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Under Pressure: Macroinvertebrate Community Responses to Agriculture in Temporary Streams

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ABSTRACT

1. Temporary streams dominate global river networks and thus often occur in catchments dominated by agricultural land uses. Drying and agriculture can exert similar stressors on aquatic communities, for example, by decreasing dissolved oxygen concentrations and increasing fine sediment deposition. However, little is known about the effects of agriculture in driving taxonomic and trait variability in temporary stream communities. Therefore, we compared the effects of agricultural land use on variability in taxonomic and functional macroinvertebrate communities in temporary and perennial streams.
2. We used 98 macroinvertebrate samples collected from sites with perennial ($n = 49$) and temporary ($n = 49$) flow in southern England. We quantified the spatial extent of agriculture surrounding each site, assigned samples to high ($n = 62$) and low ($n = 36$) agricultural land use categories, and tested whether variability in community composition differed between perennial and temporary reaches and between high and low agricultural categories. We also tested whether the occurrence of temporary stream specialist species was influenced by agriculture.
3. Regardless of agricultural land use, temporary reach communities were more variable than those in perennial reaches, suggesting that drying is a bigger influence than agriculture on stream communities. Within temporary reaches, communities were comparably variable regardless of agriculture, whereas agriculture increased variability among perennial reach communities. The occurrence of temporary stream specialists was unaffected by agriculture.
4. Our results suggest that tolerance of drying by temporary stream communities confers tolerance of agriculture. This co-tolerance of drying and agriculture may occur because temporary stream communities typically comprise species that experience agriculture and drying as comparable pressures. These species include temporary stream specialists that tolerate a wide range of environmental conditions, including drying.
5. Although temporary stream communities and their specialist species may be co-tolerant of drying and agriculture, these and other human pressures are intensifying, with potentially detrimental impacts on their long-term stability.

1 | Introduction

Agriculture threatens the integrity of riverine ecosystems globally (Mateo-Sagasta et al. 2017; Reid et al. 2019). Agricultural pressure alters rivers by introducing runoff carrying pollutants including fine sediment, inorganic nutrients and pesticides; increasing water temperatures via the loss of riparian vegetation; modifying flow regimes and channel morphology and reducing dissolved oxygen availability (Fu et al. 2004; Hao et al. 2008; Almeida et al. 2023). The resultant reduction in habitat quality

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and availability influences aquatic communities, with effects ranging from the elimination of sensitive species to shifts in structure and function (Wood and Armitage 1997; Dodds 2007; Sánchez-Bayo et al. 2016). Additionally, the global prevalence of agriculture means that it often co-occurs with other anthropogenic and natural pressures, compounding effects on riverine communities (Botwe et al. 2015; Gerth et al. 2017; Bashir et al. 2020). For example, temporary streams—which sometimes dry out due to both natural and anthropogenic influences—dominate global river networks (Messager et al. 2021; Datry et al. 2023), and are widespread in cool, wet temperate climates (Stubbington et al. 2017). Temporary streams thus often occur in agricultural areas (Armitage and Bass 2013; Karaouzas et al. 2018; White et al. 2018), exposing their communities to both agricultural and drying pressure (Botwe et al. 2015; Gerth et al. 2017).

Stream drying entails a decline in aquatic habitat availability and diversity, including the loss of all flowing surface water and the restriction of any remaining water to isolated pools and/or subsurface sediments. This decline and loss of aquatic habitat occurs seasonally in many temporary streams, with dry phases typically persisting for weeks to months in temperate climates (Stubbington et al. 2017). In addition, aquatic communities in temporary streams can be exposed to multiple abiotic stressors during flowing phases, including elevated fine sediment deposition and nutrient concentrations, and decreasing dissolved oxygen concentrations as water temperature and the density of respiring aquatic organisms increase (Stubbington et al. 2011b; Gómez et al. 2017; von Schiller et al. 2017). Biotic interactions including competition and predation also intensify as aquatic habitats contract (Stubbington et al. 2011a; Aspin and House 2022). As a result, temporary stream communities are typically dominated by generalist species with resistance and/or resilience traits that promote their persistence despite regular disturbance by drying (Bogan et al. 2017).

The stressors exerted by drying and agriculture are broadly comparable: decreased aquatic habitat diversity, increased water temperatures, increased fine sediment and nutrient concentrations, and lower dissolved oxygen availability (Figure 1a; Allan 2004; Withers et al. 2014; dos Reis Oliveira et al. 2019). At local spatial scales, these stressors typically result in species-poor, stress-tolerant communities (Delong and Brusven 1998; Gutiérrez-Cánovas et al. 2015; Gething 2021), although spatial variability in the type and intensities of stressors can result in high taxonomic and trait variability among sites (Warwick and Clarke 1993; Valdivia et al. 2011; Kuzmanovic et al. 2017). Thus, temporary stream communities may be filtered to contain taxa which also tolerate multiple stressors associated with agricultural pressure (Vinebrooke et al. 2004; Storey 2016), thus experiencing lower taxonomic and trait variability between agricultural and non-agricultural stream sites compared to perennial streams.

Although generalist taxa can dominate, the stress-tolerant communities of temporary streams also include rare, specialist macroinvertebrate species which have adaptations such as drying-tolerant life stages (Delucchi and Peckarsky 1989; Tapia et al. 2018; Macadam et al. 2021). These species include mayflies and stoneflies from families that are generally sensitive to common agricultural stressors such as low dissolved oxygen concentrations and elevated fine sediment (Armitage et al. 1983; Extence et al. 2013). For example, the occurrence of the temporary stream specialist mayfly *Paraleptophlebia werneri* and stonefly *Nemoura lacustris* in drainage ditches and streams in agricultural landscapes across southern England (Gething et al. 2021; also see Vilenica et al. 2021) indicates that they may be co-tolerant of drying and agricultural pressures, unlike their co-sensitive congeners (Chadd et al. 2017). Thus, like temporary stream communities more broadly (Storey 2016), these specialist species may be unaffected by agricultural land uses, which they experience as comparable to the drying-related stressors to which they are adapted.

We analysed a dataset describing macroinvertebrate communities in groundwater-dominated streams to assess the effects of agricultural land use on taxonomic and trait variability in temporary and perennial reaches. We hypothesised that (H1) community variability between areas with higher and lower agricultural land use is lower in temporary than in perennial

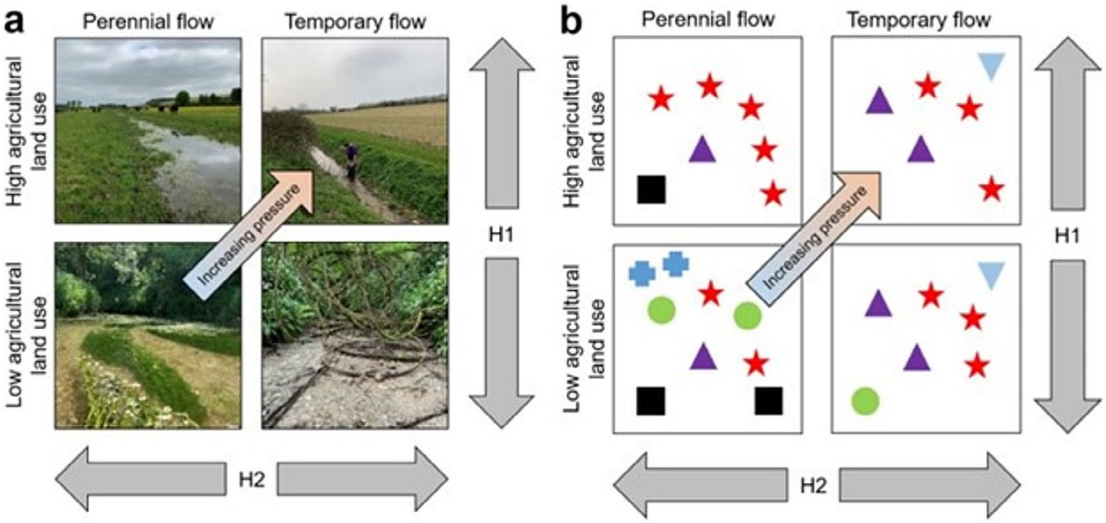

FIGURE 1 | The (a) habitats and (b) hypothesised community shifts with differing combinations of temporary and perennial flow and high and low agricultural land use. Grey arrows show the habitats compared by hypotheses (H) 1 and 2; symbols represent different taxa or traits.

reaches (Figure 1b) because drying filters communities in temporary streams to a subset of tolerant taxa, promoting co-tolerance of agriculture; (H2) community variability between temporary and perennial reaches is lower in areas with higher agricultural land use (Figure 1b) because their communities are filtered to retain only tolerant taxa/traits; and (H3) the occurrence of temporary stream specialist species is unaffected by agricultural land use because their adaptations to comparable drying-related stressors promote co-tolerance of agriculture.

2 | Methods

2.1 | Study Area

This study was conducted at 37 sites on seven tributary streams of the Hampshire Avon, southern England (Table 1, Figure 2). The region has a temperate oceanic climate (Cfb: Kottek et al. 2006), with annual minimum and maximum air temperatures of (mean ± SD) 6.1°C± 3.9°C and 15.0°C± 5.7°C, respectively, and mean annual rainfall of 754 mm (Met Office 2022). The Hampshire Avon catchment has primary land uses of pastoral (42%) and arable agriculture (39%: National River Flow Archive, 2021). The area is underlain by a chalk aquifer that experiences seasonal fluctuations in groundwater levels (Berrie 1992; Sear et al. 1999), resulting in surface streams with temporary and perennially flowing reaches (Table 1). The streams had 3–8 sampling sites each, with distances between adjacent sites in a catchment ranging from 0.23 to 8.3 km.

2.2 | Data Collection

2.2.1 | Aquatic Macroinvertebrates

Aquatic macroinvertebrate samples were collected by Wessex Water (a public water supply company) from 37 sites in spring, summer, and autumn 2006 and 2007 using a standard 3-min kick

TABLE 1 | Number of sites and samples collected from temporary (T) and perennial (P) reaches of seven streams in southern England.

	Sites	T sites	P sites	Samples	T samples	P samples
Chitterne Brook	4	3	1	5	3	2
Fonthill Brook	3	2	1	8	4	4
Nine Mile River	4	4	0	8	8	0
River Bourne	7	5	2	14	6	8
River Ebble	7	5	2	25	13	12
River Till	8	4	4	23	12	11
River Wylye	4	2	2	15	3	12
Total	37	25	12	98	49	49

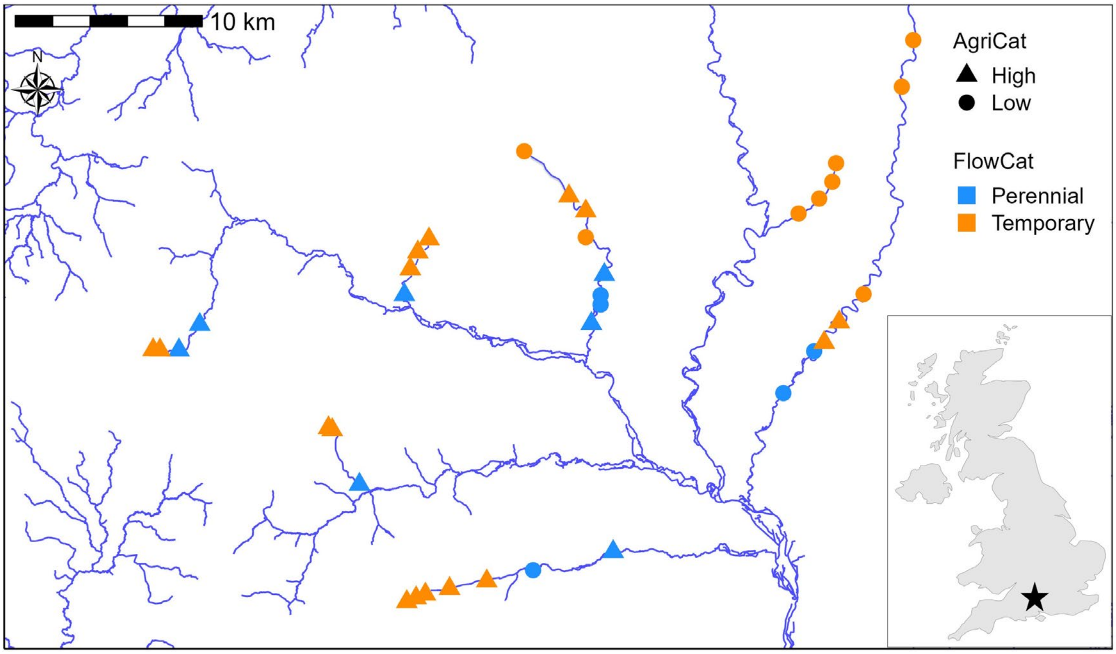

FIGURE 2 | The study area (black star) marked with sites that have perennial (blue) and temporary (orange) flow regimes, and high (triangles) and low (circles) amounts of agricultural land use.

sampling methodology supplemented by a 1-min hand search (Murray-Bligh and Griffiths 2022; Stubbington et al. 2024). In the laboratory, macroinvertebrates were identified predominantly to species level, except Diptera, which were identified to the lowest practical level between species and family (mostly genus). Some individual Coleoptera, Ephemeroptera, Gastropoda, Hirudinea, Lepidoptera, and Trichoptera were identified to genus or family level. All taxa were recorded as present/absent.

2.2.2 | Flow Permanence, Physicochemical Characteristics and Land Use

In the 3 years prior to macroinvertebrate sampling, sites were visited once per month and the presence/absence of surface water recorded. To characterise stressors indicative of agricultural land use, substrate samples were collected at each site in spring 2006 and 2007. A hole saw (10 × 5 cm) was twisted into the streambed at 6–8 representative locations and the extracted substrate aggregated into a 2.5-L composite sample. Substrate samples were returned to the laboratory, air dried, and sieved to determine the relative proportions of silt (< 0.06 mm), sand (0.06–2 mm), gravel (2–64 mm) and cobbles (> 64 mm). Total phosphorus ($\mathrm{mg\,kg^{-1}}$) and total oxidised nitrogen ($\mathrm{mg\,kg^{-1}}$) were determined for each substrate sample in a UKAS approved laboratory.

Land use buffers with a 100-m radius around each macroinvertebrate sampling site were extracted from the UK Land Cover Map 2007 (Morton et al. 2014) using Quantum GIS v.3.16 (QGIS Development Team 2021). We selected this radius because, based on Sponseller et al. (2001) and Feld (2013), such local riparian land uses influence the distribution of common agricultural pollutants such as fine sediment. This radius also prevented overlap of land use characterisations among sites.

2.3 | Data Analysis

2.3.1 | Data Preparation

To allow comparisons between reaches with contrasting flow permanence regimes, sites were assigned to a flow permanence category (FlowCat): temporary or perennial. Temporary sites were those at which water was recorded as absent in ≥ 1 of the 36 months. In total, 49 samples were collected from temporary and perennial reaches (Table 1), with the UK Centre for Ecology & Hydrology's grid-to-grid flow model (Bell et al. 2009) predicting a mean (±SD) discharge of $0.50 \pm 0.02\,\mathrm{m^3\,s^{-1}}$ (range: 0–$2.23\,\mathrm{m^3\,s^{-1}}$) in temporary reaches and $0.84 \pm 0.02\,\mathrm{m^3\,s^{-1}}$ (0.14–$6.70\,\mathrm{m^3\,s^{-1}}$) in perennial reaches. Temporary reaches had flowed for (mean ± SE) 14.9 ± 9.7 months and been dry for 21.1 ± 9.7 months, with flow resuming 2–34 months prior to macroinvertebrate sampling. Time since wetting can be a key control on community composition (Sarremejane et al. 2020). To evaluate the influence of variability in time since flow resumption on our conclusions, we added time since wetting to the models detailed in Section 2.3.2. Models including only FlowCat and both FlowCat and time since wetting supported the same conclusions and are reported in Section 3 and Supporting Information, respectively.

We generated a categorical variable (AgriCat) to represent the broad effects of agriculture. First, we applied indicator 'species' analysis (IndVal: Dufrêne and Legendre 1997; typically applied to biotic assemblage data) to a Euclidean distance matrix containing four abiotic variables: total phosphorus, total oxidised nitrogen, silt and sand (i.e., common agricultural pollutants). We repeated IndVal 98 times, in which the boundary for 'high' and 'low' agriculture were sequentially increased from 1% to 99% of total land use. For each iteration, we calculated the root-mean-square (RMS) of IndVal scores for the four abiotic variables. Iterations with lower RMS value signified that the abiotic variables had a low specificity and fidelity to each category (i.e., approximately half of the material recorded for each abiotic variable was above and below the threshold). The lowest RMS values occurred at 80% agricultural land use, and thus we used this threshold to assign samples to high ($n = 62$) and low ($n = 36$) AgriCats. To ensure that samples close to the threshold did not disproportionately influence our conclusions, we repeated all analyses while excluding 12 samples (four and eight from the low and high AgriCats, respectively) for which 70%–90% (i.e., ±10% of the 80% threshold) of total land use was agriculture. Analyses including and excluding these 12 samples produced comparable results, and thus we present analyses that include all samples.

The 80% threshold resulted in high AgriCat samples with (mean ± SD) 96.3% ± 5.2% (min.: 81.6%, max.: 98.5%) agricultural land use, compared to 49.8% ± 19.5% (0.0%–74.2%) in low AgriCat samples. Temporary and perennial reaches were comparably represented in high (31 temporary and 31 perennial samples) and low (18 and 18) AgriCats.

To minimise the influence of macroinvertebrate identification to multiple taxonomic levels (e.g., to species, genus and family), we assigned taxa to a single most likely taxon (Cuffney et al. 2007), with 85%, 11% and 4% of taxa assigned to species, genus, and family, respectively.

To characterise functional composition, we used three biological traits (maximum size, respiration and locomotion) with 20 modalities and two ecological 'traits' (i.e., environmental preferences: trophic and temperature preference) with six modalities that respond to both drying and agricultural stressors (Table S1, Tachet et al. 2010; Schmidt-Kloiber and Hering 2015). We weighted the affinity of each taxon to multiple modalities within a trait using a fuzzy coding approach, to represent intra-taxon trait variability (Chevenet et al. 1994). We represented species with their species trait profile and represented genera and families with the average trait profile of all species in that taxon (Demars et al. 2012). Where species-level information was not available, we used the highest resolution profile available (mostly genus). Trait modalities ranged from zero (no affinity) to three or five (high affinity; Tachet et al. 2010). Due to differing numbers of modalities within traits, we standardised modalities so that each trait summed to one, thus representing the relative abundance of each modality per taxon and ensuring equal weighting of the five traits (Demars et al. 2012; England et al. 2021). We multiplied the resulting taxa-by-trait matrix by the taxa-by-sample matrix to obtain a trait-by-sample matrix for analysis.

2.3.2 | The Effect of Flow Permanence and Agriculture on Macroinvertebrate Communities

To characterise communities for testing of H1 and H2, we first Sørensen transformed the taxa-by-sample matrix and Bray-Curtis transformed the trait-by-sample matrix to represent taxonomic and functional composition, respectively. We then summarised variability in the taxonomic and functional matrices by calculating the distance between each sample and the centroid (i.e., multivariate dispersion: Warwick and Clarke 1993; Benkwitt et al. 2019) of each FlowCat and AgriCat using permutational analyses of multivariate dispersions (PERMDISP2: Anderson 2006). We used the distance of samples from FlowCat (H1) and AgriCat (H2) centroids as response variables in linear models. Preliminary analyses identified significant differences in composition among seasons and years, which we controlled by nesting season within year (hereafter, Season) as a random intercept in all models.

To assess taxonomic and trait variability within temporary and perennial reaches in relation to agricultural land use (H1), we used a linear model to test whether the distance of samples from each FlowCat centroid differed between FlowCat and AgriCat and their interaction (Table S2). Acceptance of H1 required variability among temporary FlowCat samples to be comparable in each AgriCat *and* to be lower than that among perennial FlowCat samples.

To assess taxonomic and trait variability between high and low AgriCat reaches in different FlowCats (H2), we replicated the H1 linear model, with the distance of samples from each AgriCat centroid as the response variable and the interaction of AgriCat and FlowCat as predictors (Table S2). Acceptance of H2 required variability among high AgriCat samples to be comparable in each FlowCat *and* to be lower than that among low AgriCat samples.

Where differences in variability between FlowCats and between AgriCats were detected, we quantified the contribution of each taxon/trait modality to differences using similarity percentage analysis (SIMPER: Clarke 1993) over 9999 permutations. We considered a taxon/trait modality as driving differences between categories if SIMPER $p < 0.05$ and contributions to overall differences were $\geq 5\%$.

To contextualise our testing of differences in variability (i.e., H1 and H2), we also tested for differences in community composition between FlowCats and AgriCats (Supporting Information).

2.3.3 | The Effect of Agriculture on the Occurrence of Temporary Stream Specialists

Based on Armitage and Bass (2013) and Macadam et al. (2021), we identified two temporary stream specialists in the dataset: the mayfly *Paraleptophlebia werneri* and blackfly *Simulium latipes*. Additionally, since sample collection (2006–07) the temporary stream specialist stonefly *Nemoura lacustris* has been added to the British faunal list and has been widely recorded in the study area (Hammett 2012; Gething et al. 2021). The aquatic juveniles of *N. lacustris* are morphologically similar to those of *Nemoura cinerea* (Armitage and Bass 2013; Tapia et al. 2018) and records of this species are likely to represent a combination of *N. cinerea* and *N. lacustris* (Aspin and House 2022). We therefore analysed *N. cinerea* alongside the two other specialists.

Paraleptophlebia werneri was exclusive to temporary reaches, occuring in 12 of the 49 samples. *Simulium latipes* and *N. cinerea* occurred mostly in temporary reaches (in 17 and 22 samples, respectively), but were also recorded in 1 and 2 perennial reach samples, respectively. To enable detection of responses to agriculture, we therefore used only temporary reach samples to test H3. We used occurrences of the three specialists as response variables and AgriCat as a fixed effect in binomial generalised linear mixed-effect models (Table S2). Acceptance of H3 required the occurrence of specialists to be unaffected by AgriCat.

To enable the absence of a temporary stream specialist response to agriculture to be interpreted as evidence supporting H3 (rather than a false negative), we reran the H3 model for all taxa associated with (i.e., which had $>90\%$ of their occurrences in) one FlowCat. We used this $>90\%$ threshold to enable comparison with specialists, which had 92%–100% of occurrences in temporary reaches. We discounted taxa with ≤ 10 occurrences in their FlowCat, because ≤ 10 occurrences were insufficient to assess the influence of AgriCat. Thus, we applied the linear model used to test H3 to four and 21 taxa which had $>90\%$ of their occurrences in temporary and perennial reach samples, respectively.

We quantified variance attributable to the fixed and random effects using marginal R^2 (R^2M) and conditional R^2 (R^2C). For models with a difference of <0.01 between R^2M and R^2C, we removed Season to improve model parsimony. For H1 and H2, we visualised variability in taxonomic (i.e., Sørensen) and functional (Bray–Curtis) communities using two-dimensional non-metric multidimensional scaling (NMDS) ordinations with 500 iterations. For ordinations with high stress (>0.2, i.e., taxonomic composition in temporary reaches) we replotted the NMDS using 3 dimensions. We conducted all analyses in R v.4.0.3 (R Core Team 2020), using the packages biomonitoR (Laini et al. 2022), DHARMa (Hartig 2020), indicspecies (De Caceres and Legendre 2009), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017) and vegan (Oksanen et al. 2019).

3 | Results

Macroinvertebrate communities comprised 237 taxa from 86 families. The non-biting midge family Chironomidae occurred in all samples. The other most frequent taxa overall were the worm *Eiseniella tetraedra* (in 98% of samples), the mayfly *Baetis rhodani* (90%) and the blackfly *Simulium ornatum* (80%). Perennial reaches supported 189 taxa (79.7% of total) and (mean ± SD) 42.6 ± 12.1 taxa per sample, whereas temporary reaches supported 167 taxa (70.5%) and 23.1 ± 9.9 taxa per sample. In temporary reaches, *E. tetraedra* (100%) and *B. rhodani* (86%) occurred most frequently, whereas in perennial reaches *E. tetraedra*, the amphipod *Gammarus pulex*, and the riffle beetle *Elmis aenea* were most frequent (98%–100%). High and low AgriCat reaches supported 209 taxa (88% of total) and 178 taxa (75%), respectively, and supported 31.4 ± 13.5 and 35.4 ± 16.4 taxa per sample, respectively. *Eiseniella tetraedra* (98% and 100% of samples) and *B. rhodani* (89% and 92%) were the most frequently occurring taxa in both high and low AgriCats. Perennial reaches supported 39.3 ± 12.4 and 48.2 ± 9.3 taxa per sample in high and low AgriCat, respectively, while temporary reaches supported 23.4 ± 9.3 and 22.7 ± 11.0 taxa per sample in high and low AgriCats, respectively.

Functional communities in temporary and perennial reaches both had the same 25 of 26 modalities. Low AgriCat reaches supported 24 modalities, missing maximum size: > 8 cm, whereas all 25 modalities were present in high AgriCat reaches.

3.1 | H1. Community Responses to Agriculture in Temporary and Perennial Reaches

AgriCat did not influence taxonomic variability in temporary reaches (estimate ± SE = −0.04 ± 0.02, $p = 0.101$, $\mathrm{R}^2\mathrm{M} = 0.321$, Figures 3a and S1). In perennial reaches, taxonomic variability was greater in high than low AgriCat reaches (estimate ± SE = 0.05 ± 0.02, $p = 0.033$, Figure 3b). No individual taxon drove differences between AgriCats in perennial reaches (all SIMPER < 5% and/or $p > 0.05$), suggesting concurrent responses of multiple taxa as driving community variability. Functional variability was unaffected by AgriCat in temporary (estimate ± SE < 0.01 ± 0.01, $p = 0.884$, $R^2\mathrm{M} = 0.317$, Figure 3c) and perennial (estimate ± SE = 0.01 ± 0.01, $p = 0.299$, Figure 3) reaches.

3.2 | H2. The Effect of Agriculture on Differences in Community Variability Between Temporary and Perennial Reaches

Taxonomic variability was higher in temporary reaches than perennial reaches in high ($p < 0.001$, $R^2\mathrm{M} = 0.471$, $R^2\mathrm{C} = 0.561$, Figure 4a) and low ($p < 0.001$, Figure 4b) AgriCats, although differences in variability were less pronounced in high (estimate ± SE = 0.08 ± 0.02) than low (0.20 ± 0.02) AgriCat reaches. Functional variability was higher in temporary than perennial reaches in high ($p < 0.001$, $R^2\mathrm{M} = 0.293$, $R^2\mathrm{C} = 0.319$, Figure 4c) and low ($p < 0.001$, Figure 4d) AgriCats. Differences in functional variability between FlowCats were comparable (both estimate ± SE: 0.04 ± 0.01) in both AgriCats. No individual taxon

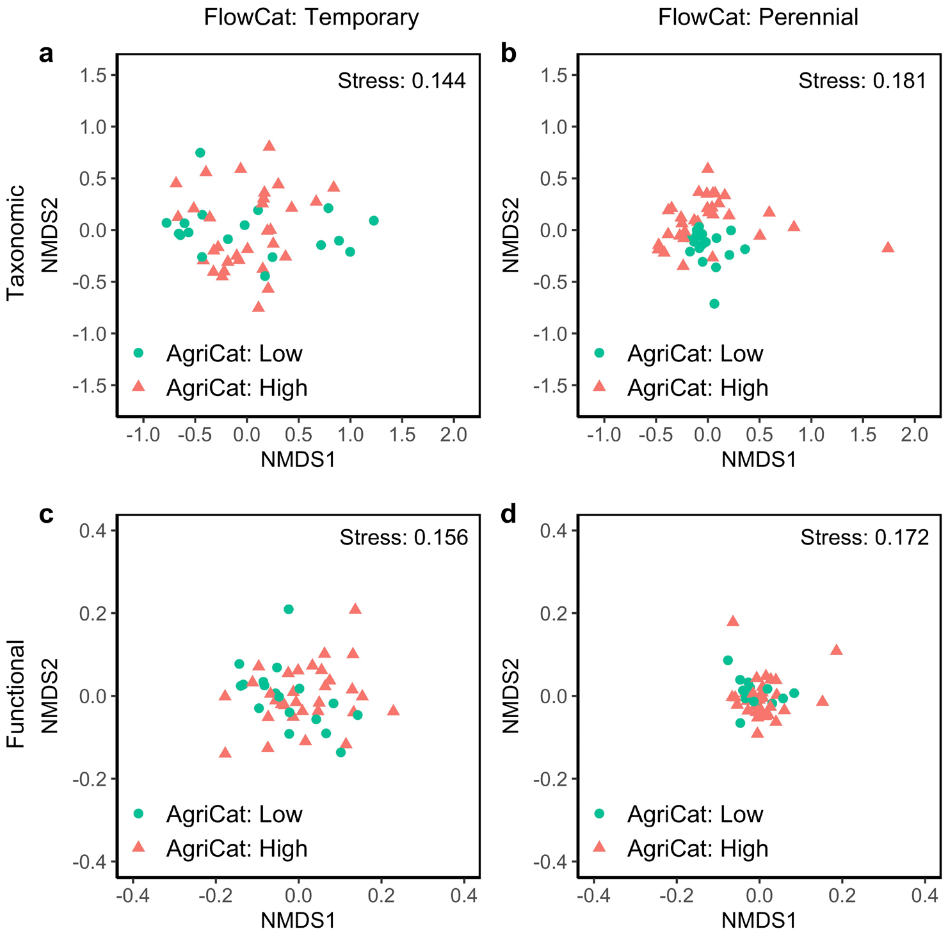

FIGURE 3 | Non-metric multidimensional scaling (NMDS) ordination of taxonomic (a, b) and functional (c, d) variability in relation to agricultural land use categories (AgriCats) in temporary (a, c) and perennial (b, d) reaches. (a) NMDS1 and NMDS2 of a three-dimensional ordination; see Figure S1 for plots of NMDS1 and NMDS2 against NMDS3.

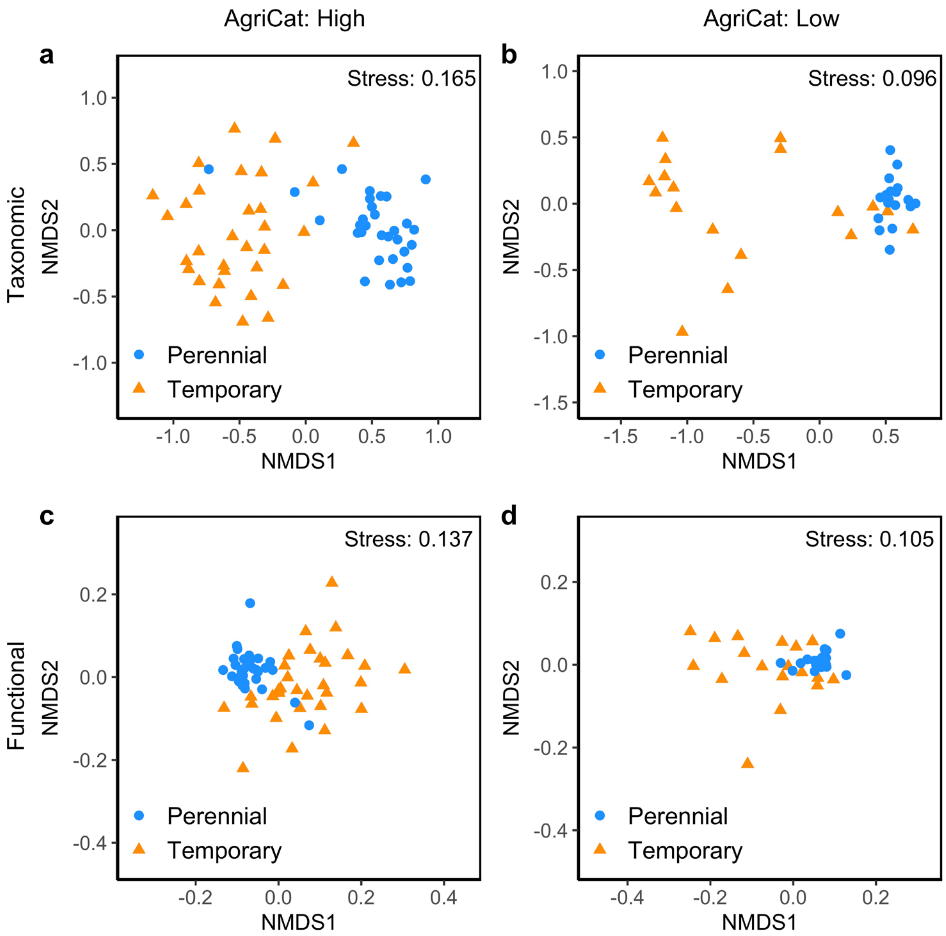

FIGURE 4 | Non-metric multidimensional scaling (NMDS) ordination of taxonomic (a, b) and functional (c, d) variability in relation to flow categories in high (a, c) and low (b, d) agricultural land use category (AgriCat) reaches.

or trait drove differences between FlowCats (all SIMPER: $<5\%$ and/or $p > 0.05$).

3.3 | H3. The Effect of Agriculture on the Occurrence of Temporary Stream Specialists

AgriCat did not significantly influence the occurrence of any specialist species ($p = 0.205$–0.337, $R^2\text{M} = 0.023$–0.040, $R^2\text{C} = 0.184$–0.679, Figure 5), although the occurrence of *P. werneri* and *N. cinerea* was moderately higher in high AgriCat reaches (number of occurrences in low: high AgriCat samples: 3:9 and 6:16, respectively). All four other taxa associated with temporary reaches were recorded more frequently in high AgriCat, and this association was significant for the bivalve *Pisidium personatum* ($p = 0.031$, $R^2\text{M} = 0.079$, $R^2\text{C} = 0.630$) and the blackfly group *Simulium aureum* ($p < 0.001$, $R^2\text{M} = 0.063$, $R^2\text{C} = 0.579$, Figure 5). Five of the 21 taxa associated with perennial reaches were affected by AgriCat. The mayfly *Baetis muticus* ($p = 0.042$, $R^2\text{M} = 0.264$, $R^2\text{C} = 0.276$) was associated with high AgriCat, whereas the mayflies *Ecdyonurus dispar* ($p = 0.016$, $R^2\text{M} = 0.148$) and *Caenis rivulorum* ($p = 0.028$, $R^2\text{M} = 0.141$, $R^2\text{C} = 0.445$), the caddisfly *Mystacides azurea* ($p = 0.002$, $R^2\text{M} = 0.294$, $R^2\text{C} = 0.325$) and the gastropod *Physa fontinalis* ($p = 0.009$, $\text{R}^2\text{M} = 0.226$) occurred more frequently in low AgriCat samples (Figure 5).

4 | Discussion

Despite agricultural land use being one of the most prevalent causes of environmental degradation in river ecosystems (Pereira et al. 2010), and despite temporary streams dominating global river networks (Messager et al. 2021), few studies have characterised agricultural impacts on temporary stream biodiversity. We assessed the effects of co-occurring stream drying and agricultural pressure on variability in macroinvertebrate communities. Taxonomic and functional variability among communities in temporary reaches were unaffected by agriculture, whereas community variability in perennial reaches was higher in reaches with more agriculture, supporting our first hypothesis (H1) and suggesting that adaptations to drying promote co-tolerance of agriculture among temporary stream communities (Storey 2016; Loskotová et al. 2023). Taxonomic and functional communities were more variable in temporary reaches relative to perennial reaches regardless of agriculture, contrary to H2. The consistently higher variability among temporary stream communities suggests that drying may be a stronger influence on aquatic communities than agricultural land use (Leigh and Datry 2017). The occurrence of temporary stream specialist species was unaffected by agriculture, supporting H3 and suggesting that such specialists may live in a wide range of natural to impacted temporary habitats (e.g., Chalkley 2006; Salmela and Savolainen 2013; Tapia et al. 2018).

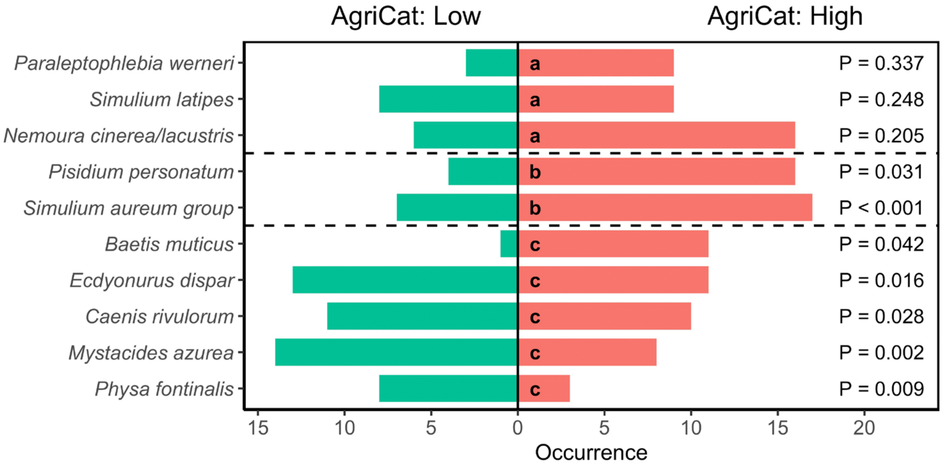

FIGURE 5 | The occurrence of temporary stream specialists (a), and taxa with a similar association with temporary (b) and perennial (c) reaches in the low (green) and high (red) agricultural land use categories (AgriCat). P values denote the significance of associations between each species and either AgriCat.

4.1 | H1. Community Responses to Agriculture in Temporary and Perennial Reaches

Temporary reach communities were comparably variable regardless of agricultural land use, supporting H1 and likely reflecting the hypothesised adaptations to drying that promote tolerance of other pressures (e.g., agriculture: Storey 2016; Loskotová et al. 2023). For example, both drying and agriculture can reduce dissolved oxygen concentrations (Gómez et al. 2017; dos Reis Oliveira et al. 2019), and thus taxa that tolerate low dissolved oxygen survive in temporary streams (Pardo and García 2016; Straka et al. 2019), streams impacted by agricultural pollution (e.g., nutrient enrichment: Kazanci and Başören 2010; Başören and Kazanci 2012) and potentially streams exposed to both pressures (e.g., Jones et al. 2023). In contrast to communities in temporary reaches, communities in high AgriCat reaches with perennial flow typically comprised fewer taxa that tolerate agricultural stressors. These results suggest that communities were filtered by site-specific sets of agricultural stressors, resulting in higher among-site variability in high compared to low AgriCat perennial reaches (Genito et al. 2002).

Like taxonomic variability, the functional variability of communities in temporary reaches was comparable regardless of agriculture. This functional co-tolerance likely arises because the predictable, seasonal flow patterns in the study streams (Berrie 1992; Sear et al. 1999) promote functional redundancy (i.e., communities of taxa with similar functional traits: Boersma et al. 2014; Vander Vorste et al. 2016) and because drying promotes co-tolerance of agriculture among their communities (Storey 2016). Thus, traits that promote tolerance of drying allow temporary stream communities to maintain a comparable state of variability when additional pressures (e.g., agriculture) are applied.

The functional variability of communities in perennial reaches was comparable between AgriCats, suggesting that—as in temporary reaches—perennial reach communities have functional redundancies that promote their tolerance of agriculture. However, the greater taxonomic variability among communities in high AgriCat perennial reaches suggests that their functional redundancy is due to a subset of generalist taxa which can tolerate agriculture. The cumulative effect of multiple, intensifying pressures (e.g., abstraction, sewage pollution, climate change: Palmer-Felgate et al. 2008; Watts et al. 2015; White et al. 2018) may result in increased functional variability and a loss of taxa and traits from perennial sites, with potential consequences throughout the river network (Datry et al. 2023). For example, nearby perennial reaches supply colonists to temporary reach communities (Fournier et al. 2023) and a change in the number and identity of colonists from perennial reaches may influence both the composition and compositional variability of communities in temporary reaches.

4.2 | H2. The Effect of Agriculture on Differences in Community Variability Between Temporary and Perennial Reaches

Taxonomic and functional variability were higher in temporary reaches than perennial reaches regardless of agriculture, contrary to H2. The consistently higher variability among temporary reaches possibly reflects that different flow durations (i.e., 2–34 months) and likely differing drying intensities filtered communities to site-specific assemblages that can tolerate site-specific hydrological conditions (Storey 2016; Arias-Real et al. 2022). Although more variable than perennial reaches, temporary reach communities shared a co-tolerance of agriculture (see H1). Thus, the effects of drying were observed regardless of agriculture, suggesting that drying is a core driver of community variability (Leigh and Datry 2017). Communities in perennial reaches were more variable in high relative to low AgriCat (see H1), and thus differences in variability between temporary and perennial reach communities were less pronounced in high AgriCat, as per H2. Again, this likely reflects that agriculture filtered communities to site-specific assemblages and thus increased among-site variability in high AgriCat. Differences in functional variability between communities in temporary and perennial reaches were comparable regardless of AgriCat, further supporting that agricultural pressure is secondary relative to drying effects.

4.3 | H3. The Effect of Agriculture on the Occurrence of Temporary Stream Specialists

The temporary stream specialists *Paraleptophlebia werneri*, *Simulium latipes* and *Nemoura cinerea* (likely including records of *Nemoura lacustris*) occurred in temporary reaches regardless of agriculture, supporting H3. The other four taxa that were almost exclusive to temporary streams all occurred more frequently in high AgriCat reaches, two of which (*Pisidium personatum* and *Simulium aureum* group) were significantly associated with high AgriCat, suggesting that—as for the wider community—their adaptations to drying promote co-tolerance of agriculture (Storey 2016; Loskotová et al. 2023). Temporary stream specialists such as *N. lacustris* and *P. werneri* occur in habitats ranging from springs (Biondi et al. 2022; Kabir et al. 2024) to perennial ponds (Salmela and Savolainen 2013) and temporary agricultural ditches (Chalkley 2006), as well as being widespread in temporary streams (Tapia et al. 2018; Bunting et al. 2021). Thus, temporary stream specialists may tolerate a broad spectrum of environmental conditions, including drying (Sarremejane et al. 2019).

For aquatic macroinvertebrates, drying equates to increasingly harsh physicochemical conditions, increased competition for space and resources, and increased risk of predation (Stubbington et al. 2011b; Gómez et al. 2017; von Schiller et al. 2017). Thus, drying can leave stretches of a river network uninhabitable for species that cannot tolerate such conditions. This exclusion of drying-sensitive species may promote the survival of temporary stream specialists by reducing competition and predation (House and Tapia 2014; Aspin and House 2022). By this mechanism, temporary stream specialists may prefer minimally impacted (i.e., non-agricultural) or even perennial (Prenda and Gallardo-Mayenco 1999) sites, but may be excluded from such reaches by their competitors and/or predators. Despite this potential exclusion from their preferred habitats, adaptations to drying make temporary stream specialists co-tolerant of other pressures, promoting their survival in numerous aquatic habitats (e.g., Chalkley 2006; Salmela and Savolainen 2013; Tapia et al. 2018) with a range of hydrological, morphological, and physicochemical conditions (e.g., Prenda and Gallardo-Mayenco 1999; Errochdi et al. 2014; Vilenica et al. 2021).

5 | Implications for Monitoring and Further Research

Pressures influencing an ecosystem are often hierarchical, with a dominant pressure overriding most or all of the influence of subordinate pressures (*sensu* Côté et al. 2016; Barrett et al. 2023). For example, water quality can be dominant, attenuating the effects of climatic warming (Durance and Ormerod 2009) and catchment land uses (Villeneuve et al. 2018). Our results suggest drying ranks higher than (i.e., is dominant over) agriculture in this pressure hierarchy. Dominant, higher-level pressures may promote tolerance of subordinate pressures, with communities adapted to drying being better equipped to tolerate agriculture (Storey 2016; Loskotová et al. 2023). Equally, rankings may change over time, with the influence of drying declining as flowing phases extend, resulting in the communities in perennial and temporary streams becoming increasingly comparable (Bonada et al. 2007). However, the community's capacity for co-tolerance in the face of novel and intensifying pressures remains unclear (Reid et al. 2019).

In our study, temporary reaches were consistently upstream of perennial reaches, whereas the position of AgriCats varied from upstream to downstream (Figure 2). Upstream reaches typically have higher intra-site variability (Finn et al. 2011; Kabir et al. 2024), because their relative isolation means their communities are shaped by the available colonists and site-specific conditions (e.g., flow permanence regime, land use and associated impacts on sediment composition, etc.). Thus, our finding that flow regime is of greater importance than agriculture in shaping aquatic communities is consistent with previous studies (e.g., Leigh and Datry 2017), but further research is required to determine the positions of flow permanence and site isolation in the pressure hierarchy.

Temporary stream specialists are widespread, both geographically and in terms of the habitats they occupy (e.g., Bogan et al. 2017; Gething et al. 2021; Gething 2024). Here, the co-tolerance of agriculture by species including *N. cinerea* and *P. werneri* challenges their grouping with congeners (i.e., within the Nemouridae and Leptophlebiidae) that have higher dissolved oxygen requirements, and which are less tolerant of agriculture and other human pressures (Paisley et al. 2014).

Conceptually, complex multi-level hierarchies govern community dynamics and the distribution of specialist species throughout river networks (Barrett et al. 2023), and thus limit the effectiveness of biomonitoring activities which aim to detect human impacts in temporary streams (Buffagni et al. 2009; Wilding et al. 2018; Stubbington et al. 2022). A greater understanding of how existing, intensifying, and emerging stressors will interact to alter the pressure hierarchy and thus influence aquatic communities could inform actions designed to support the resilience of riverine ecosystems in a period of unprecedented environmental change.

Author Contributions

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All environmental and ecological data used in the study are available from Wessex Water Services Ltd. upon request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.