Ecological effects of a supra-seasonal drought on macroinvertebrate communities differ between near-perennial and ephemeral river reaches

Running title: Aquatic macroinvertebrate biodiversity following supra-seasonal drought

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Abstract

The duration, intensity and frequency of hydrological droughts are predicted to increase significantly over the 21^{st} century globally, threatening the long-term stability of lotic communities. In this paper we examine the recovery and recolonization of macroinvertebrate taxa in ephemeral and near perennial reaches of the River Lathkill (UK) after a supra-seasonal drought event. Following flow resumption, species accumulation (recolonization) occurred rapidly over a four-month period, with a steady increase observed thereafter. Taxonomic richness was significantly higher in the section with near perennial flow after the first month of the study than the naturally ephemeral reach. Serial correlation was observed in the near perennial section but not in the upstream ephemeral reach. Serial correlation in the near perennial section may reflect: (1) the ongoing process of recovery or (2) the macroinvertebrate community following a new ecological trajectory. Our results suggest that supra-seasonal droughts may cause initial reductions in lotic diversity during stream desiccation events but may re-set ecological succession and / or temporarily provide new ecological niches, thereby supporting increased taxonomic diversity when the full range of hydrological conditions are considered. Quantifying the recovery of ecological communities following supra-seasonal drought can provide information to help develop ecologically effective conservation and management strategies.

Key words: aquatic conservation, biodiversity, community composition, disturbance, ephemeral streams, lotic habitat.

Introduction

Global climate models predict that the duration, intensity and frequency of drought events are likely to increase significantly over the 21st century (Prudhomme et al. 2014). Climatic variability combined with increasing abstraction pressures and the construction of artificial impoundments to supply increasing human populations globally, is likely to increase the number of waterbodies that experience channel drying (Larned et al. 2010), extend the duration of drying events in waterbodies that already experience dewatering (Benejam et al. 2010; Rahiz and New 2013; Skoulikidis et al. 2017) and lead to significant changes to biological communities, such as the loss of taxa poorly adapted to drying events (Datry et al. 2014).

Supraseasonal drought is defined here as an extended duration of reduced rainfall and surface water availability over multiple seasons or years (Lake 2011). This differs from seasonal drought which is characterised by seasonal reductions in rainfall and water availability, such as those regularly experienced in semi-arid or Mediterranean ecosystems (Gasith and Resh 1999). Extreme, high magnitude but low frequency supra-seasonal events may significantly increase the spatial and temporal extent of stream drying (Boulton 2003; Wood and Armitage 2004) and in some instances affect historically perennially flowing sites (Stubbington et al. 2015).

Surface water drying is a primary determinant of aquatic floral and faunal diversity and community structure in intermittent lotic ecosystems (Lake 2003; Stubbington et al. 2011; Aspin et al. 2018), with streambed drying events commonly being associated with reductions in aquatic diversity (Soria et al. 2017). Following streambed drying, harsh environmental conditions selectively remove taxa which are dependent on surface flow and good water quality (Wood and Petts 1999; Datry et al. 2013) and may cause an increase in faunal densities and competition as habitat availability is reduced (James et al. 2008). However, recovery of flow and the recolonization of aquatic flora and fauna following channel drying in intermittent streams can be rapid, reflecting the range of traits / adaptations which promote resilience and resistance in temporary waterbodies (Fritz and Dodds 2004; Stubbington and Datry 2013; Vander Vorste et al. 2015; Sarremejane et al. 2017). Resistance can be enhanced due to strong dispersal capacity with taxa being able to migrate from the stream as it dries and rapidly recolonize when flow resumes (Leigh et al. 2016). Resilience can be facilitated by physiological and morphological traits that enable drought survival *in situ* (e.g., short life cycles, desiccation resistant eggs or adult life stages able to persist in moist sediments; Williams 2006; Vander Vorste et al. 2015). Resilience strategies may be strongly influenced by the presence of refuges, such as nearby perennial pools, the hyporheic zone, perennial downstream reaches or patches of moist leaf litter, proximal to intermittent streams (Chester and Robson 2011; Hill and Milner 2018).

In streams that experience regular or predictable drying, the effect of seasonal drought on aquatic communities may be compared to those of perennially flowing systems (Côté and Darling 2010; Vander Vorste et al. 2015; Chessman 2015). Typically, perennial streams have high ecosystem stability and may be dominated by a limited number of highly abundant flora and fauna (Fisher 1983; Milner et al. 2008). However, supra-seasonal droughts and the subsequent recolonization and recovery period may encourage the development of distinct faunal assemblages (Boulton 2003; Chadd et al. 2017), and may help maintain, and in some instances, enhance habitat and faunal diversity at the landscape scale. Supra-seasonal droughts potentially open new ecological niches for some organisms following the removal or reduction in abundance of numerically dominant and highly competitive taxa or through the disturbance and re-setting of ecological succession trajectories. For example, the gradual drying and ponding of surface water in a river channel as it dries may provide suitable conditions for colonization by a wide range of taxa associated with lentic conditions (Sheldon et al. 2010; Hill and Milner 2018).

While the process of recolonization and recovery following stream drying and drought events within seasonally intermittent waterbodies has been widely studied (Boulton 2003), there is a paucity of research examining aquatic biodiversity following supra-seasonal drought events (Lake 2003). This is particularly apparent in temperate regions due to the difficulties associated with collecting long-term data and predicting the onset and termination of supra-seasonal drought events. In arid landscapes, Bogan et al. (2015) found that robust recovery after a supra-seasonal drought occurred in streams with historically predictable intermittency, with these communities demonstrating both resistance and resilience mechanisms. In the same study, the response of perennial macroinvertebrate communities to supra-seasonal drought differed due to a lack of resistance traits in the pre-drought community; long lived (>1 year) weak dispersing macroinvertebrates were replaced by short lived (<1 year) strong dispersers that were able to rapidly recolonize.

A supra-seasonal drought in the UK between December 2010 and April 2012 (Parry et al. 2013), which caused channel drying in both historically perennial and ephemeral reaches of the River Lathkill, provided a unique opportunity to examine the response of macroinvertebrate communities to flow recovery. As a result, this is one of the first studies to examine ecological responses to supra-seasonal drought from communities in ephemeral and historically perennial flow sites in temperate regions. This study aimed to characterise the recolonization of aquatic macroinvertebrate communities of naturally ephemeral and near perennial sites (flowing except under extreme drought conditions) in the River Lathkill (UK) following a high magnitude supra-season drought.

Materials and Methods

Study sites

The River Lathkill (Derbyshire, UK) is a groundwater-fed river in the White Peak area of the Peak District National Park. Land-use in the catchment is predominantly low intensity grazing on unimproved grassland (Stubbington et al. 2016). The perennial source originates at Bubble Springs (SK 2049 6612, 159m AOD; Figure 1) and the entire catchment of the river above the springs is underlain by Carboniferous limestone.

A total of 11 sites within two sections upstream of the perennial source (Bubble Springs), based on their historic flow permanence (after Wood et al. 2005), were studied. Naturally ephemeral sites comprised the headwater sites (Sites 1-6; Figure 1) which typically experience surface water drying for at least six-months per-annum, although flows can occur in response to high rainfall events (two to four times per year; Stubbington et al. 2016). Exposed limestone bedrock with boulder to gravel size clasts dominated headwater sites. Finer organic rich sediments with patches of semi-aquatic and terrestrial flora were also present. The second downstream section comprised five near perennial sites; three sites which dry most years for a short period (typically around 2 weeks but up to 2 months) depending on meteorological conditions, and two sites that have dried only once in the last 30 years (Sites 7-11; Figure 1). The substratum at sites with near perennial flow consisted predominately of mixed alluvial deposits (sand to cobble sized angular clasts) with instream vegetation dominated by mosses and liverworts (Stubbington et al. 2011). All study sites were upstream of the confluence between the R. Lathkill and the River Bradford (Figure 1).

Hydroclimatic conditions

The 2010-2012 supra-seasonal drought affected large parts of England, particularly southern and midland areas (Parry et al. 2013). By the end of March 2012, 14 of the previous 24 months had recorded <70% of average rainfall across lowland England (10 of those recorded <55% of average rainfall: Marsh et al. 2013). As a result, the channel was dry upstream of the perennial source (Bubble Springs) and both study reaches (ephemeral and near perennial sites) remained dry for the longest duration since the start of monitoring in 1998. After a nine-month dry period, flow resumed in the ephemeral headwaters but dried again in mid-March 2012 for ca. 28 days (Stubbington et al. 2016). The supra-seasonal drought ended abruptly in April 2012 which experienced double the monthly average rainfall (Parry et al. 2013). As a result, surface flow resumed throughout the near perennial reach in April 2012 and the channel experienced flowing conditions throughout the remainder of the study. Overall, 2012 was the wettest year in England since 1910 (Parry et al. 2013). Flow remained ephemeral in the ephemeral reach and streambed drying occurred on three additional occasions; (1)

ca. 28 days from mid-March 2012, (2) ca. 39 days from mid-May 2012; and (3) ca. 46 days from early August 2012 (Stubbington et al. 2016). Regional monthly mean temperatures for 2012 were within 0.5 ^{o}C of the long-term average (1961-1990; Met Office 2015).

Macroinvertebrate sampling

Aquatic macroinvertebrate samples were collected from 11 sites along the R. Lathkill at monthly intervals where possible (some samples could not be taken during high flow events or dry periods) between December 2011 and September 2012. A total of 138 samples were collected; 72 from the ephemeral and 66 from the near perennial reach (Figure 1b). Two additional macroinvertebrate sampling events were undertaken in November 2012 and February 2013. Samples comprised a three-minute kick sample (using a pond net fitted with l mm mesh) divided equally between mesohabitats present. Aquatic macroinvertebrate samples were preserved in the field with 4% formaldehyde solution prior to processing and identification in the laboratory. The majority of macroinvertebrate taxa were identified to species level but Diptera, Leuctridae, Baetidae, Sphaeriidae and Planariidae were resolved to family level and Oligochaeta, Tricladida (non-Planariidae) and Collembola were recorded as such.

Statistical analysis

To examine temporal changes in diversity and the relative abundance of individual taxa over time mixed-effects models were fitted to selected taxon and community metrics. Prior to statistical analysis, data were examined to ensure they met the assumptions of statistical tests (e.g., normal distribution). The following taxa; *Asellus aquaticus, Gammarus pulex, Isoperla grammatica, Serratella ignita,* Baetidae and *Perlodes mortoni* were selected for further investigation as they typically occurred in greater abundances and in multiple samples throughout the study period. The month of sample collection and sample sites were fitted as random effects to account for potential spatial and temporal dependence, and month and intermittence (ephemeral and near perennial) were fitted as fixed interacting factors. Taxonomic richness was tested via a Generalised Linear Mixed Effects Model (GLMM) fitted using a Poisson distribution and log link structure via the '*glmer*' function in the lme4 package (Bates et al. 2018). Community abundance and abundances of individual taxa were tested via a Linear Mixed Effects Model (LMM) using the '*lmer*' function in the lme4 package with the restricted maximum likelihood (REML) estimation function. Abundances were log10(x+1) transformed to normalise residuals prior to model fitting. Conditional R^2 (proportion of variance explained by the fixed and random factors; r^2 c) values were extracted using '*rsquared.glmm*' function in the MuMIn package (Bartoń 2018). To account for the non-linear association of *I. grammatica* with time, a third order polynomial model was fitted. This technique has been shown to reliably model nonlinear associations without model overfitting (Kennen et al. 2014). Species accumulation plots were constructed to examine the rate of recolonization over time for ephemeral and near perennial sites and a linear model fitted to assess the rate of invertebrate colonisation differed over time between ephemeral and near perennial sites. All univariate analyses were conducted using R version 3.2.3 (R Development Core Team 2015).

Heterogeneity of macroinvertebrate communities between the ephemeral and near perennial reaches was assessed using Analysis of Similarity (ANOSIM) and visualised using Non-metric Multidimensional Scaling (NMDS) ordination plots (using Bray Curtis dissimilarity). To identify changes in community composition among months in ephemeral and near perennial sites, spearman rank correlations (RELATE) and centroid NMDS ordination plots were examined. A monthly similarity matrix (Bray-Curtis) for each site was compared to a linear sequence (the sampling months in this study) to examine if similarity among macroinvertebrate assemblages was higher in adjacent sampling months than in more distant sampling months (*Serial* RELATE; Clarke and Gorley 2006). Distances among centroid matrices were constructed by calculating the averages (e.g., the centroid - the centre-point of all replicates for each month in multi-dimensional space) in the 'Bray-Curtis space' of macroinvertebrate compositions from the replicate samples for each month (Anderson et al. 2008). Centroid NMDS ordinations were generated using the distance among centroid matrices.

Similarity Percentage analysis (SIMPER) was used to determine which species were driving the differences in community composition between ephemeral and near perennial sites. Faunal abundance data was log transformed prior to ANOSIM, NMDS, centroid NMDS, SIMPER and RELATE analysis, which was undertaken in PRIMER V7 (PRIMER-E Ltd, Plymouth, UK).

Results

Spatial macroinvertebrate diversity and variability in community composition in ephemeral and near perennial reaches

Following the supra-seasonal drought (2011-2013), a total of 101 taxa were recorded from the ephemeral (total: 65 taxa, mean: 7.1, range: 3-13) and near perennial sites (total: 85 taxa, mean: 14.6, range: 5-25) during the 12 surveys from the 11 sample sites. Of the 101 taxa recorded between 2011-2013, the most widely distributed taxa were: Chironomidae, Tipulidae, Simuliidae, Oligochaeta, *A. aquaticus*, *G. pulex* (recorded at all 11 sites) and, Baetidae, *G. truncatula* and *Nemurella picteti* (recorded at 10 sites). The most diverse orders were Trichoptera (23 taxa), Coleoptera (21 taxa), Plecoptera (14 taxa) and Diptera (14 taxa).

Taxonomic richness (df=9, t=3.905, p=0.004) and total relative abundance (df=9, t=3.615, p=0.006) were significantly higher in near perennial than ephemeral sites (Figure 2). No significant differences in the abundance of *A. aquaticus, I. grammatica, S. ignita,* Baetidae and *P. mortoni* between near perennial and ephemeral sites were recorded; however, *G. pulex* had significantly greater abundances in near perennial than ephemeral sites (df=9, t=2.425 p=0.038). Significant differences were observed in macroinvertebrate community composition between ephemeral and near perennial sites (ANOSIM *r*=0.457 p=0.01; Figure 3a). The top four macroinvertebrate taxa identified by SIMPER to be driving the differences in macroinvertebrate community composition between ephemeral and near perennial sites were *A. aquaticus* (contributing 6% to the dissimilarity) which were recorded in greater abundances in ephemeral sites and Baetidae (8.4% dissimilarity), Chironomidae (7.3% dissimilarity) and *I. grammatica* (6% dissimilarity) which were recorded in greater abundances from near perennial sites. A total of 16 taxa were unique to ephemeral and 35 taxa to near perennial sites (see Supplementary Material Part 1).

Temporal diversity and variability in community composition in ephemeral and near perennial reaches

At a regional scale, a steep increase in taxonomic richness was recorded in ephemeral and near perennial sites over the first three months after flow resumed (December 2011 to March 2012), with a more gradual increase in taxa richness in ephemeral and near perennial sites from month 4 (April 2012) to the end of the study (Figure 4). Species accumulation was determined to be significantly greater in near perennial sites ($t_{3,23}$=2.604, p=0.017), although the rate of colonisation over time did not differ between ephemeral and near perennial sites ($t_{3,23}$=0.390, p=0.7; Figure 4). At an alpha scale, both taxonomic richness (GLMM) and total abundance (LMM) were significantly greater (p<0.001) in the near perennial sites and demonstrated little variation over time (Figure 2, Table 1). When examining individual reaches, mean taxonomic richness in the ephemeral sites was similar (between 5-10 taxa) among all sampling months, whilst in the near perennial sites taxonomic richness was highest 2-3 months after flow resumed (February 2012 and March 2012), but was similar (between 10-15 taxa) for the other sampling periods (Figure 2a). Mean macroinvertebrate abundance increased rapidly up to 3-months after flow resumed in near perennial flow sites (March 2012) and subsequently declined gradually thereafter to the end of the survey period (Figure 2b). Similarly, mean abundance increased rapidly up to 3 months after flow resumed in ephemeral sites, but was more variable in the proceeding months, decreasing at month 4 (April 2012 - reflecting spate conditions) and month 6-9 (June-September 2012- reflecting the periods of desiccation in ephemeral sites headwaters: Figure 2b).

Abundances of *A. aquaticus* increased monthly in ephemeral and near perennial sites ($p<0.001$ in both instances; Table 1), reaching their greatest abundance in the final survey month (Feb 2013; Figure 5a) but demonstrated no differences by intermittence ($p>0.05$; Table 1). *G. pulex* abundances were consistently and significantly greater in near perennial sites than ephemeral sites (Table 1). *G. pulex* abundance was broadly similar over the 12-months after flow resumed in ephemeral sites before rising to a peak in the final sampling month. In near perennial sites, *G. pulex* abundance was stable for 5-months after flow resumed (Dec 2011- April 2012) but was markedly reduced during month 6-7 (May and June 2012) as flow declined (Figure 5b). *I. grammatica* was more abundant in near perennial sites than ephemeral sites (Table 1) and was initially recorded 4 months after flow resumed in ephemeral sites, and 3 months after flow resumed in near perennial sites (Figure 5c). Abundances of *I. grammatica* peaked 3 months after flow resumed (March 2012) in ephemeral sites and 5 months after flow resumed (May 2012) in near perennial sites. However, its abundance declined throughout the summer months and only increased again 11 months after flow resumed (Nov 2012; Figure 5c). *S. ignita* was not recorded from ephemeral sites during the 2011-2013 study and was first sampled in near perennial sites three months after flow resumed (Feb 2012), reaching its greatest abundance 5 months after flow resumed (May 2012) and declining thereafter (Figure 5d). In ephemeral and near perennial sites, Baetidae demonstrated highly variable abundances throughout the survey period. Baetidae, first recorded 2 months after flow resumed (Feb 2012) in near perennial sites and three months after flow resumed (March 2012) in ephemeral sites, reached highest abundance 7-8 months after flow resumed in the two study sections (Figure 5e). Temporal changes in Baetidae populations were determined to be significantly different (Table 1) with near perennial abundances increasing at a faster rate compared to ephemeral sites. *P. mortoni* was initially recorded 4 months after flow resumed (April 2012) in ephemeral sites and remained consistent throughout the remainder of the study (Figure 5f). In near perennial sites, *P. mortoni* was first recorded 6 months after flow resumed (June 2012) with abundances increasing rapidly and peaking 8 months after flow resumption (August 2012; Figure 5f). Abundances of *P. mortoni* were significantly greater in near perennial sites and varied between sections over time (Table 1). Across ephemeral sites, *A. aquaticus, G. pulex, I. grammatica* and Baetidae all demonstrated a reduction in abundance from the 3^{rd} to 4^{th} month after flow resumed (March 2012 to April 2012), although abundance of *P. mortoni* increased in this period. In addition, *A. aquaticus,* Beatidae, *P. mortoni* and *I. grammatica* demonstrated reduced abundances from the 8th to 9th month after flow resumed (August 2012 to September 2012) in ephemeral sites (Figure 5a, b, c, e, f).

Spearman's rank correlations comparing the similarity matrices of monthly macroinvertebrate communities were statistically significant for near perennial sites (Table 1) demonstrating a strong serial correlation (Figure 3c). In ephemeral sites, 5 of the 6 sites displayed low and non-significant ρ values demonstrating a weak serial correlation (Table 2) and did not follow serially in the centroid NMDS biplot (Figure 3b – particularly 3-5 months after flow resumed, March-April 2012); only site 3 recorded a significant Spearman's rank correlation (Table 2).

Discussion

Macroinvertebrate recolonization of ephemeral and near perennial reaches following a supra-seasonal drought

Following the resumption of surface flow after the supra-seasonal drought, we found rapid macroinvertebrate recolonization (species accumulation) on the R. Lathkill with the cumulative number of taxa plateauing after approximately 6 months. Similar findings have been recorded from streams in Georgia, USA and Berkshire, UK (Wright et al. 2004; Churchel and Batzer 2006) where rapid recolonization of streams was observed immediately following the onset of flow after drought, and species accumulation also beginning to plateaux after 5 to 6 months.

Different recolonization processes, however, probably operated in the ephemeral and near perennial sites of the R. Lathkill examined. Ephemeral sites in the headwaters and are hydrologically more isolated from perennial water sources. The lack of lateral or longitudinal connectivity and frequent channel drying in ephemeral sites suggests that resilience strategies may have been an important mechanism for the rapid recolonization in this section of the river. Many taxa have developed adaptations to survive *in-situ* in dry river beds such as producing diapause eggs (e.g., the macroinvertebrate seedbank; Stubbington and Datry, 2013), having short development times (Lytle and Poff 2004; Bogan and Lytle 2011) or persisting in damp leaf patches and sub-surface water in the hyporheic zone (Stubbington et al. 2009a, 2011, although this is not the case for all rivers; Datry 2012). In this study, *A. aquaticus* recolonized quickly after flow resumed in the ephemeral sites, potentially surviving the period of flow desiccation as small individuals in damp sediments and organic matter in the hyporheic zone (Leberfinger and Herrmann 2010; Vadher et al. 2017).

Near perennial flow sites were located between the ephemeral headwaters and the fully perennial river further downstream. The return of lateral and longitudinal aquatic connectivity between the perennial zone and near perennial sites is likely to have been an important factor influencing the recolonization of this section of the river. Previous studies have demonstrated that perennial reaches may act as a refuge for taxa capable of dispersal (Chester and Robson 2011; Bogan et al. 2015), with rapid recolonization after the drought event being possible in this study from the proximal perennial zone via resistant mechanisms (life stages) such as aerial dispersal, or through upstream migration (Williams and Hynes 1976; Verberk et al. 2008; Chester et al. 2015). The coleopteran, *Agabus guttatus* was recorded as early as two months after flow resumed in near perennial sites and previous studies have indicated them to be one of the first predators to aerially colonise intermittent reaches (Davy-Bowker et al. 2002; Stubbington et al. 2016). Further, the significantly greater abundances of *G. pulex* in near perennial sites may reflect this species rapid ability to recolonize from perennial reaches downstream (White et al. 2018) and through vertical connectivity with the hyporheic zone (Stubbington et al. 2009) and subterranean caves (Wood et al. 2005). Based on the results of this study, the effective recolonization of biological communities to drought in ephemeral and near perennial reaches is likely to be the result of a combination of resistance and resilience strategies (Bogan et al. 2015).

The mean number of taxa remained consistent throughout the sampling months in ephemeral sites but a peak in richness was recorded in near perennial sites during February 2012. A significant rainfall event prior to sampling in February 2012 increased the discharge in the R. Lathkill and may have provided connectivity to facilitate upstream migration of taxa from the perennial reaches downstream. The loss of surface flow in ephemeral sites on three separate occasions during the sampling period may explain the reductions in abundance of *A. aquaticus, G. pulex*, *P. mortoni, I. grammatica* and Baetidae at months 3 and 4, and months 8 and 9, as it is likely many of the taxa were unable to complete their life-cycle and those that did may have had to disperse as flow receded (Dobrin and Giberson 2003).

Macroinvertebrate communities within ephemeral sites did not display a serial correlation, with adjacent sampling months being heterogeneous. This may be the result of the loss of surface flow on a number of occasions during the study period (March, May and August 2012) continually re-setting succession and re-starting the community recolonisation process (Sponsellor et al. 2010). This suggests that ephemeral stream reaches are in a constant state of resetting of community succession, with recovery and recolonization only partially occurring until they are re-set by the next drying event. In contrast, after the first month of the study, flow was continuous throughout the near perennial section following the supra-seasonal drought and as such macroinvertebrate assemblages in these sites demonstrated serial correlation, with adjacent sampling months being most similar, and the first and last sample recording the greatest heterogeneity in community composition. In perennial rivers, macroinvertebrate assemblages typically follow a seasonal cycle (e.g., successive winter communities record similar community assemblages: Giller and Twomey 1993; Leunda et al. 2009) and therefore, the significant serial correlation recorded in near perennial sites indicates that two possible ecological processes may be occurring in the R. Lathkill: *(i)* recolonization and ecological recovery are ongoing. Despite the rapid recolonization by many taxa, the full recovery of macroinvertebrate communities had not occurred during the study period, as communities from January 2012 and February 2013 were most heterogeneous. This suggests that the ecological effect of the supra-seasonal drought on macroinvertebrate communities was evident for multiple seasons following the event (Churchel and Batzer 2006; Bogan and Lytle 2011), with ecological recovery being a long-term process (Wood and Petts 1999; Churchel and Batzer 2006) that typically takes significantly longer than hydrological recovery; and *(ii)* the supra-seasonal drought may have reset the ecological trajectory of the macroinvertebrate community which is possibly now heading towards a new ecological equilibrium (Bogan and Lytle 2011), reflecting the high heterogeneity between samples. Supra-seasonal drought may cause macroinvertebrate assemblages to permanently differ from pre-drought assemblages. For example, research by Bogan and Lytle (2011) on intermittent streams in Arizona has shown that supra-seasonal drought can cause regime shifts in invertebrate community composition from long-lived sedentary taxa to smaller short-lived and highly vagile taxa.

If taken in isolation, supra-seasonal droughts appear to have a negative effect on ecosystems, causing an initial decline in taxonomic diversity during the period of stream desiccation (Lake 2003; Boulton and Lake 2008; Aspin et al. 2019). However, when recolonization is examined over longer timescales, supra-seasonal droughts may actually facilitate the development of environmental conditions to support a higher diversity through; (1) a reduction in competition and predation pressure (supra-seasonal drought removed key predators and dominant taxa such as *G. pulex*); (2) an increase in the availability and number of habitats (environmental niches: Ricklef & Schluter, 1993), as succession is re-set and dominant environmental / ecological pressure are reduced and; (3) enabling new taxa (that may be outcompeted in later succession lotic habitats) to utilise the increased spatio-temporal environmental and biotic niches. However, it is unclear whether the macroinvertebrate communities in the R. Lathkill will maintain this high diversity, whether successional processes are ongoing, or if the community will be reset to follow another new ecological trajectory following the next flow cessation event.

Climate change and the increase in water abstraction from growing human populations is likely to increase the number of rivers that experience drying (Larned et al. 2010), the severity / duration of drying events (Rahiz and New 2013) and could lead to irrevocable changes to biological communities and a loss of taxa that are ill adapted to drying (Datry et al. 2014). Currently, consideration of supra-seasonal drought and management in lotic freshwaters is impeded by the lack of knowledge and information available (Arscott et al. 2010). Future research should be directed towards the long-term monitoring of macroinvertebrate communities before, during and after supra-seasonal droughts to provide the information needed to fully quantify the ecological impacts of these disturbances, understand the mechanisms and strategies macroinvertebrates use to persist / recolonise rivers following an extreme drying event, identify possible regime shifts in intermittent freshwater communities and identify strategies to manage drought impacts. For example, ensuring newly intermittent streams are connected with drought refuge sites may facilitate a rapid recovery post-disturbance (Robson et al. 2011).

Spatial variability of macroinvertebrate communities between ephemeral and near perennial sites

Taxonomic richness was consistently greater within near perennial sites than the headwater ephemeral sites and significant differences in macroinvertebrate assemblages were observed between the two study sections, following the 2011 supra-seasonal drought. Ephemeral sites were subject to multiple drying events during 2012 and increasing flow intermittence has been shown to significantly reduce taxonomic diversity across most biogeographic regions (Datry et al. 2013). Further, flow desiccation in ephemeral sites (which continually re-sets communities) may remove taxa sensitive to drying, while near perennial sites remained wet throughout the study and recolonization could progress providing variable physicochemical and biological conditions for a wide range of taxa to exploit. Taxonomic richness and community assemblage differences may also be the result of spatial organisation of colonist sources (connectivity). The hydrological isolation of ephemeral sites from the perennial reaches reduces the potential for colonisation (Bogan et al. 2015) while hydrological connectivity to the downstream perennial zone provides near perennial sites with a readily available and diverse source of colonists to enhance taxonomic richness and develop a heterogeneous community composition.

Conclusion

This study has demonstrated that aquatic macroinvertebrate taxa can rapidly recolonise lotic habitats after supra-seasonal drought episodes. The impact of supra-seasonal drought on macroinvertebrate communities may persist for multiple seasons after the event, as the communities may not have reached the end-point of recovery during the study period. The results of this study also suggest that supra-seasonal droughts may cause some communities to head towards a new ecological equilibrium rather than recover to their pre-disturbance composition; making the assessment of the end point of recovery more difficult. Supra-seasonal droughts may therefore effectively re-set ecological succession and during the initial recovery / recolonisation phase, and provide ecological and environmental space for new taxa to colonise. Quantifying the recolonisation and recovery of biological communities to extreme disturbances such as supra-seasonal drought is vital to provide the information required to ensure the persistence of biodiversity through the implementation of ecologically effective conservation and management strategies.

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Tables

Table 1 - Univariate analysis for differences in taxonomic richness, total abundance and abundance of individual taxon associated with intermittence (ephemeral and near perennial, n=2), month (n =12) and the interaction of these factors.

Metric	**Intermittence**		**Month**		**Month x Intermittence**		R^2c
	Stat value	p value	Stat value	p value	Stat value	p value	
Taxonomic richness	4.34	**<0.001**	-0.77	0.443	0.15	0.880	62.56
Abundance	3.80	**<0.001**	0.75	0.450	-0.62	0.619	62.11
Baetidae	1.63	0.103	-1.24	0.214	3.56	**<0.001**	70.48
Asellus aquaticus	-1.61	0.106	3.40	**<0.001**	-0.41	0.682	67.02
Seretella ignita	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Gammarus pulex	2.50	**0.012**	1.59	0.110	-0.63	0.530	57.06
Isoperla grammatica	5.04	**<0.001**	6.70, -6.52, 6.39	<0.001	-0.564	0.574	42.76
Perlodes mortoni	2.57	**0.026**	-2.45	**0.025**	4.79	**<0.001**	46.01

609 Table 2 - Spearman's rank correlation coefficients calculated among temporal macroinvertebrate

610 communities (serial RELATE analyses) at each site.

	Site	Spearman's correlation (ρ)
Ephemeral sites	1	0.013
	2	0.255
	3	0.572***
	4	0.079
	5	0.178
	6	0.055
Near perennial sites	7	0.626***
	8	0.593***
	9	0.635***
	10	0.609***
	11	0.539***

*** p<0.01

611

Figure captions

Figure 1 – Location of study river (a) and sampling reach and sites (b): ephemeral sites comprises sites 1- 6 and near perennial comprises sites 7-11.

Figure 2 - Number of taxa (a) and $\log_{10}$ macroinvertebrate abundance (b) across the sampling period in ephemeral (E) and near perennial (NP) river reaches on R. Lathkill (UK). *Surface flow was maintained in near perennial sites throughout the study period. Flow remained ephemeral in ephemeral sites and streambed drying occurred for; (1) ca. 28 days from mid-March 2012, (2) ca. 39 days from mid-May 2012; and (3) ca. 46 days from early Aug 2012.*

Figure 3 – NMDS ordination of macroinvertebrate assemblages from near perennial and ephemeral study sites (a) and; centroid NMDS plots of macroinvertebrate communities from the 12 sampling periods in ephemeral (b) and near perennial sites (c).

Figure 4 - Species accumulation plot for the months sampled from the ephemeral and near perennial sites) river reaches on R. Lathkill (UK). *Surface flow was maintained in near perennial sites throughout the study period. Flow remained ephemeral in ephemeral sites and streambed drying occurred for; (1) ca. 28 days from mid-March 2012, (2) ca. 39 days from mid-May 2012; and (3) ca. 46 days from early Aug 2012.*

Figure 5 - Mean *Asellus aquaticus* (a) *Gammarus pulex* (b) *Isoperla grammatica* (c) *Serratella ignita* (d) Baetidae (e) and *Perlodes mortoni* (f) abundance from each sampling month from ephemeral (ephemeral sites: E) and near perennial (near perennial sites: NP) study sites on the R. Lathkill (UK). *Surface flow was maintained in near perennial sites throughout the study period. Flow remained ephemeral in ephemeral sites and streambed drying occurred for; (1) ca. 28 days from mid-March 2012, (2) ca. 39 days from mid-May 2012; and (3) ca. 46 days from early Aug 2012.*

Figure 1

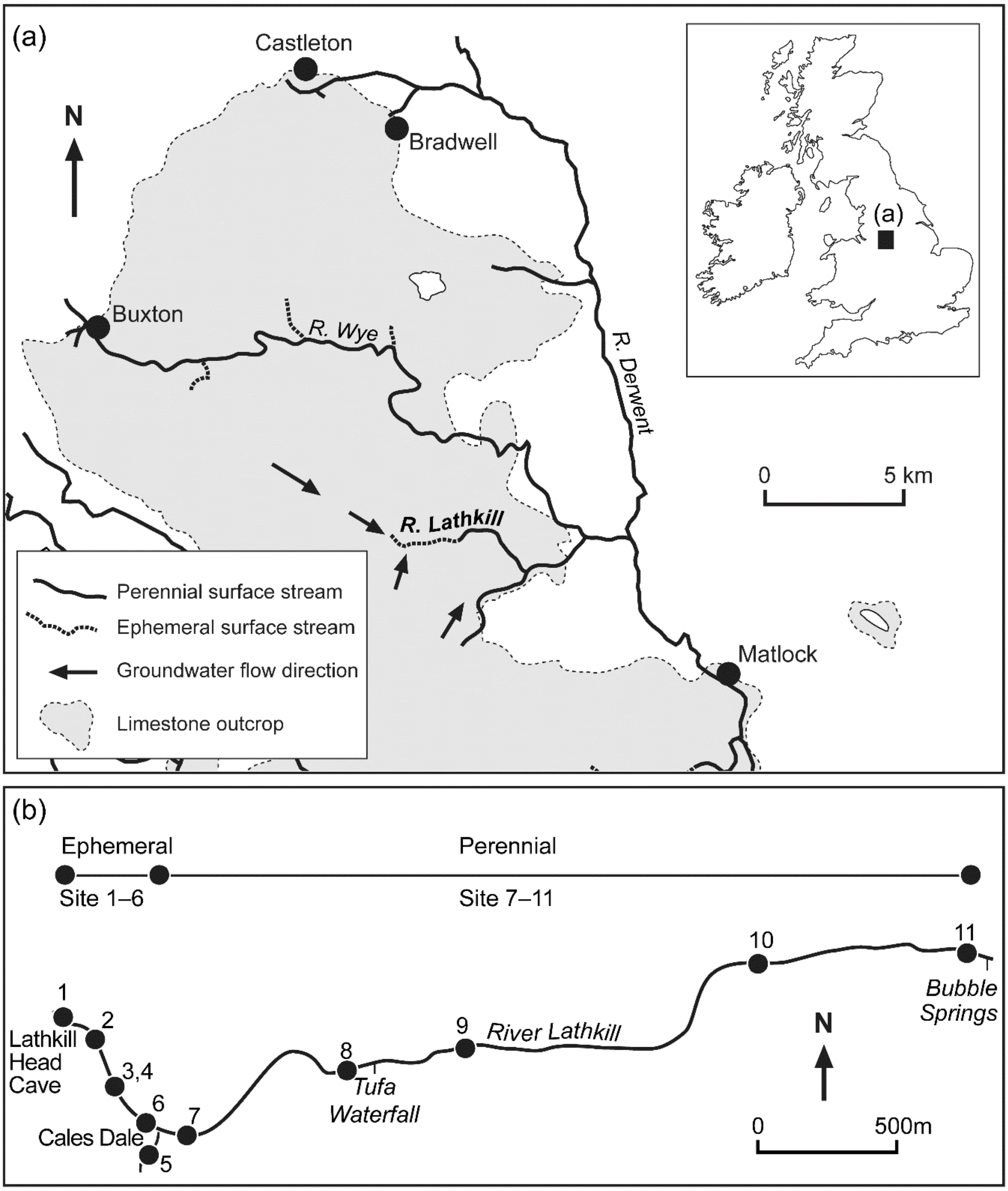
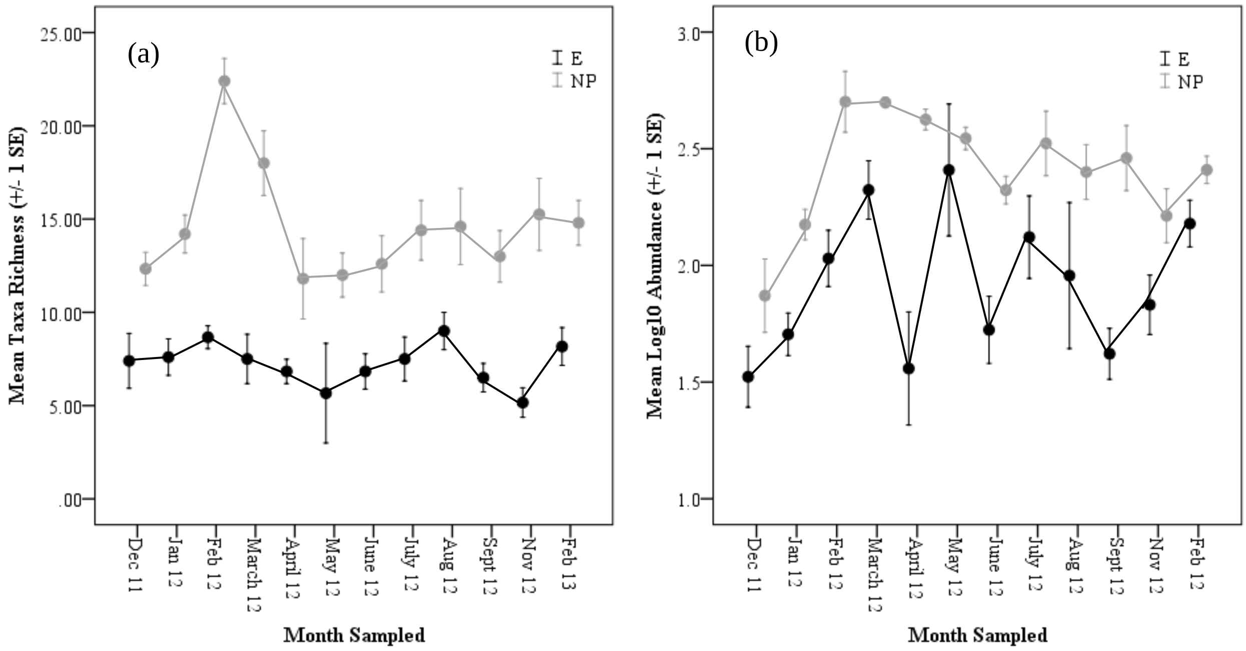

(a)
Castleton
Bradwell
N
Buxton
R. Wye
R. Derwent
R. Lathkill
Matlock
0
5 km
Perennial surface stream
Ephemeral surface stream
Groundwater flow direction
Limestone outcrop
(b)
Ephemeral
Perennial
Site 1–6
Site 7–11
1
2
Lathkill
Head
Cave
3,4
6
7
Cales Dale
5
8
Tufa
Waterfall
9
River Lathkill
10
11
Bubble
Springs
N
0
500m

Figure 2



(a)
Mean Taxa Richness (+/- 1 SE)
25.00
20.00
15.00
10.00
5.00
.00
E
NP
Dec 11
Jan 12
Feb 12
March 12
April 12
May 12
June 12
July 12
Aug 12
Sept 12
Nov 12
Feb 13
Month Sampled
(b)
Mean Log10 Abundance (+/- 1 SE)
3.0
2.5
2.0
1.5
1.0
E
NP
Dec 11
Jan 12
Feb 12
March 12
April 12
May 12
June 12
July 12
Aug 12
Sept 12
Nov 12
Feb 12
Month Sampled

Figure 3

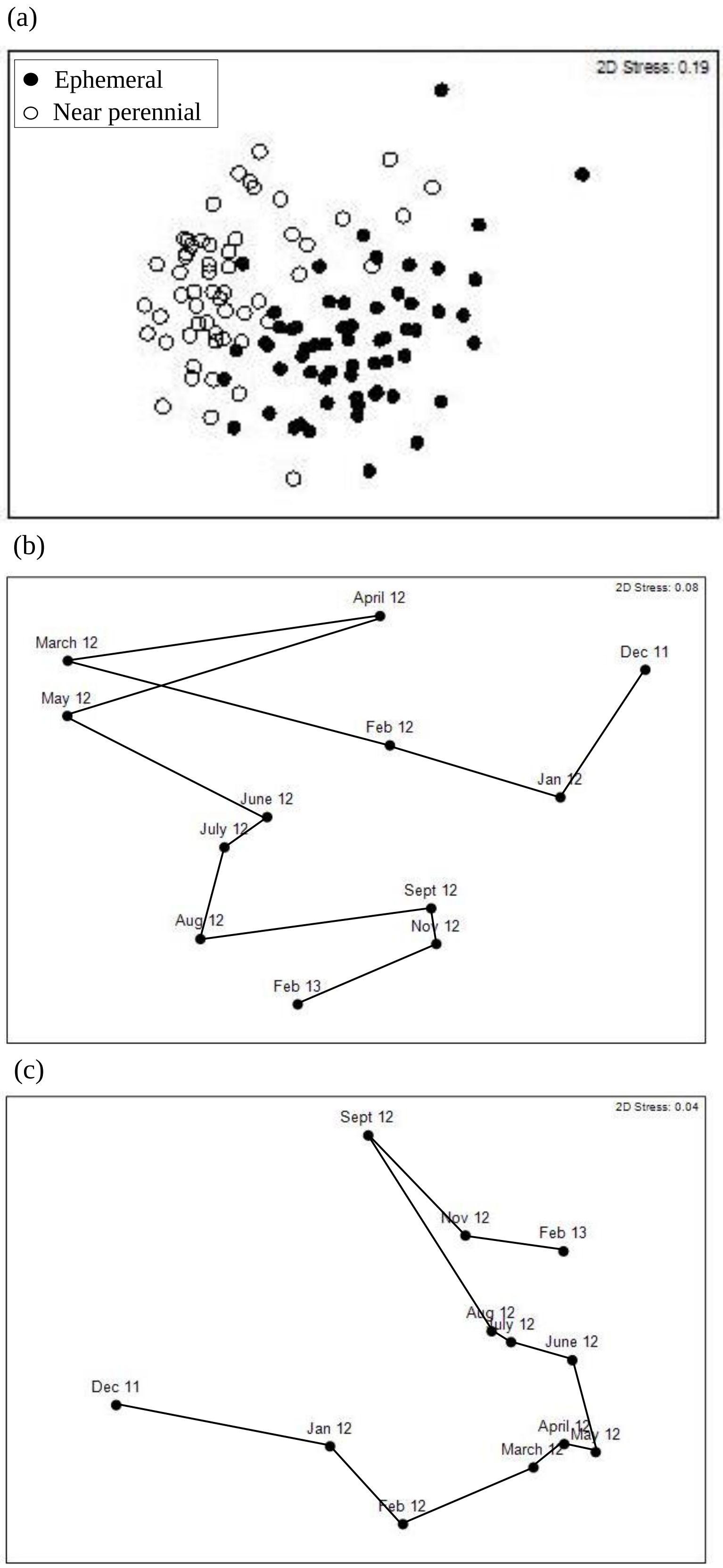

(a)
Ephemeral
Near perennial
2D Stress: 0.19
(b)
2D Stress: 0.08
April 12
March 12
Dec 11
May 12
Feb 12
Jan 12
June 12
July 12
Sept 12
Aug 12
Nov 12
Feb 13
(c)
2D Stress: 0.04
Sept 12
Nov 12
Feb 13
Aug 12
July 12
June 12
Dec 11
Jan 12
April 12
May 12
March 12
Feb 12

Figure 4

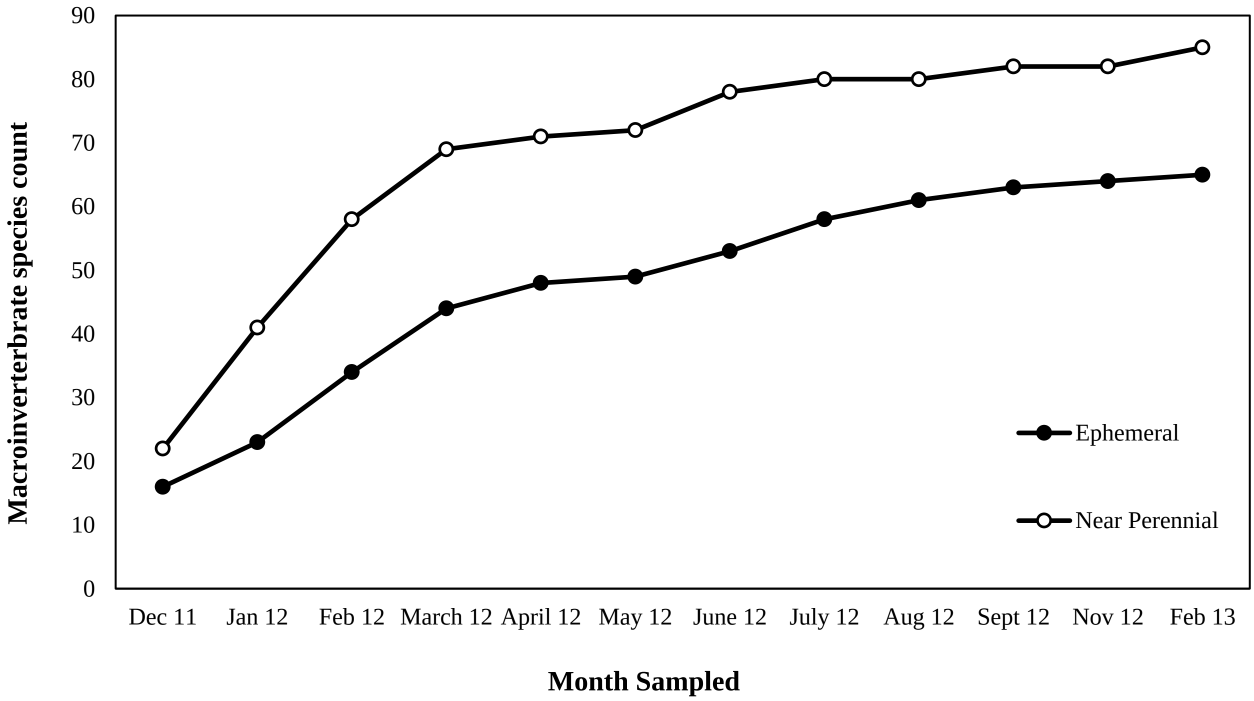
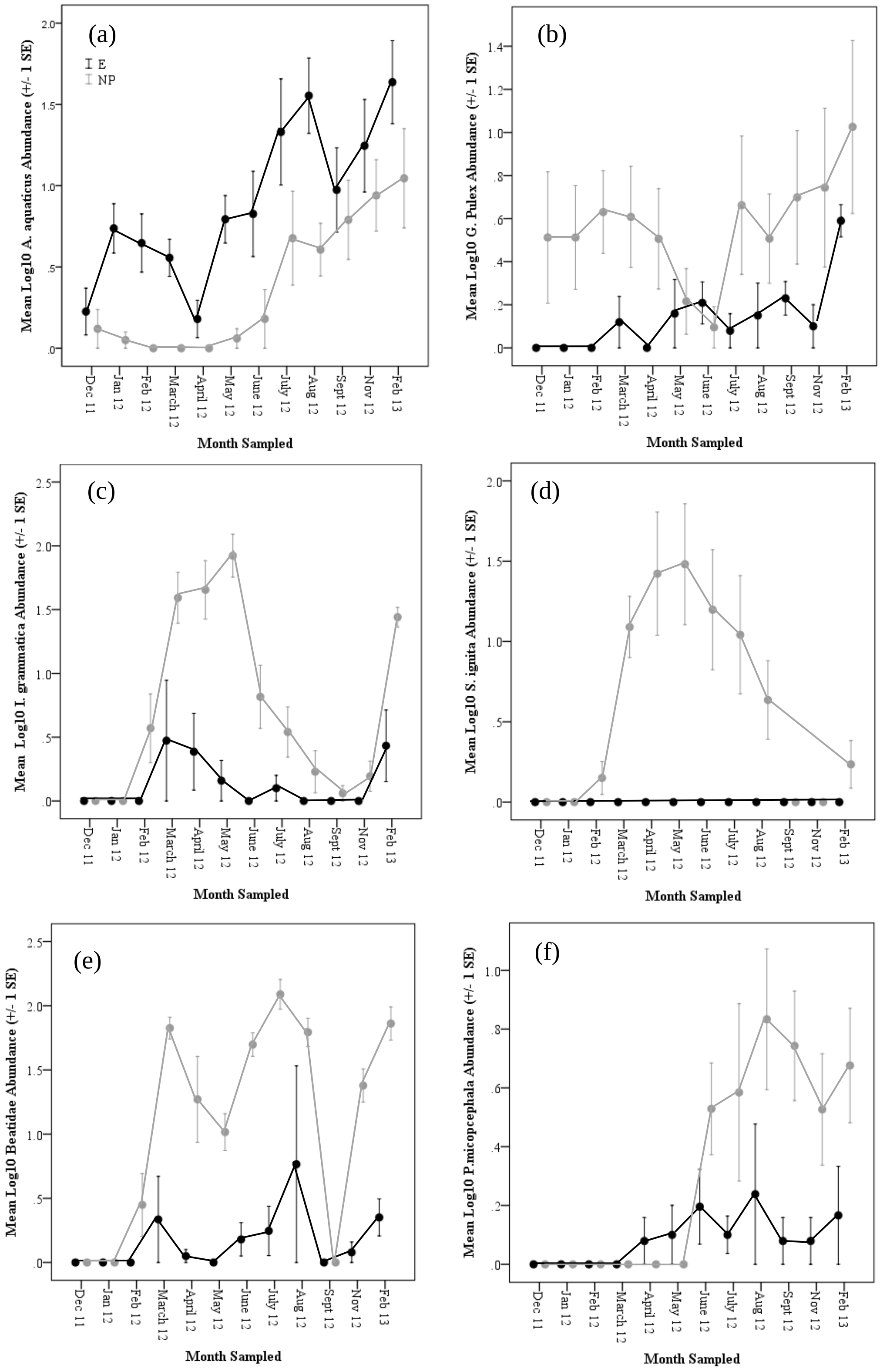

Macroinvertebrate species count
0
10
20
30
40
50
60
70
80
90
Dec 11
Jan 12
Feb 12
March 12
April 12
May 12
June 12
July 12
Aug 12
Sept 12
Nov 12
Feb 13
Month Sampled
Ephemeral
Near Perennial

Figure 5


(a)
E
NP
Mean Log10 A. aquaticus Abundance (+/- 1 SE)
(b)
Mean Log10 G. Pulex Abundance (+/- 1 SE)
(c)
Mean Log10 I. grammatica Abundance (+/- 1 SE)
(d)
Mean Log10 S. ignita Abundance (+/- 1 SE)
(e)
Mean Log10 Beatidae Abundance (+/- 1 SE)
(f)
Mean Log10 P.micopcephala Abundance (+/- 1 SE)
Dec 11
Jan 12
Feb 12
March 12
April 12
May 12
June 12
July 12
Aug 12
Sept 12
Nov 12
Feb 13
Month Sampled