included in the model, suggesting hydrology was the synchronizing agent.

2.5.4. Model fitting and diagnostics

For all models, abundance data were natural log(x+1) transformed and hydrological covariates were z-scored. Models were fitted using maximum likelihood and an expectation-maximization algorithm with <1000 iterations per model. If error variances tended towards zero, we considered the model to be 'degenerate' and fitted a simpler MAR model (Holmes, Ward, & Scheuerell, 2020; Table S4). All parameters (i.e., model variance and covariate effect sizes) were assessed using bootstrapped 95% confidence intervals. For each set of community and metapopulation models, we selected the best-fitting models with an information-theoretic approach (Burnham & Anderson, 2002) using corrected Akaike's information criteria (AICc). We considered models with a ΔAICc <4 as equally good (Anderson, 2008). For each site, we tested collinearity between LocalFlow and RegFlow using variance inflation factor (VIF) analysis, and considered VIF <3 as non-collinear and <5 as moderately collinear (James, Witten, Hastie, & Tibshirani, 2013). We checked that model residuals did not display a trend, significant departures from a normal distribution, or temporal autocorrelation (using the auto-correlation function, ACF).

2.6. Estimating quasi-extinction risk under drought scenarios via simulations

To test H3, we simulated invertebrate metapopulation trajectories under a set of drought scenarios (Table S5). Scenarios varied in the number of time steps (six-month periods) with drought (i.e., a spatially extended drying event), the number of drought events (i.e., discrete drought periods), and their sequence (i.e., the order of drought vs. non-drought time steps). Specifically, we used the mean and minimum observed RegFlow values (Figure 2) to create 124 scenarios spanning six years, reflecting variation in hydrology over 12 six-month periods (Table S5). Scenarios ranged from no drought to an uninterrupted six-year drought i.e., all time steps with mean or minimum RegFlow values, respectively (Table S5).

We then used MARSS models to generate plausible trajectories of each functional group and widespread taxon under the 124 scenarios. We used estimated coefficients from the stochastic (i) and flow-group (iii) MARSS metapopulation models, and set initial abundance values (x_0) as the mean site-specific abundance of that state (taxon or functional group abundance). For each scenario, we ran 1000 simulations and calculated the minimum abundance value per site and the minimum total abundance value across sites. We then calculated the number of simulations in which invertebrate abundances would reach an 80% decline threshold, a measure of quasi-extinction risk (Semmens et al., 2016; Wilson, Kendall, & Possingham, 2011). *Local quasi-extinction risk* was then calculated as the proportion of site-specific realizations that reached the quasi-extinction threshold, and *regional quasi-extinction risk* as the proportion that crossed the threshold when pooling abundance across sites. The latter captured the probability of all populations 'crashing' at the same time, i.e., metapopulation-level risk. We explored changes in quasi-extinction risks in response to the number of six-month periods affected by a drought across all scenarios, later termed *drought incidence*, expecting that the more six-month periods a drought spans, the greater its severity. We compared risks from observed data with simulated predictions (Appendix 2). We also tested the sensitivity of our simulation approach to the sequence of drought events by examining if quasi-extinction risk varied across scenarios that had the same drought incidence but different number of events (Appendix 3).

We used R version 3.5.0 (R Core Team 2018) for all analyses, including the packages *MARSS* (Holmes et al., 2020) to fit and compare model structures and to estimate quasi-extinction risk; *usdm* (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014) for VIF analyses; *indicspecies* (De Cáceres & Legendre, 2009) for indicator species analysis; *codyn* (Hallett et al., 2016) to calculate synchrony; and *ggplot2* (Wickham 2016) for figures.

3. Results

3.1. Hydrological conditions: seasonal drying and supraseasonal drought

All streams were hydrologically variable, but generally displayed high coherence in periods of high and low flows, with two gauging stations recording flows <0.01 $m^3 s^{-1}$ during the study period (Figure S1). However, sites differed widely in their drying patterns: four of the 20 sites were perennial, nine were near-perennial, and seven were intermittent (Figure 2). The two droughts (2005–2006, 2011–2012) were characterized by low discharge (LocalFlow) and regional hydrological connectivity (RegFlow; Figure 2), and only <60% of the river network kept flowing. In contrast, two distinct wet periods occurred in 2008–2009 and 2012–2014 (Figure 2). Thus, this study captures a wide range of local and regional hydrological conditions—including sites that dry seasonally and sites that dry during supraseasonal events—as well as variation in hydrological connectivity (i.e., fragmented vs. connected network states).

3.2. Taxonomic and functional community description

Community abundance fluctuated across sites, seasons, and years, ranging from 573 ± 458 to 2082 ± 868 individuals per sample. Overall, the most abundant taxa were *Gammarus* sp., Chironomidae, *Baetis rhodani*, *Agapetus* sp. and *Simulium* sp., which accounted for 45.5%, 9.8%, 4.2%, 2.9%, and 2.8% of all recorded individuals, respectively. The eight functional groups (Table 1, Figure S2) represent different combinations of traits conferring resistance and resilience to drought (Tables S2 and S6). All functional groups were represented among the widespread taxa (Table S3), but taxa with low resistance and resilience strategies were relatively less prevalent at intermittent sites (Table S7).

Resistance groups comprised taxa with dormant forms (*Resist_Dormancy*), aerial respiration (*Resist_Respir*), and/or interstitial space use (*Resist_Substrate*); taxa with none of these traits were coded as *Resist_None*. Resilience groups included aquatic obligates (*Resil_Aqua*), and taxa with slow (*Resil_Slow),* intermediate (*Resil_Medium*), and fast (*Resil_Fast*) colonization capacities (Table 1). Widespread taxa abundance accounted for –93% of their respective functional groups (Appendix 1, Table S9).

3.3. Community responses to hydrological variation

We found evidence that hydrology controlled community variability in 40% of the communities, for which the best models included only hydrological covariates (Table S8). Hydrology and stochastic models were equally good for 35% of communities and stochastic models were the only best model for the remaining 25%. Among the best models providing strong evidence for hydrological control, LocalFlow or RegFlow were each selected as a single covariate in 25% of models and in combination in the remaining 50% (Table S8).

Invertebrate abundance increased with discharge, regardless of resistance strategy (except *Resist_Respir*; Figure 3a). The effect size of LocalFlow increased with declining long-term flow permanence (Flow%), particularly for *Resist_Dormancy* and *Resist_Substrate* groups (Figure 3a). This suggests that variation in local discharge became a stronger control on the abundance of taxa in these resistance groups as flow permanence declined. Responses to RegFlow were heterogenous across sites and resilience strategies: abundances increased, decreased, or did not respond to RegFlow (Figure 3b). The negative effects of RegFlow generally increased with decreasing flow permanence, particularly for the *Resil_Aqua* and *Resil_Fast* groups (Figure 3b). This suggests that hydrological contraction of the river network (i.e., lower RegFlow) favoured taxa in such resilience groups, particularly at intermittent sites.

3.4. Metapopulation responses to hydrological variation

All functional groups and widespread taxa showed some level of spatial synchrony (Figure S3). Flow-group models were selected as the best MARSS models for two functional groups: *Resil_Slow* and *Resist_None,* and three taxa*: Elmis aenea*; *Agapetus* sp. and *Hydropsyche* sp., indicating strong effects of RegFlow on the abundance of these metapopulations (Table 2). *Resil_Slow* and *Resist_None* group abundances increased consistently across flow permanence groups as hydrological connectivity increased, suggesting similar responses across sites (Figure 4a). In addition, the covariance of these groups was largely captured by RegFlow, as suggested by the decrease in covariance/variance values and the overlap of confidence intervals with zero for the flow-group model compared to the stochastic model (Figure 5, Appendix 4). These results indicate that hydrological connectivity was a key driver of population covariation (Figure 5a). In contrast, responses of other groups were variable and model covariance was little affected by RegFlow (Figures 4a and 5, Appendix 4), indicating that their covariation was not driven by hydrology. For example, abundances of *Resist_Dormancy* taxa increased with RegFlow*,* but only at perennial sites; *Resist_Respir* taxa showed the opposite pattern, but only at intermittent sites. The four other functional groups showed non-significant responses to RegFlow, indicating weak or heterogenous responses across sites with comparable flow regimes (Figure 4a).

Similar patterns were observed when examining metapopulations of widespread taxa (Figure 4b). Whereas *E. aenea* abundance increased with RegFlow across flow permanence groups, *Agapetus* sp., *Pisidium* sp., and *Hydropsyche* sp. increased with RegFlow only in some groups (Figure 4b), and *Asellus aquaticus* decreased with RegFlow but only at intermittent sites (Figure 4b). These observations indicate that some, but not all taxa are vulnerable to spatial synchronization if a river network contracts (i.e., if RegFlow decreases; Figure 5b, Appendix 4). Sensitivity analyses showed that model trends and significance for most functional groups were not affected by the removal of widespread taxa (Appendix 1).

3.5. Simulations and associated quasi-extinction risk estimates

Mean local and regional (i.e., metapopulation-wide) quasi-extinction risks increased with drought incidence for *Resil_Slow* and *Resist_None* groups, particularly for scenarios with ≥6 drought time steps (i.e., ≥3 years) of interrupted or uninterrupted drought (Figure 6). Risks for other functional groups remained relatively stable (Figure S4). Local and regional risks increased simultaneously with drought incidence for *Agapetus* sp., *E. aenea and Hydropsyche* sp. (Figure 6). For other taxa, which did not respond strongly to RegFlow (Figure 4), regional quasi-extinction risks remained relatively stable as drought incidence increased (Figure S4). Basal local quasi-extinction risk (i.e., the risk at drought incidence = 0) varied from 0 to 0.7 (Figures 6 and S4), indicating that some taxa were more prone to local critical declines due to highly variable population dynamics, as captured by high state process error variance (Appendix 4). Local quasi-extinction risk values were higher in observed than in simulated data, but patterns of increasing risks with drought incidence were similar (Appendix 2). Because we compared multiple functional groups and taxa, relative differences in quasi-extinction risk may be more reliable than absolute risk values.

4. Discussion

The ecological impacts of drought on freshwater ecosystems have been largely described at local (Aspin et al., 2019; Ledger, Edwards, Brown, Milner, & Woodward, 2011) and regional scales (Bêche et al., 2009; Jaeger et al., 2014; Rolls, Heino, & Chessman, 2016). Our study explored whether drought can also synchronize local responses in river networks, destabilizing ecological communities via cross-scale interactions. We used time-series analyses of spatially replicated long-term data to examine invertebrate community and metapopulation responses to local and network-scale hydrological variation, and to estimate quasi-extinction risk under a range of drought scenarios. We found that community responses to drought were highly variable, and differed among taxa with traits conferring contrasting resistance and resilience to drought (H1). Whereas taxa with no or few resistance and resilience traits declined synchronously with the spatial extent of drying, the responses of other taxa were spatially heterogeneous (H2). Notably, drought incidence increased metapopulation-wide quasi-extinction risk for drought-sensitive taxa (H3). These results indicate that even if portfolios of resistance and resilience traits promote ecological rescue at the community level, drought may increase extirpation of drought-sensitive species by spatially synchronizing their population fluctuations. This example of the Moran effect highlights the need to consider metapopulation dynamics when forecasting climate-driven risk of biodiversity loss in river networks.

4.1. Drought influences metapopulation synchrony in river networks

Populations may decline synchronously if disturbances exceed species' resistance or resilience capacities and are spatially correlated across a landscape (i.e., the Moran effect: Hudson & Cattadori, 1999; Moran, 1953). Drought can exacerbate population extinction risk across biotic groups such as plants (Anderegg, Anderegg, Kerr, & Trugman, 2019), terrestrial insects (Kahilainen, van Nouhuys, Schulz Torsti, & Saastamoinen, 2018), and fish (Vander Vorste, Obedzinski, Nossaman Pierce, Carlson, & Grantham, 2020). Although limited research indicates the role of synchrony in driving these risks—particularly in freshwater ecosystems—some evidence exists. For example, floods can coordinate juvenile fish mortality across catchments (Cattanéo, Hugueny, & Lamouroux, 2003), dam-induced hydropeaking can synchronously filter out non-adapted invertebrates along river main stems (Ruhi et al., 2018), and low-flow periods can cause concurrent declines in invertebrate taxa adapted to fast-flowing environments (Huttunen et al., 2014). Understanding the mechanistic basis of drought-driven synchronization, and how it controls metapopulation persistence, is key to predicting drought impacts at the river network scale.

As river networks contracted, the abundance of taxa with no or limited resistance and/or resilience strategies declined. These vulnerable taxa included limpets, caddisflies, and riffle beetles adapted to fast-flowing waters (Tachet et al., 2010), which typically respond within days of drying and can take years to recolonize (Sarremejane et al., 2019). Their local and regional quasi-extinction risks drastically increased after three drought years, suggesting that drought-induced critical thresholds (Aspin et al., 2019) could drive populations towards demographic crashes (van Bergen et al., 2020). However, conflicting with H2, some taxa classified as having relatively high resilience and resistance capacities, such as *Agapetus* sp., were at risk of drought-driven extinction. The *Agapetus* sp. metapopulation showed the highest synchrony levels, indicating particular sensitivity to spatially extended disturbances such as drought. Although this caddisfly genus may overwinter as dormant eggs (Anderson & Bourne, 1974), this resistance strategy may not promote summer dry-phase persistence (Alvarez & Pardo, 2005). Alternating periods of drought and average conditions allowed the regional extinction risk of *Agapetus* sp. to stay low (Appendix 3), suggesting that fluctuating hydrological conditions may allow drought-vulnerable taxa with strong resilience capacity to recover between drought events.

Equally, a few taxa were favoured as drought severity increased. For ‘pioneer’ taxa such as *Simulium*, positive responses could reflect an ability to recolonize within weeks following a disturbance (Bogan, Boersma, & Lytle, 2013; Malmqvist, Rundle, Brönmark, & Erlandsson, 1991; Sarremejane et al., 2019). Equally, dispersal of flow-dependent organisms (such as *Gammarus* sp.) is often constrained by the dendritic structure of river networks (Carrara, Altermatt, Rodriguez-Iturbe, & Rinaldo, 2012; Tonkin et al., 2018). Contrasting taxon-specific responses could thus reflect differences in connectivity among populations with different dispersal capacities. However, we only assessed responses of widespread taxa, which are typically connected to many other populations within a landscape, and observed differences thus likely result from differences in functional traits, not connectivity. We contend that limited rescue effects could make some stream metapopulations particularly vulnerable to synchrony-driven extinctions.

4.2. Resilience and resistance strategies promote asynchrony, dampening risk

Drivers of community dynamics differed across sites, and non-hydrological and hydrological drivers both influenced community dynamics. Variability in responses among communities could reflect compositional differences. Community responses to a given disturbance are often mediated by the resistance and resilience capacities of their constituent species. Whereas some communities were driven largely by the effects of local hydrology on taxon resistance strategies, others were more influenced by regional processes, owing to the dispersal of resilient taxa, or a combination of drivers operating across both spatial scales. Communities may also respond stochastically to hydrological variability if all species are highly resistant and/or resilient, if density-dependent biotic interactions control changes in abundances, and/or if other environmental factors or dispersal override the effect of hydrology. For example, mass effects may obscure hydrological effects in highly connected communities, if a continuous influx of individuals allows communities to remain stable despite disturbances (Brown & Swan, 2010; Huttunen et al., 2017). In addition, the relative importance of local niche filtering, dispersal, and stochastic processes on community assembly can change over space and time in response to natural disturbance regimes (Cañedo-Argüelles et al., 2020). Such spatiotemporal variability should promote asynchronous responses at the metacommunity level, allowing species from relatively unimpacted communities to rescue those at impacted sites.

We found that metapopulations responses to increasing drying extent were not spatially coordinated for taxa with some form of resistance (*Resist_Dormancy, Resist_Substrate*) or resilience strategy, including aquatic dispersal (*Resil_Aqua*), small wings, intermediate fecundity, and short life cycles (*Resil_Fast*). These heterogeneous responses could reflect differences in local habitat conditions that locally buffer the effects of hydrological or climatic drivers, a phenomenon known as the portfolio effect (Schindler, Armstrong, & Reed, 2015). Populations occupy optimal and suboptimal habitats, and impacts of regional-scale disturbances may be most pronounced for populations inhabiting the latter (Moore, McClure, Rogers, & Schindler, 2010; Schindler et al., 2010).

At the functional level, differences in resistance and resilience strategies among taxa may also have promoted response diversity. Although the local extinction risks of some resistant and/or resilient taxa increased with drought incidence (e.g., *Baetis rhodani* and *Pisidium* sp.), asynchrony moderated regional extinction risks. For instance, although mayflies including *B. rhodani* are sensitive to decreases in flow velocity and drying (Chadd et al., 2017), they can persist in remnant aquatic habitats (Verdonschot, van Oosten-Siedlecka, ter Braak, & Verdonschot, 2015) and are often among the first taxa to recolonize post disturbance from within-reach and catchment-wide refuges (Sarremejane et al., 2019). In contrast, *Pisidium* sp. clams have low mobility but their populations can persist during drying events (Herbst, Cooper, Medhurst, Wiseman, & Hunsaker, 2019; Stubbington, Gunn, Little, Worrall, & Wood, 2016). These results advance the notion that despite drought, species with contrasting resistance and/or resilience capacities can maintain populations in a mosaic of habitats through source-sink dynamics.

4.3. Future directions and implications for conservation

Few studies have considered how cross-scale interactions may limit our capacity to conserve biodiversity in the face of environmental change (Altermatt et al., 2020; Chase et al., 2019; Erős et al., 2020). Here, we characterized ecological responses to a range of flow regimes in headwater systems, but caution should be exercised before generalizing our results. First, responses to hydrological changes may vary with network position, with mass effects tending to dominate in mainstems but not in isolated headwaters (Brown & Swan, 2010; Sarremejane, Mykrä, Bonada, Aroviita, & Muotka, 2017). Population stability may thus be higher in well-connected mainstems (Huttunen et al., 2017), which are also less prone to drying than headwaters. However, non-hydrological anthropogenic stressors typically increase with progression downstream, potentially leading to interactions between flow intermittence and poor water quality (Soria et al., 2020). Second, our simulation-based estimates are likely conservative because they are based on past conditions. Future increases in drought severity could further fragment networks and imperil metapopulations by constraining species dispersal and habitat ranges (Jaeger et al., 2014). Similarly, asynchronous responses for taxa identified to genus could have resulted from unmeasured response diversity within a genus—leading us to overestimate stability. Finally, larger spatial and temporal scales, and more precise measures of environmental variation (e.g., physically based hydrological modelling) should be considered, to evaluate how our estimates of network-scale quasi-extinction risk translate into true species extirpations across a region. Future research could address these limitations, and explore how observed patterns in drought-driven synchrony affect ecosystem functions (e.g., Truchy et al., 2020).

From an applied perspective, our results indicate that adaptive management strategies promoting asynchrony could help to protect biodiversity as droughts become longer, more frequent, and more intense (Spinoni et al., 2018). Metapopulation asynchrony could be promoted by designing diverse portfolios of flow conditions by coordinating operations of e.g., water abstraction and dam releases within a watershed (Palmer & Ruhi, 2019; Tonkin et al. 2021). Similarly, understanding habitat-level contributions to asynchrony could help to identify river sections that sustain network-scale biodiversity, promoting metapopulation resilience via dispersal in space and time (Buoro & Carlson, 2014; Rogosch & Olden, 2019). Climate change vulnerability assessments often focus on identifying species-specific habitat suitability and refuges under ranges of average and extreme conditions (Markovic, Carrizo, Kärcher, Walz, & David, 2017). However, such efforts generally overlook ecological impacts arising from cross-scale interactions (e.g., changes in spatial synchrony among populations), and large-scale resilience (Wilby, 2020; Williams et al., 2020). Our study highlights that both the spatial scales of climate-driven flow alteration and the role of drought as a large-scale synchronizing driver warrant greater attention in future research. Other widespread impacts such as land-use change and associated landscape homogenization, and biological invasions, could also synchronize population responses across rivers (Patrick et al. 2021). We call for further research to assess the generalizability of our results, and the potential for interacting factors to drive (meta)community and (meta)population synchronization as natural ecosystems continue to be increasingly exposed to sets of multiple stressors.

Conclusion

Freshwater invertebrate abundance and diversity have increased in parts of Europe in recent decades, with water quality improvements sometimes offsetting impacts of climate change (Pilotto et al., 2020; van Klink et al., 2020; Vaughan & Gotelli, 2019; Vaughan & Ormerod, 2014). However, spatially synchronous responses to extreme climatic events such as supraseasonal droughts could represent an underappreciated risk. River drying is increasingly common due to climate change and overallocation of water resources (Döll & Schmied, 2012), and is likely to intensify further as droughts become more frequent and severe in many regions, including much of Europe (Spinoni et al., 2018). Increasingly fragmented stream networks, and intermittence in previously perennial rivers, may further compromise access to refuges and recolonization post-drying (Jaeger et al., 2014), accentuating the patterns described herein. Our analytical approach may be transferred to other stream networks for which spatially replicated hydrological and biological time-series data exist, and may help to increase realism when forecasting climate-driven risk of biodiversity loss.

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Data Availability Statement

The data that support the findings of this study are openly available in figshare at http://doi.org/[doi], reference number [xxx]

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TABLE 1 Resistance (*Resist*) and Resilience (*Resil*) functional-group characteristics, example taxa, and total number of taxa in each group.

Abbreviation	**Description**	**Example taxa**	**Number of taxa**
Resist_None	No resistance forms, spiracles or ability to move into interstitial spaces.	Limpets: *Ancylus fluviatilis*; caddisflies: *Hydropsyche* sp., *Goera* sp.; leeches: *Glossiphonia* sp., *Helobdella* sp.	18
Resist_Dormancy	Presence of resistant and/or dormant forms (eggs, cocoon etc.). Spiracles absent; no ability to move into interstitial spaces.	Caddisflies: *Agapetus* sp., *Limnephilus* sp.; true flies: Ceratopogonidae; mussels: *Sphaerium* sp.; snails: *Radix balthica*	19
Resist_Substrate	Ability to move into interstitial spaces. In most cases (except for elmid beetles and *Gammarus* sp.), presence of resistant and/or dormant forms.	Beetles: *Elmis aenea;* crustaceans: *Asellus aquaticus, Gammarus* sp.; mayflies: *Baetis rhodani*; true flies: Chironomidae; mussels: *Pisidium* sp.	12
Resist_Respir	Respiration through spiracles present. In some cases (e.g., *Simulium* sp.), presence of other resistance strategies.	True flies: Tipulidae, *Simulium* sp.; beetles: *Haliplus* sp.	5
Resil_Aqua	Winged adult life stage absent (i.e., aquatic obligates); long adult life span (>1 year); short life cycle (<1 year); low fecundity (<100 eggs)	*Ancylus fluviatilis, A. aquaticus, Gammarus* sp.*, Glossiphonia* sp., *Helobdella* sp., *Pisidium* sp., *R. balthica, Sphaerium* sp.	21
Resil_Fast	Small wings; short adult life span (<1 week to <1 month); short life cycle; intermediate fecundity (100–1000 eggs)	*Agapetus* sp., *B. rhodani,* Chironomidae, Ceratopogonidae, *Simulium* sp.	17
Resil_Medium	Medium wings; intermediate adult life span (>1 week to <1 month); short life cycle; intermediate fecundity	*Goera* sp., *Limnephilus* sp., *Hydropsyche* sp., Tipulidae	10
Resil_Slow	Small wings; intermediate adult life span (>1 month); long life cycle (>1 year); low fecundity.	*Elmis aenea*, *Haliplus* sp.	5

TABLE 2 Comparison of MARSS metapopulation models, including AICc values for models of each functional group and widespread taxon, and three model structures assessing metapopulation responses: 1) stochastic, i.e., no effect of regional hydrological connectivity (*RegFlow*) was allowed; 2) site-specific RegFlow effects; and 3) RegFlow effects constrained by flow permanence regime (*flow-group*). Models with a Δ AICc <4 from the best model are indicated in bold. * indicate when MAR models were used due to degenerate variances (see section 2.5.4). See Table 1 for functional group abbreviations.

		RegFlow	
	Stochastic	**Site-specific**	**flow-group**
Functional group			
Resil_Aqua	**1875.38**	1903.26	**1878.53**
Resil_Fast	**1781.76**	1795.41	**1782.40**
Resil_Medium	**1861.62***	1897.68*	1866.21*
Resil_Slow	1394.16	1378.72	**1368.30**
Resist_None	1494.83	1496.21	**1472.24**
Resist_Dormancy	**1813.31**	1830.31	**1812.90**
Resist_Substrate	**1864.91**	1889.99	**1868.70**
Resist_Respir	**2029.90***	2059.71*	**2028.54***
Taxa			
Agapetus sp.	1889.65	1908.26	**1879.07**
Asellus aquaticus	1610.30	**1603.42**	**1602.00**
Baetis rhodani	**1863.04**	1890.85	1867.17
Elmis aenea	1382.55	1368.70	**1346.47**
Gammarus sp.	**2031.04**	2167.84*	**2034.78**
Hydropsyche sp.	1614.38*	1637.93*	**1607.14***
Pisidium sp.	**1711.63**	1724.56	**1709.42**
Simulium sp.	**2106.81***	2136.94*	**2104.17***

FIGURE captions

FIGURE 1 Hypothesized, multi-scale effects of drought (yellow band) on local communities and regional metapopulations, as influenced by species-specific resistance and resilience capacities. Different species (shapes) may have high or low resistance abilities (orange or blue fill, respectively), and high or low resilience abilities (pink or grey outlines, respectively, a). At the community level (b, **H1**), asynchronous fluctuations in species abundances can promote community stability in e.g., total local abundance (grey line). At the metapopulation level (c), individual populations (dashed lines) generally have asynchronous dynamics that stabilize regional metapopulations (solid line), in particular among taxa with strong resistance capacities (orange) (**H2**). However, at high drought severity, population synchrony may increase drastically in space, reducing metapopulation stability of less resistant taxa (blue) and potentially driving metapopulations toward extinction (**H3**).

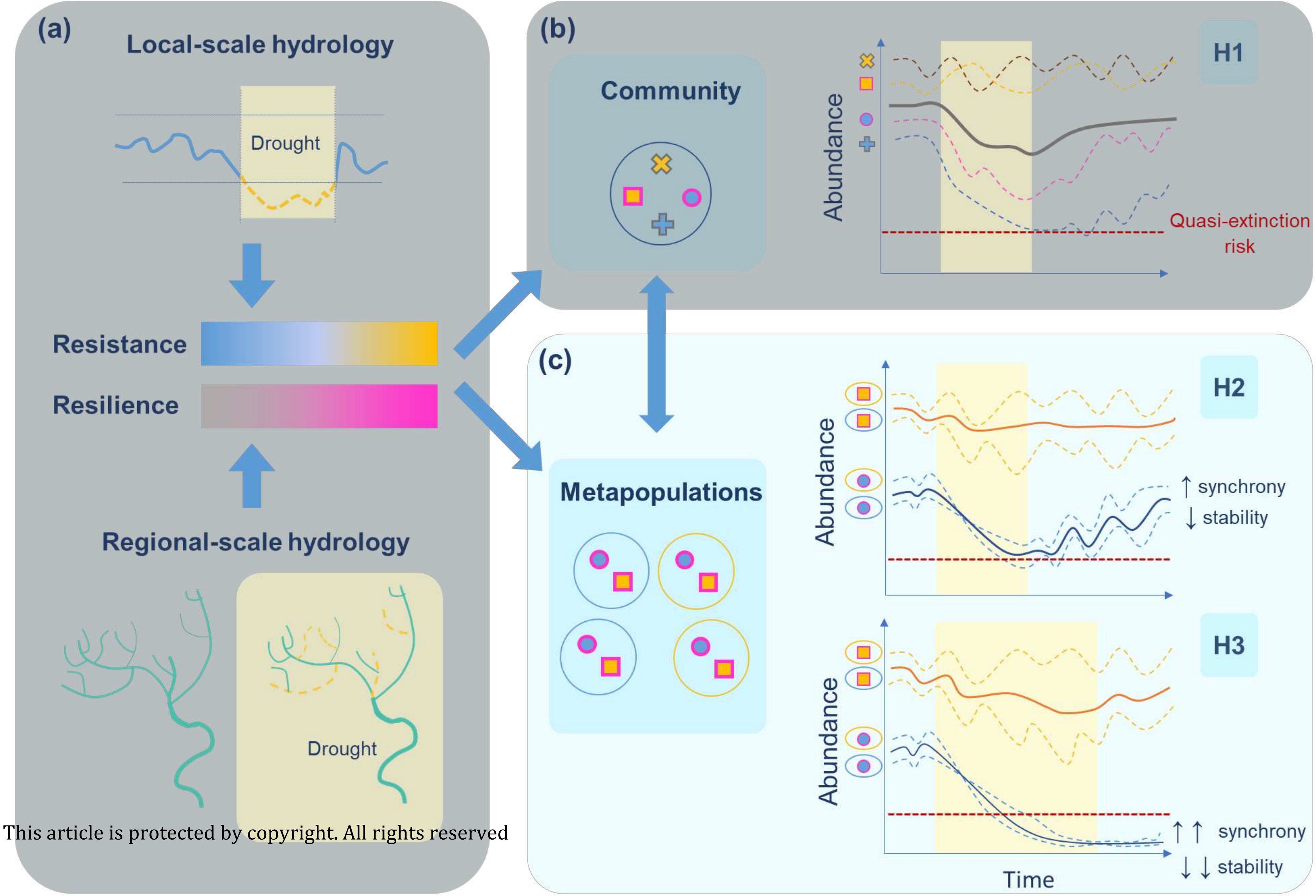
FIGURE 2 Map of the 20 study sites (a), and temporal change in (b) regional and (c) local hydrological conditions (*RegFlow* and *LocalFlow*, respectively). In (a), dot colours indicate flow permanence regimes (IR = intermittent, NPR = near-perennial, PR = perennial), calculated as the % of months flowing (Flow%) between 2004 and 2018. RegFlow and LocalFlow were calculated for six-month periods (i.e., March–August and September–February). RegFlow was measured as the proportion of reaches flowing within the network (in %) and the mean (± SE) LocalFlow was measured as mean daily discharge ($m^3.s^{-1}$) across sites. Six-month periods with RegFlow or LocalFlow values below the 80th percentile are indicated in yellow (dry periods), and those above the 20th percentile are shown in dark blue (wet periods).

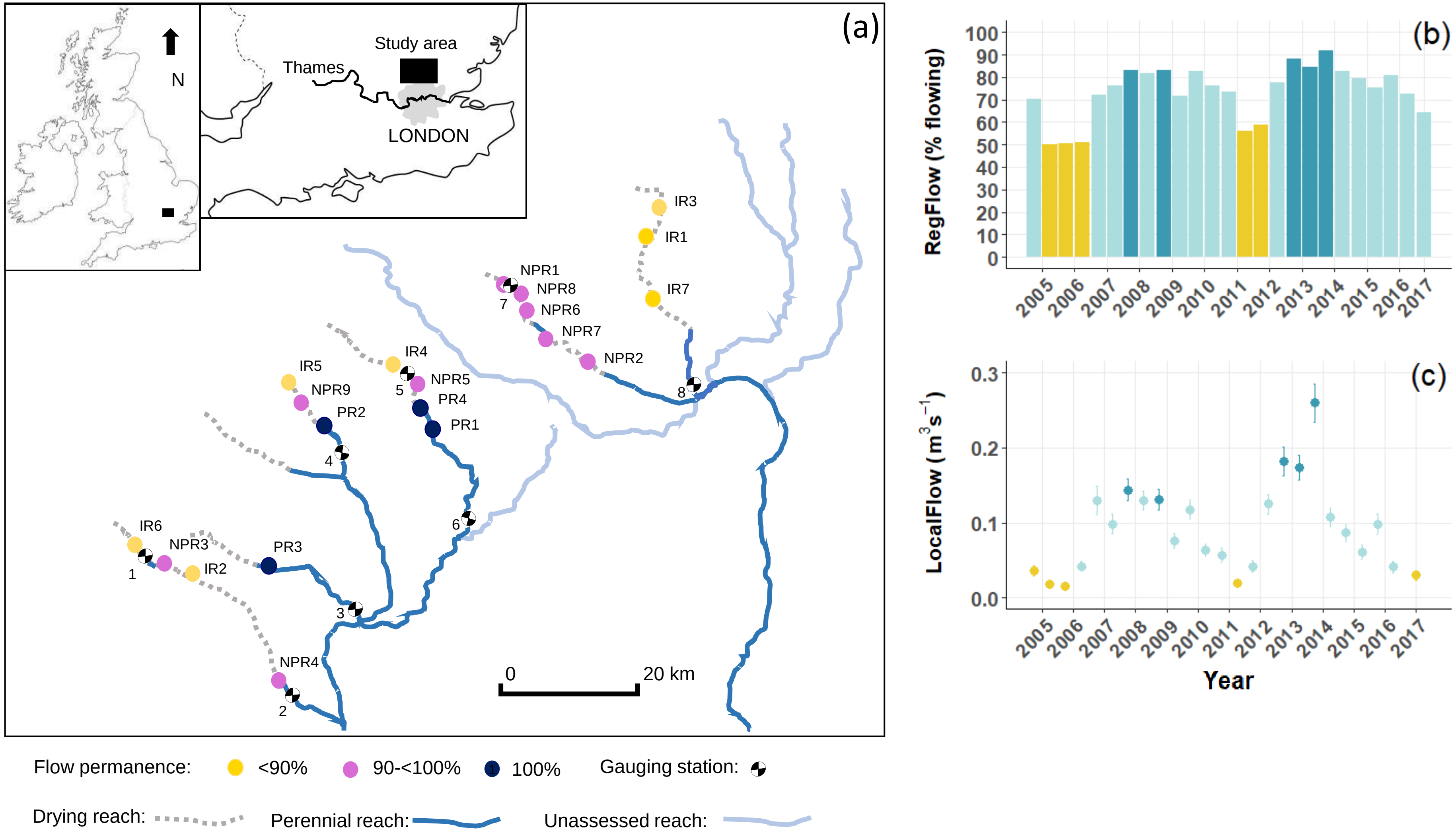
FIGURE 3 Effect sizes of local and regional hydrological covariates on invertebrate functional groups, as estimated by MARSS community models. Flow permanence (%) indicates whether sites had perennial, near-perennial, or intermittent flow regimes. *LocalFlow* represents local hydrological conditions (mean daily discharge, in m^3 s^{-1}), and *RegFlow* represents regional hydrological connectivity (extent of flowing reaches, in %). Filled and open symbols and solid and dashed error bars indicate significant and non-significant effects respectively, based on whether bootstrapped 95% confidence intervals overlap with zero. Positive effects indicate increases in invertebrate abundances as hydrological covariates increase (and vice versa). Only results for functional-group models with ΔAICc <4 are reported, excluding communities for which the best models were stochastic or taxon-specific. Curves were plotted using a generalized additive model smoothing function, and capture an interaction, i.e., whether hydrological effects depend on site flow permanence regimes. Functional group abbreviations are defined in Table 1.

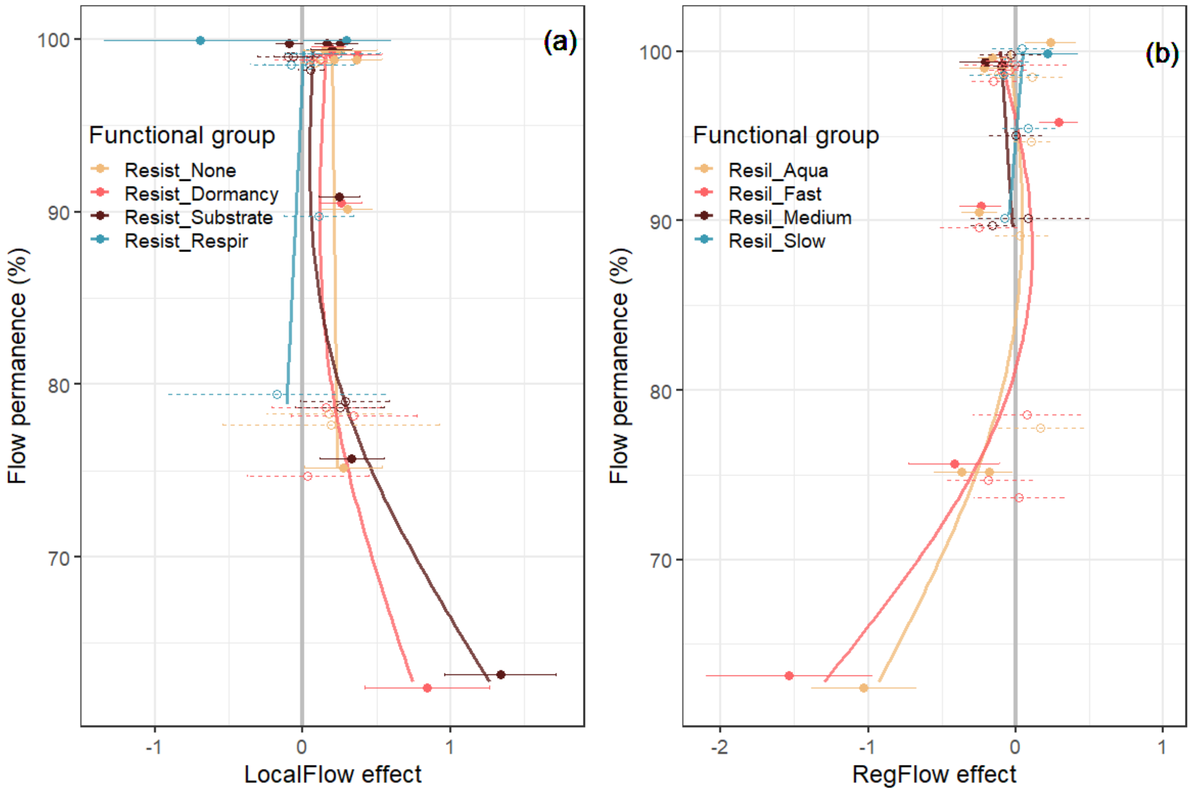
FIGURE 4 Effect size of regional hydrological conditions (*RegFlow*) on invertebrate metapopulations, as estimated by MARSS metapopulation models for (a) functional groups, and (b) widespread taxa. We compared inferences across sites with different flow permanence regimes (IR = intermittent, NPR = near-perennial, PR = perennial). Solid and transparent symbols and error bars indicate significant and non-significant effects, respectively (the latter have 95% confidence intervals overlapping with 0). See Table 1 for functional groups abbreviations.

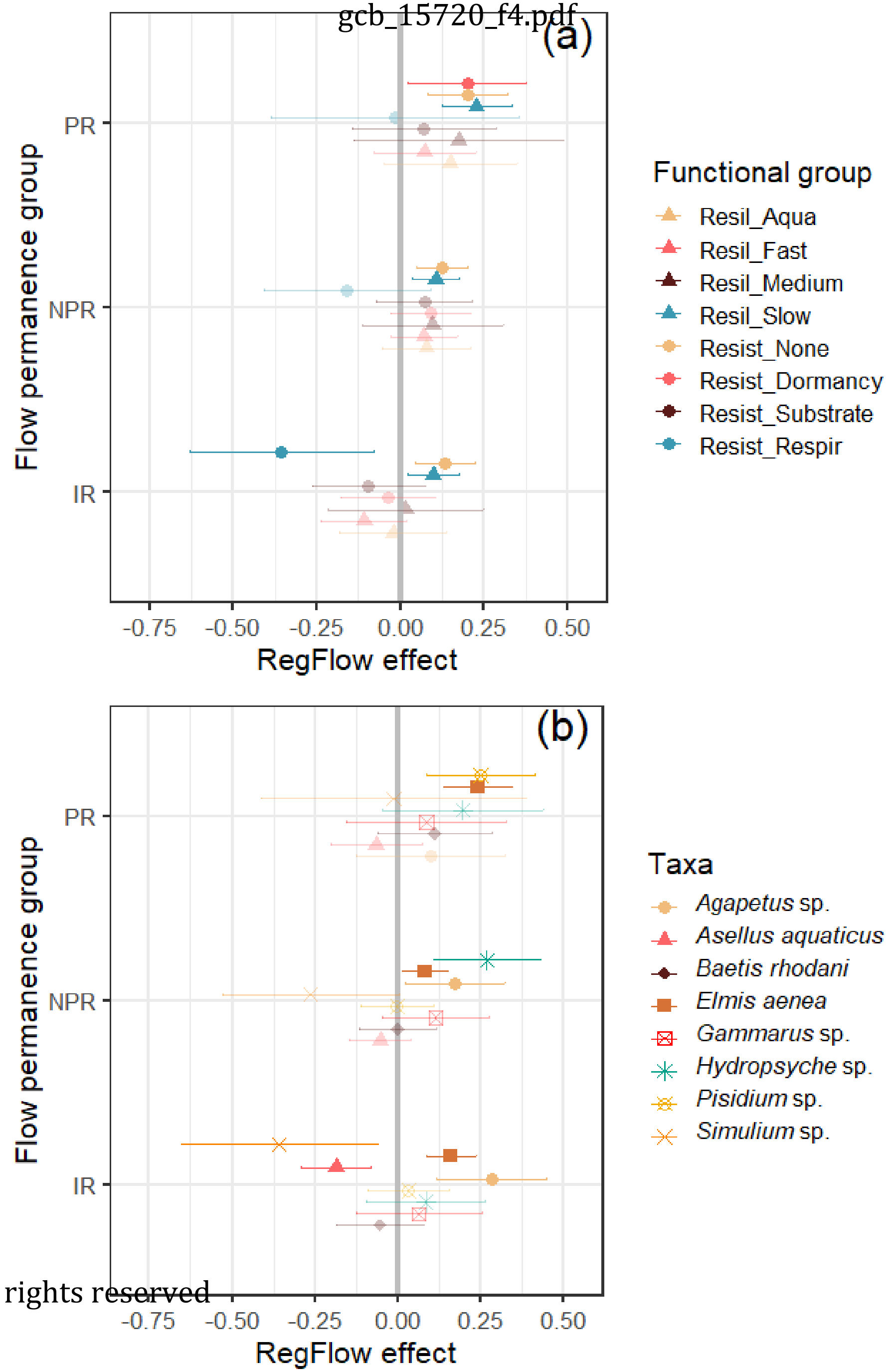
FIGURE 5 Patterns in process error covariance standardized by process error variance, as estimated from the ***Q*** matrix of MARSS or MAR metapopulation models for (a) each functional group, and (b) each widespread taxon. We compared stochastic covariance models (model iv in Table S4, open symbols) to flow-group covariance models (model v in Table S4; filled symbols), to examine whether including hydrology as a covariate subsumed process error ('unexplained') covariance. Dotted error bars indicate non-significant effects (i.e. 95% confidence intervals overlapping with zero, or 'unexplained' coordinated fluctuations not being statistically significant). See Table 1 for functional group abbreviations, and Appendix 4 for patterns in process error variance (Figure S8) and process error covariance (Figure S9), respectively.

FIGURE 6 Responses of local (yellow) and regional (orange) quasi-extinction risks to drought incidence derived from metapopulation simulations. Dotted lines show results from the stochastic model (i.e. with no hydrological covariate) and solid lines results from the flow-group models across 124 scenarios with varying drought incidence (i.e., spanning 0 to 12 six-month periods). Only groups and taxa which showed significant metapopulation responses to hydrological connectivity (RegFlow) are presented. Other results are in Figure S3. Regression curves were fitted using a locally estimated scatterplot smoothing (loess) function

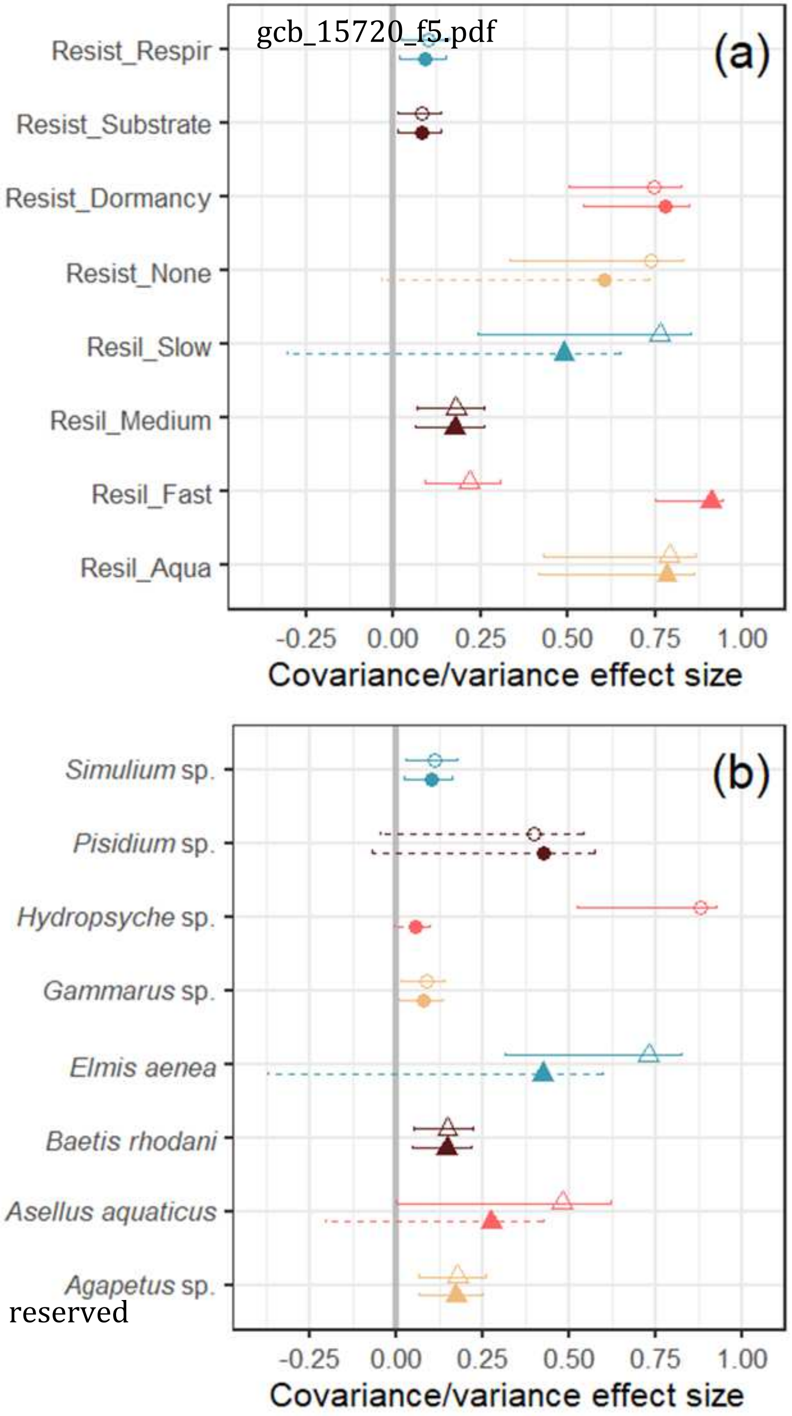

(a)
Local-scale hydrology
Drought
Resistance
Resilience
Regional-scale hydrology
Drought
(b)
Community
Abundance
H1
Quasi-extinction risk
(c)
Metapopulations
Abundance
H2
↑ synchrony
↓ stability
Abundance
H3
↑↑ synchrony
↓↓ stability
Time

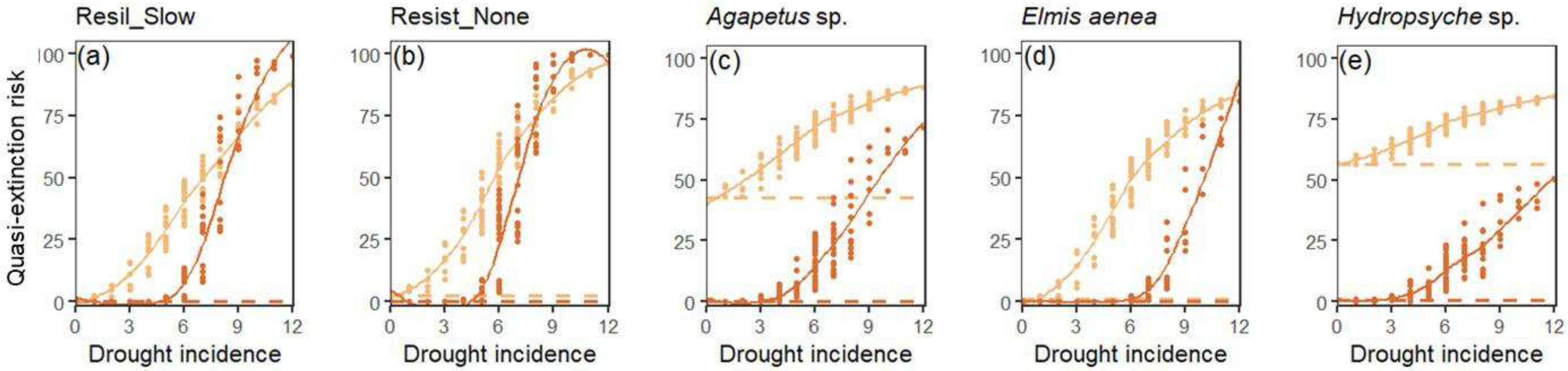

(a)
N
Study area
Thames
LONDON
IR3
IR1
IR7
NPR1
NPR8
NPR6
NPR7
NPR2
7
8
IR4
NPR5
PR4
PR1
5
6
IR5
NPR9
PR2
4
IR6
NPR3
IR2
PR3
1
3
NPR4
2
0
20 km
Flow permanence: <90% 90-<100% 100% Gauging station:
Drying reach: Perennial reach: Unassessed reach:
(b)
RegFlow (% flowing)
100
90
80
70
60
50
40
30
20
10
0
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
(c)
LocalFlow ($m^3 s^{-1}$)
0.3
0.2
0.1
0.0
Year


(a)
Functional group
Resist_None
Resist_Dormancy
Resist_Substrate
Resist_Respir
Flow permanence (%)
100
90
80
70
-1
0
1
LocalFlow effect
(b)
Functional group
Resil_Aqua
Resil_Fast
Resil_Medium
Resil_Slow
Flow permanence (%)
100
90
80
70
-2
-1
0
1
RegFlow effect


(a)
Flow permanenence group
PR
NPR
IR
-0.75
-0.50
-0.25
0.00
0.25
0.50
RegFlow effect
Functional group
Resil_Aqua
Resil_Fast
Resil_Medium
Resil_Slow
Resist_None
Resist_Dormancy
Resist_Substrate
Resist_Respir
(b)
Flow permanenence group
PR
NPR
IR
-0.75
-0.50
-0.25
0.00
0.25
0.50
RegFlow effect
Taxa
Agapetus sp.
Asellus aquaticus
Baetis rhodani
Elmis aenea
Gammarus sp.
Hydropsyche sp.
Pisidium sp.
Simulium sp.

gcb_15720_f5.pdf




Resil_Slow
Resist_None
Agapetus sp.
Elmis aenea
Hydropsyche sp.
(a)
(b)
(c)
(d)
(e)
Quasi-extinction risk
0
25
50
75
100
Drought incidence
0
3
6
9
12