





Working 9 to 5: Diurnal Variability in Terrestrial Invertebrate Activity Does Not Compromise Ecosystem Health Assessments in Dry Stream Channels

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ABSTRACT

Temporary streams are impacted by climate change and other anthropogenic pressures, but fluctuating water levels complicate ecological assessments. Terrestrial invertebrate communities may enable dry-phase assessments, but their sampling can be resource intensive. We assessed diurnal variability in the capacity of two methods (hand searching and pitfall trapping) to rapidly characterise terrestrial invertebrate assemblages and their responses to environmental conditions when channels are dry. The methods provided comparable estimates of richness and abundance at any time of day (i.e., morning, midday and evening), and among sites with different dry-phase durations, air temperatures and proportions of fine sediment. Differences in taxonomic assemblage composition were detected among sites with differing dry-phase durations, air temperatures and proportions of fine sediment, suggesting that the effects of natural and human-influenced environmental stressors can be detected despite intermittence. Assemblage composition differed between methods, but not among times of day, suggesting diurnal activity patterns need not hinder assemblage characterisation in dry streams. Taxon-specific preferences for dry-phase duration, silt and sand suggest that biomonitoring indices which distinguish the influence of drying from human impacts could be developed. Monitoring over shorter periods may provide managers, regulators and citizen scientists with opportunities to increase the representation of terrestrial assemblages in ecosystem health assessments for temporary streams.

1 | Introduction

Temporary streams, which alternate between wet and dry phases, are the world's dominant lotic ecosystem type (Messager et al. 2021) and are becoming more common due to climate change and direct anthropogenic pressures including abstraction (Chiu et al. 2017; Sauquet et al. 2021; Zipper et al. 2024). The occurrence of wet and dry phases mean that temporary stream communities include aquatic and terrestrial fauna (Corti and Datry 2016; Stubbington et al. 2017; Steward et al. 2022), both

of which require inclusion in holistic assessments of stream health (Stubbington et al. 2017, 2018; Gething 2024). However, fluctuating water levels complicate assemblage sampling in temporary streams (i.e., aquatic sampling methods cannot be applied in the dry phase and vice versa). As a result, temporary stream communities are often excluded from biomonitoring programmes, especially terrestrial assemblages during dry phases (Stubbington et al. 2019). Thus, the effectiveness of in-channel dry-phase sampling methods and how terrestrial assemblages may be more readily characterised remains unclear.

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As temporary streams dry, their channels are rapidly colonised by terrestrial invertebrates, which form communities that are taxonomically diverse and responsive to a range of environmental stressors, making them effective biomonitors (Maelfait and Hendrickx 1998; Rainio and Niemelä 2003; Koivula 2011). For example, ground beetles (family: Carabidae) are common in riverine environments including dry streams (e.g., Steward et al. 2011; Gething 2025a), and their distributions are influenced by variables such as shade (Thiele 1977), sediment composition (Eyre et al. 2001; Baiocchi et al. 2012), the availability of food (O'Callaghan et al. 2013; Gething 2025b) and water (Bates et al. 2007), and the duration of a dry phase (Rosado et al. 2015; Bunting et al. 2021). Additionally, in-channel activity patterns are moderated by diurnal/diel cycles, and associated light and temperature changes (Luff 1978; Tuf et al. 2012). Natural and anthropogenic variation in these factors influences speciesspecific movement within/into/out of the channel (Bates et al. 2006; Kolesnikov et al. 2012; Langhans and Tockner 2014), and thus assemblage composition. Any characterisation of the relationships between terrestrial invertebrate assemblages and human pressures may thus also need to represent intermittence and short-term (e.g., diurnal) variability.

Terrestrial invertebrate assemblages are typically sampled from ecosystems including dry streams using hand searching and/or pitfall trapping (e.g., Corti and Datry 2016; Sánchez-Montoya et al. 2016). Pitfall traps are typically left in place for 7–28 days and primarily collect ground-dwelling species (Siewers et al. 2014), whereas hand searches often last 20–60 min (Webb et al. 2022) and capture more taxa that are capable of flight (Alexander 2014; Bunting et al. 2021). Thus, the concurrent use of both methods maximises the number of taxa captured (Andersen 1995; Gobbi et al. 2018; Webb et al. 2022). However, temperature-driven fluctuations in invertebrate activity (Tuf et al. 2012; Saska et al. 2013) may lead these methods to sample different taxa during hotter/cooler part of the day. Therefore, the time of day may influence characterisations of terrestrial assemblages and thus impact inferences of ecosystem health.

Citizen scientists can increase the collection of data used to assess ecosystem health, and can produce high-quality datasets that rival those collected by professionals (Kosmala et al. 2016). However, the taxonomic richness of terrestrial invertebrates means that identifying all groups to lower (i.e., family, genus or species) taxonomic levels is challenging, time-consuming and potentially expensive. Thus, determining an identification level that balances sufficient characterisation of terrestrial assemblages and their responses to environmental conditions with surveyors' time and skills could promote more frequent and widespread dry-phase biomonitoring (Hayes 2022).

We assessed diurnal variability in the capacity of hand searching and pitfall trapping to characterise terrestrial invertebrate assemblages and their responses to variation in environmental conditions in dry stream channels. We hypothesised that: (H1) diurnal variability in environmental conditions (e.g., temperature) and associated changes in invertebrate activity alter assemblage characterisation; and (H2) methods can distinguish assemblage responses to environmental stressors indicative of human activity despite the effects of drying. For each hypothesis,

we also assessed the influence of the taxonomic identification level on characterisation of assemblages and their responses to environmental conditions.

2 | Method

2.1 | Study Area

We conducted this study in Hampshire, UK, which has a temperate oceanic climate (Cfb: Kottek et al. 2006) with mean \pm SD annual minimum and maximum air temperatures of $6.1^{\circ}\text{C} \pm 3.9^{\circ}\text{C}$ and $15.0^{\circ}\text{C} \pm 5.7^{\circ}\text{C}$, respectively and mean annual rainfall of 754 mm (Met Office 2022). The area is underlain by a chalk aquifer, meaning that surface stream flows are controlled primarily by seasonal fluctuations in groundwater levels (Sear et al. 1999). When groundwater levels are low, the upper reaches of many streams dry out (Berrie 1992; Sear et al. 1999), typically between late spring and mid-autumn.

During July 2022, we sampled three (upper, middle, lower) sites with temporary flow regimes on each of two streams, Bourne Rivulet and Candover Brook. Their catchments have a comparable amount of arable (Bourne Rivulet and Candover Brook: 50.4% and 51.4%), grassland (mostly pasture: 29.0% and 28.4%), woodland (13.5% and 14.1%) and urban/suburban (3.4% and 4.0%) land cover (National River Flow Archive 2022a, 2022b). We defined each sampling site as an approx. 20-m channel length in which habitat characteristics represented the wider reach. The Bourne Rivulet lower and middle sites and middle and upper sites were separated by 1.2 and 3.6 km, respectively. The Candover Brook sites were separated by 0.9 and 2.0 km, respectively. Site locations were selected based on Environment Agency observations which indicated that the upper, middle and lower sites on the Bourne Rivulet and their corresponding Candover Brook sites typically dry at a similar time (i.e., ±1 week). Sites on both streams dry from upstream to downstream and, at the time of sampling, had been dry for 1-6 weeks. All sites are in or <350 m downstream of pastures, and livestock have direct access to the channel. The sites receive runoff from roads and agricultural land during flowing phases, and are mown during dry phases.

2.2 | Data Collection

To characterise site-specific environmental conditions that may be influenced by human activities, we visually estimated the relative proportions of each sediment grain-size class (i.e., % gravel, sand and silt) to the nearest 5%. We visually estimated shade (% cover to the nearest 10%), and recorded relative humidity (%) and air temperature (°C) at three equidistant points along the channel bed.

At each site, we sampled terrestrial invertebrates by hand searching and short-duration (5–6h) pitfall trapping. We conducted 30-min hand searches in three periods: early morning (06.00–07.30), at midday (12.00–13.00) and early evening (17.00–18.30). Hand searches involved manual disturbance of all habitats between the base of the banks in a 10-m long channel section and collection of

all observed invertebrates using an aspirator (n=2 streams $\times 3$ sites $\times 3$ time periods $\times 1-2$ samples =25). The number of hand-search samples ranged from three to six per site because sites/sampling periods were attended by one or two samplers, each searching a different longitudinally adjoining section with comparable habitat conditions. We retained all samples to maximise assemblage characterisation and account for the potential variability in our analyses, as detailed in 2.4 Data analysis.

Within 5 m of the hand-search area(s), in a channel section with comparable habitat conditions, we set six pitfall traps (i.e., plastic cups; 8-cm diameter, 10-cm height) in the morning by burying them in the bed, with the cup lip level with surface sediments, and 1/3 filling them with ethylene glycol to preserve trapped organisms. We emptied the pitfall traps at midday and pooled the contents of the six cups into one 'morning' sample. We then reset the traps at midday and collected them in the evening following the same procedure, creating one 'afternoon' sample (total n=12, i.e., one morning and one afternoon sample per site). We identified invertebrates to the lowest practical resolution, with 23%, 1%, 52% and 24% of individuals identified to species, genus, family and order, respectively.

2.3 | Data Preparation

To avoid artificially altering assemblage composition, we assigned taxa identified to multiple levels (e.g., *Porcellio scaber* and *Porcellio*) to the single most likely taxon (*sensu* Cuffney et al. 2007). The triplicate humidity and temperature readings were used to calculate a mean summarising sample-specific conditions.

To test H1–2, we calculated taxa richness (the number of taxa per sample) and activity density (the number of individuals per sample, hereafter 'abundance': see Adis 1979), and summarised taxonomic assemblage composition (i.e., taxa abundance per sample, hereafter 'taxa composition') as a log+1 transformed Bray-Curtis dissimilarity matrix. To characterise the influence of taxonomic resolution, we also calculated family richness (the number of families or higher taxa per sample, where the higher taxon was morphologically distinct, e.g., Hymenoptera other than Formicidae) and order richness (the number of orders per sample). We summarised family and order-level assemblage composition using a method comparable to that described for taxa composition.

2.4 | Data Analysis

To assess diurnal variability in response variables (i.e., taxa, family and order richness, and abundance) and their capacity to represent assemblage responses to environmental conditions, we ran linear mixed-effects models (LMM) using the R package lme4 (Bates et al. 2015). To meet model assumptions of residual normality (as tested using the DHARMa package: Hartig 2020), we log+1 transformed the response variables. To account for potential sources of additional variability, we modelled response variables with combinations of two random intercepts (handsearch sampler and stream: see Burnham and Anderson 2002; Brown et al. 2018), and selected the most parsimonious structure using Akaike's information criterion corrected for small sample sizes (AICc). The final structure for richness and abundance

models included catchment and sampler, respectively, as a random intercept. To determine whether the time of sampling influenced captures by pitfall traps and hand searching (H1), we used sampling period, method and their interaction as predictors (i.e., fixed effects).

To test whether assemblage responses to dry-phase duration and environmental variables potentially indicative of human impacts can be distinguished (H2), we used stepwise variance inflation factor analysis to identify collinearity among environmental variables (i.e., each grain-size class, shade, relative humidity and temperature, threshold = 3: Zuur et al. 2010). Silt was negatively and positively associated with gravel and shade, respectively, and temperature was negatively correlated with humidity. Therefore, we excluded gravel, humidity and shade from statistical analyses.

To model the effects of dry-phase duration, we ordered sites from upstream to downstream as a categorical variable (hereafter 'longitudinal position'). Longitudinal position was favoured over a continuous variable (e.g., the absolute distance between sites) because water is a key resource around which terrestrial communities assemble (McCluney and Sabo 2012; Gething et al. 2022), and the longitudinal rate of drying (and thus availability of water) differs between the streams. The final model included longitudinal position to represent dry-phase duration and two-way interactions between longitudinal position and silt, sand and temperature as predictors. For all LMMs, we distinguished the variance explained by the predictors and random factor using marginal (R^2 M) and conditional (R^2 C) R^2 , calculated using the MuMIn package (Bartoń 2020).

To assess diurnal variability in taxa composition and its response to environmental conditions, we ran permutational multivariate analysis of variance (PERMANOVA: Anderson 2017) over 9999 iterations using the vegan package (Oksanen et al. 2019). For both hypotheses, PERMANOVA used a log+1 transformed Bray-Curtis dissimilarity matrix as a response and included a permutation scheme restricted by stream. PERMANOVA predictors followed the structures outlined for LMMs: sampling period, method and their interaction to test H1; and longitudinal position and two-way interactions between longitudinal position and silt, sand and temperature to test H2. To assess the influence of multiple hand-search samplers on compositional analyses, we also ran all PERMANOVAs including only samples collected by the primary hand searcher (who collected samples from all sites during all periods). We report results of analyses of all samples, except where a result differs due to the inclusion of the additional hand-search sampler, in which case we report results of both analyses.

To determine whether significant PERMANOVA results represented true differences in assemblage composition or variation among levels of categorical predictors (i.e., differences in multivariate dispersion among methods, periods and longitudinal positions), we used permutational analyses of multivariate dispersions (PERMDISP2: Anderson 2006). We calculated dispersion within levels of each predictor (e.g., between hand-search samples and between pitfall-trap samples in the method predictor) using the vegan package, and tested for differences in dispersion using a one-way ANOVA.

We quantified the contribution of each taxon to dissimilarity between categorical predictor levels using similarity percentage analysis (SIMPER: Clarke 1993) over 9999 permutations. We considered a taxon as driving differences if SIMPER p < 0.05 and contributions to overall compositional differences were $\geq 5\%$. To test H2, we used Pearson correlation coefficients (r) to characterise relationships between common taxa (i.e., those occurring in ≥ 10 samples) and continuous environmental predictors (i.e., silt, sand and temperature).

We visualised assemblage composition in relation to method, period and longitudinal position using two-dimensional non-metric multidimensional scaling (NMDS) ordinations based on log+1 transformed Bray-Curtis distance matrices over 500 iterations. Continuous environmental predictors were applied to NMDS ordinations using envfit (Oksanen et al. 2019).

We conducted all analyses in R v.4.0.3 (R Core Team 2020).

3 | Results

Environmental conditions varied among streams, longitudinal positions and periods (Table 1). Silt was 40% and 80% of total sediment at lower sites and 20% and 55% at middle sites, being consistently higher in the Candover Brook than the Bourne Rivulet. Upper sites on both streams had the same amount of silt (30%). Sand comprised 10% and 20% of sediment at lower and 20% and 40% of sediment at upper sites, being higher in the Bourne Rivulet. At middle sites, sand made up 20% and 40% of total sediment, being higher in the Candover Brook.

We recorded 1768 individuals from 72 taxa, with a mean \pm SD of 11.6 ± 4.0 taxa and 47.8 ± 29.2 individuals per sample. The most abundant orders were Coleoptera (beetles: 432 individuals, 24.4% of total abundance), Araneae (spiders: 331, 18.7%) and Hymenoptera (sawflies, wasps, bees and ants: 259, 14.7%: Figure 1).

TABLE 1 | Mean ± SD air temperature, relative humidity and shade at all sites, Bourne Rivulet and Candover Brook sites, sites at lower, middle and upper longitudinal positions and during morning, midday and evening sampling periods.

		Air temperature (°C)	Relative humidity (%)	Shade (%)
Streams	All sites	22.2±5.5	59.4 ± 14.7	56.7 ± 35.8
	Bourne Rivulet	22.3 ± 5.4	59.0 ± 15.6	33.3 ± 30.8
	Candover Brook	22.0 ± 5.9	59.8 ± 14.6	80.0 ± 23.5
Longitudinal positions	Lower	22.4 ± 5.1	61.6 ± 13.7	66.7 ± 44.6
	Middle	20.9 ± 6.0	61.5 ± 19.1	48.3 ± 46.2
	Upper	23.2 ± 6.2	55.2 ± 12.1	55.0 ± 5.5
Sampling periods	Morning	15.6 ± 2.9	77.0 ± 7.6	53.3 ± 42.7
	Midday	25.2 ± 2.7	52.0 ± 8.0	65.0 ± 32.7
	Evening	25.7 ± 2.9	49.3 ± 7.1	51.7 ± 36.6

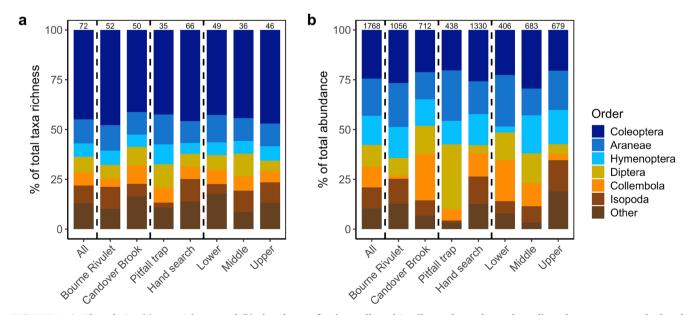


FIGURE 1 | The relative (a) taxa richness and (b) abundance of orders collected in all samples and samples collected per stream, method and longitudinal position. Values at the top of each bar represent the number of taxa/individuals. [Color figure can be viewed at wileyonlinelibrary.com]

3.1 | H1. Diurnal Variability of Sampling Methods

Taxa richness was comparable between pitfall-trap and hand-search samples ($p\!=\!0.911$: Figure 2a), and among sampling periods ($p\!=\!0.142\!-\!0.843$, $R^2M\!=\!0.115$, $R^2C\!=\!0.268$: Figure 2c), contrary to H1. Neither method nor period affected richness at the taxa, family or order level (all $p\!>\!0.05$: see Supporting Information—H1). Similarly, abundance was comparable between methods ($p\!=\!0.770$: Figure 2b) and among periods ($p\!=\!0.059\!-\!0.611$, $R^2M\!=\!0.072$, $R^2C\!=\!0.419$: Figure 2d).

Taxa composition differed between hand-search and pitfall-trap samples (PERMANOVA: F (1)=4.059, p<0.001, R^2 =0.108), with assemblages being more consistently characterised by pitfall trapping (PERMDISP2: F (1)=31.089, p<0.001: Figure 3a). Differences between methods were

driven by adult Diptera (SIMPER: 12.9% of dissimilarity, p < 0.001), which were captured more frequently by pitfall trapping (mean \pm SD individuals per sample: 11.7 \pm 6.2) than hand searching (1.8 \pm 2.0). Hand-search samples plotted in two areas (Figure 3a): those with negative NMDS1 scores were collected from four sites (upper Candover Brook and all Bourne Rivulet sites) with less shading (mean \pm SD: 34% \pm 26%) and silt $(28\% \pm 7\%)$ than samples with positive NMDS1 scores $(96\% \pm 7\% \text{ and } 71\% \pm 13\%, \text{ respectively})$. For both methods, taxa composition was unaffected by sampling period (F(3) = 0.550,p = 0.91, $R^2 = 0.044$: Figure 3b), contrary to H1. Dispersion was comparable among periods for pitfall trapping (p = 0.644) and hand searching (p = 0.332 - 0.882). Family and order level compositional responses to method (PERMANOVA: p < 0.001) and period (PERMANOVA p > 0.05) were comparable to taxalevel responses (Supporting Information—H1).

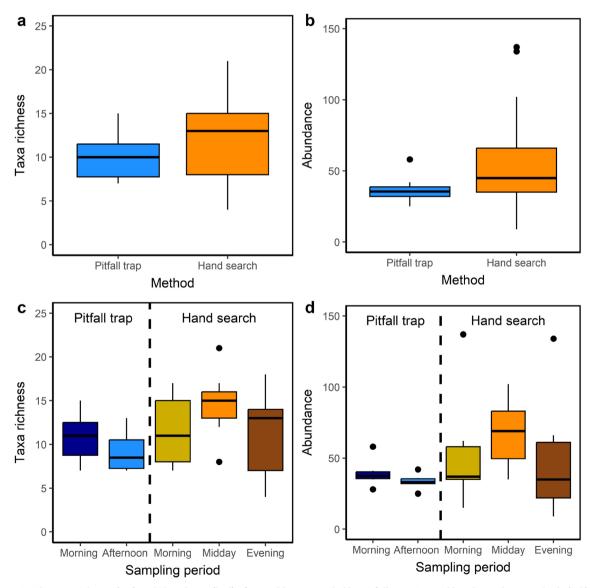


FIGURE 2 | The taxa richness (a, c) and abundance (b, d) of assemblages sampled by pitfall trapping and hand searching methods (a, b), by pitfall trapping in the morning and afternoon, and by hand searching in the morning, midday and evening periods (c, d). The centre line represents the median, boxes represent the interquartile range, whiskers represent the minimum/maximum values which are within 1.5× the interquartile range of the first and third quartiles and filled circles represent outliers. [Color figure can be viewed at wileyonlinelibrary.com]

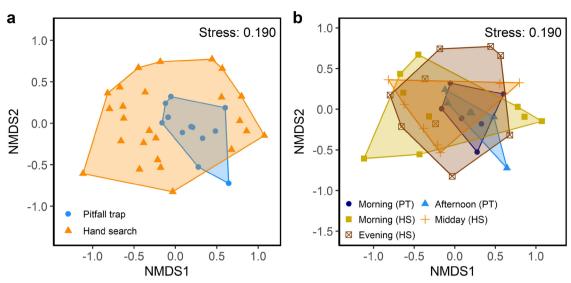


FIGURE 3 | Non-metric multidimensional scaling (NMDS) of taxa composition sampled (a) by hand searching and pitfall trapping, and (b) by pitfall trapping (PT) in the morning and afternoon, and by hand searching (HS) in the morning, midday and evening sampling periods. [Color figure can be viewed at wileyonlinelibrary.com]

3.2 | H2. Responses to Human-Influenced Stressors Despite Drying

Contrary to H2, longitudinal position (a proxy for dry-phase duration), silt, sand and temperature had no effect on taxa richness (all p = 0.095 - 0.978, $R^2M = 0.255$, $R^2C = 0.613$: Figure 4), abundance (all p = 0.157 - 0.745, $R^2M = 0.217$, $R^2C = 0.487$: Figure 5), family richness or order richness (all p > 0.05: Supporting Information—H2).

Taxa composition, but not dispersion, differed between upper, middle and lower sites (PERMANOVA: F(2)=5.697, p<0.001, $R^2=0.198$, PERMDISP2: F(2)=2.059, p=0.143: Figure 6a). Compositional differences between upper and middle sites were caused by the spider family Lycosidae (SIMPER: 8.3% of dissimilarity, p<0.001, Table 2), whereas differences between middle and lower sites were caused by the spider family Linyphiidae (8.1%, p=0.026), the beetle family Staphylinidae (7.0%, p=0.003) and adult Diptera (10.1%, p=0.029, Table 2). Differences between upper and lower sites were driven by Lycosidae (9.8%, p<0.001), Linyphiidae (7.8%, p=0.046) and the millipede family Craspedosomatidae (6.2%, p=0.008, Table 2). Taxa, family and order-level composition responded comparably to longitudinal position (Supporting Information—H2).

Silt and temperature influenced taxa composition (PERMANOVA: F $(1) = 3.080 - 8.033, \quad p = < 0.001 - 0.004,$ $R^2 = 0.053 - 0.139$: Figure 6b), offering some support for H2, but sand had no effect $(F(1)=2.269, p=0.079, R^2=0.039)$. Longitudinal position did not interact with silt, sand or temperature to influence composition (p = 0.139 - 0.206). Silt positively correlated with springtail (Collembola) abundance (Pearson's r = 0.520, p = 0.001, n = 28), and negatively correlated with Lycosidae (r=-0.453, p=0.005, n=21) and Formicidae (ant, r=-0.436, p=0.007, n=23) abundance. The abundance of Lycosidae and the isopod P. scaber was positively correlated with sand (r=0.403, p=0.013, n=21 and r=0.361, p=0.028,n=15, respectively). The abundance of no taxon correlated with temperature. Taxa, family and order-level composition responded comparably to silt, sand and temperature (Supporting Information—H2). Based on data collected by only the primary hand searcher, no relationship between temperature and taxa composition was detected (F(1)=1.920, p=0.066, $R^2=0.043$).

4 | Discussion

We assessed the effectiveness of two rapid sampling methods for characterising terrestrial invertebrate assemblages, and their responses to environmental variables indicative of human impacts in dry temporary streams. Based on univariate metrics (i.e., richness and abundance), both hand-searched and pitfalltrapped assemblages were comparable in all sampling periods, and among sites at different longitudinal positions (a proxy for dry-phase duration), silt, sand and temperatures, contrary to H1 and H2. This comparability suggests these metrics may be insufficient to detect the effects of natural and human-influenced environmental stressors on dry-phase assemblages. Assemblage composition differed between methods, but not among sampling periods, suggesting diurnal activity patterns (e.g., those driven by temperature changes: Tuf et al. 2012) need not hinder assemblage characterisation in dry temporary streams, contrary to H1. Differences in assemblage composition were detected among sites with differing dry-phase durations, silt, sand and temperatures, suggesting that the effects of natural and humaninfluenced environmental stressors can be detected despite the effects of dry-phase duration (supporting H2).

4.1 | H1. Differences in Captured Assemblages Between Methods and Sampling Periods

The richness, abundance and composition of invertebrate assemblages captured was comparable in all periods, contrary to H1 and suggesting that samples collected at any time of day may provide comparable assemblage characterisations, despite

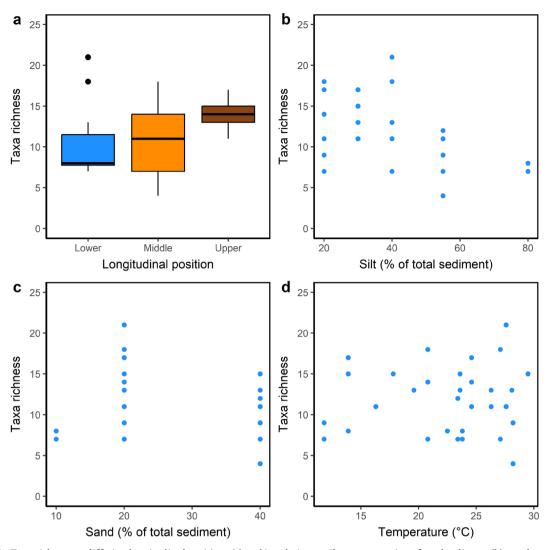


FIGURE 4 | Taxa richness at differing longitudinal positions (a) and in relation to silt as a proportion of total sediment (b), sand as a proportion of total sediment (c) and air temperature at the channel bed (d). [Color figure can be viewed at wileyonlinelibrary.com]

potential responses to diurnally variable environmental conditions (e.g., temperature: Tuf et al. 2012; Saska et al. 2013). The lack of diurnal differences among pitfall-trapped assemblages may partly reflect that the consecutive morning and afternoon samples captured similar assemblages around midday. In contrast, hand searches were more temporally distinct, being conducted for 30 min in the morning, at midday and in the evening, and thus their comparable assemblages are likely a truer representation of the in-channel communities present at different times of day. Their comparability may reflect the relatively high air temperatures (i.e., consistently above 11°C), which correlate with higher development rates, activity and hunting by many terrestrial invertebrates (Tuf et al. 2012; Vangansbeke et al. 2015; Fricke et al. 2022), allowing individuals to become and remain active from morning to evening. Similarity among sampling periods may also have been influenced by the 76% of individuals identified to family or above, obscuring differences that a finer taxonomic resolution could have detected. However, invertebrate responses are typically consistent between species and family level (Pik et al. 1999; Timms et al. 2013) and no taxon from groups that were identified to species or genus (e.g., Carabidae) was influential in driving overall dissimilarity.

Richness and abundance were comparable between hand searched and pitfall trapped assemblages, suggesting—subject to comparable sampling effort—either method may provide similar estimates of such metrics, which could be used for basic comparisons between sites or habitats (Fleishman et al. 2006). A lack of consistent differences in metrics between methods is commonly reported (e.g., Zanetti et al. 2016; Privet et al. 2020) and the observed comparability in this study may reflect an incidental comparability of effort between the shorter (0.5 h), active hand searches and the longer (5-6 h), passive pitfall traps. Regardless of cause, comparable richness and abundance values can mask differences in assemblage composition (e.g., Moorhead and Philpott 2013; Croft-White et al. 2021). Thus, inferences of ecosystem health in temporary streams should be made from assemblage composition (or specialist biomonitoring indices that summarise composition) as characterised using a consistent sampling approach (e.g., Webb et al. 2022).

Differences in pitfall-trapped and hand-searched assemblages likely reflect taxon-specific differences in abundance, habitat preferences and biological traits (e.g., Lang 2000; Engel

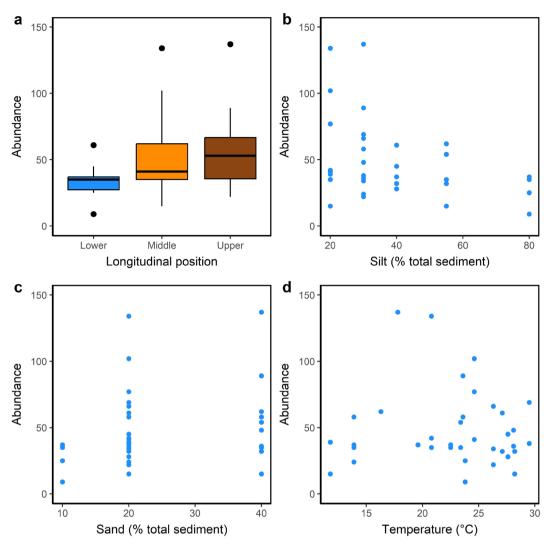


FIGURE 5 | Abundance at differing longitudinal positions (a) and in relation to silt (b), sand (c) and air temperature (d). See Figure 4 for further details. [Color figure can be viewed at wileyonlinelibrary.com]

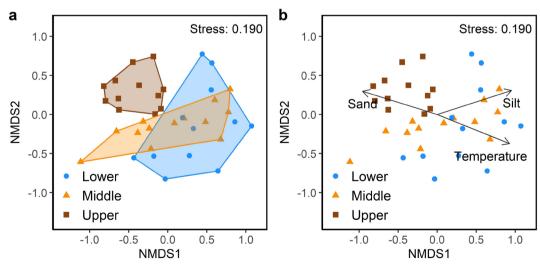


FIGURE 6 | Non-metric multidimensional scaling (NMDS) of taxa composition at sites as lower, middle and upper longitudinal positions (a), and (b) at each position in relation to silt, sand and temperature. [Color figure can be viewed at wileyonlinelibrary.com]

et al. 2017). For example, the taxon responsible for the greatest proportion of dissimilarity (adult Diptera) are motile fliers, making them difficult to collect using aspirators during hand

searches. Thus, a standardised multi-method approach (e.g., Webb et al. 2022) is likely to support comprehensive characterisations of community composition in dry temporary streams.

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TABLE 2 | Mean±SD abundance of taxa contributing to compositional differences among sites with different dry-phase durations, as represented by sites at lower, middle and upper longitudinal positions.

Taxon	Lower	Middle	Upper
Lycosidae	0.6 ± 1.0	2.2 ± 4.6	9.4 ± 5.6
Linyphiidae	7.8 ± 7.0	4.8 ± 5.0	1.8 ± 3.1
Staphylinidae	1.9 ± 2.1	7.8 ± 12.7	2.4 ± 2.1
Diptera (adult)	4.8 ± 6.2	7.5 ± 7.2	2.5 ± 3.2
Craspedosomatidae	0.7 ± 0.9	0.5 ± 0.8	8.6 ± 23.2

However, one method may be sufficient to detect environmental variability attributable to human influences, as demonstrated by the differing composition of hand-searched assemblages from sites with different amounts of shade and silt. Pitfall traps may capture most taxa caught by active searching methods (e.g., hand searching, quadrat sampling) if left in place for longer durations (Corti et al. 2013), and thus may also allow inference of human-caused environmental variability (e.g., Eyre et al. 2001).

4.2 | H2. Distinguishing the Effects of Drying From Human-Influenced Stressors

No differences in assemblage composition caused by environmental conditions were detected by richness or abundance, contrary to H2. Despite such difficulties in distinguishing the effects of drying and other stressors (Stubbington et al. 2022), the influence of dry-phase duration (represented here by longitudinal position) and human-influenced environmental stressors on assemblage composition were detected, supporting H2. The taxa influenced by longitudinal position often differed from taxa influenced by human-influenced environmental stressors, potentially enabling distinction of different environmental effects. For example, spiders were among the most responsive taxa to longitudinal position, with Lycosidae preferring upstream habitats and Linyphiidae preferring downstream habitats. This may reflect that more recent water loss at downstream sites favours Linyphiidae, which may prefer moist sediments (Hayes 2022), prey upon aquatic invertebrates (Power and Rainey 2000; Kato et al. 2004), have a high inundation tolerance (Hayashi et al. 2015) and a greater ability to colonise newly dry habitat (by "ballooning" i.e., aerial dispersal: Adis and Junk 2002; Bell et al. 2005; Blandenier 2009), relative to Lycosidae. Sites with a higher proportion of silt typically supported fewer Formicidae and Lycosidae, likely reflecting their use of interstitial spaces for hunting or shelter from predation and heat (Uetz 1979; Sosiak and Barden 2021).

Biomonitoring indices based on aquatic macroinvertebrate communities are often used to infer the biological impacts of human pressures in river ecosystems (e.g., BMWP, Armitage et al. 1983; WHPT, Paisley et al. 2014). The taxon-specific preferences for longitudinal position, silt and sand detected here highlight that such indices could potentially be developed or existing indices (e.g., Solascasas et al. 2022) adapted to characterise terrestrial assemblage responses to a range of impacts in dry temporary streams.

However, taxa that are responsive to both inundation and other human-impacted environmental conditions (e.g., Formicidae, which respond to inundation and silt: Hertzog et al. 2016) may confound responses to any such index. Thus, further taxa whose responses to human impacts can be detected despite any concurrent response to flow permanence require identification.

4.3 | Implications for Monitoring and Further Study

The capacity of hand-searching and pitfall-trapping methods to distinguish the effect of dry-phase duration from environmental conditions that may be influenced by humans highlights that, like aquatic assemblages and physical habitat characteristics (e.g., Gething et al. 2022; Stubbington et al. 2022; Shuker et al. 2023), terrestrial assemblages have the potential to contribute to ecosystem health assessments (Steward et al. 2018; Marshall et al. 2020; Hayes 2022). However, further research on whether the habitat preferences of terrestrial taxa in riparian and wider habitats are transferable to dry temporary streams is required to enable the development of dry-phase biomonitoring indices that indicate assemblage responses to natural and human-influenced environmental stressors (e.g., moisture availability, nutrient enrichment, channel modification). Further research is also needed on movement within/into/out of dry and drying channels, and the subsequent spatiotemporal arrangement of terrestrial assemblages in temporary streams. For example, terrestrial assemblages remain in distinct lateral zones relative to the waterline during wet phases (Bates et al. 2007), but how long it takes this zonation to breakdown during/after drying is unclear. Additionally, this study considered samples collected throughout the day but many terrestrial invertebrates are nocturnal (e.g., Luff 1978), further highlighting that the spatiotemporal dynamics of terrestrial assemblages during and after drying could be key in determining when, where and how to collect representative samples.

To promote the inclusion of terrestrial assemblages in ecological health assessments, sampling methods should maximise usable ecological information while minimising training and other resource requirements, and thus financial costs (Stenzel et al. 2017; Hoffmann et al. 2019). Differences in the assemblages captured by pitfall trapping and hand searching suggest that both methods are needed to comprehensively characterise dry-phase assemblages (Andersen 1995; Gobbi et al. 2018; Bunting et al. 2021), but our results indicate that one method may be sufficient to indicate ecological health. The greater effort of longer sampling periods more robustly characterises assemblages (Niemelä 1990), as can increasing the spatial, rather than temporal, extent of surveys (e.g., by setting more pitfall traps: Lövei and Magura 2011). Thus, the comparability of samples collected throughout the day suggests that shorter sampling durations (i.e., <1 day) may be applied to characterise terrestrial assemblages and their responses to environmental conditions when longer sampling periods are impractical, with more traps/ searching a wider area having the potential to compensate for these shorter periods (Lövei and Magura 2011).

Taxa, family and order-level information provided consistent support for/against each hypothesis, suggesting that coarser identification levels may be sufficient, enabling samples to be

processed more quickly and with less training. Comparable richness and abundance despite differences in environmental conditions (e.g., dry-phase duration) have been reported in the study region (Bunting et al. 2021). However, such comparability suggests that finer levels of identification may be required to elucidate environment-assemblage relationships, because such metrics do respond to drying and water availability (McCluney and Sabo 2012; Gething et al. 2022), sediment composition (Sadler et al. 2004; Baiocchi et al. 2012), habitat complexity (Shuker et al. 2023; Gething 2024) and temperature (Müller et al. 2015; Liu et al. 2021). Thus, although less comprehensive than longer, spatially extensive multi-method surveys with samples identified to species level, monitoring over shorter periods with an intermediate identification level may provide managers, regulators and citizen scientists with opportunities to incorporate terrestrial assemblages into ecosystem health assessments for temporary streams.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used in this study are available from https://doi.org/10.5281/zenodo.17664078.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. Data S1: rra70082-sup-0001-supinfo. docx. Figure S1: The family (A and C) and order (B and D) richness of assemblages sampled by hand searching and pitfall trapping methods (A and B) and sampled by pitfall trapping in the morning and afternoon, and by hand searching in the morning, midday and evening sampling periods (C and D). The centre line represents the median; boxes represent the interquartile range; whiskers represent the minimum/maximum values which are within 1.5× the interquartile range of the first and third quartiles; filled circles represent outliers. Figure S2: Non-metric multidimensional scaling of terrestrial invertebrate family (A and C) and order (B and D) composition sampled (A and B) by hand searching and pitfall trapping, and (C and D) by pitfall trapping (PT) in the morning and afternoon, and by hand searching (HS) in the morning, midday and evening sampling periods. Figure S3: The family richness sampled at differing longitudinal positions (A) and the

relationships between family richness and silt as a proportion of total sediment (B), sand as a proportion of total sediment (C) and air temperature at the channel bed (D). **Figure S4:** The order richness sampled at differing longitudinal positions (A) and the relationships between family and order richness and silt as a proportion of total sediment (B), sand as a proportion of total sediment (C) and air temperature at the channel bed (D). **Figure S5:** Non-metric multidimensional scaling of terrestrial invertebrate family (A and C) and order (B and D) composition sampled at lower, middle and upper sites (i.e., longitudinal position: A and B), and in relation to longitudinal position, silt, sand and temperature gradients (C and D).