Responses of the functional diversity of benthic macroinvertebrates to floods and droughts in small streams with different flow permanence

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Abstract

Floods and droughts are 2 of the most influential factors affecting the structure and function of benthic macroinvertebrate assemblages in stream ecosystems. Even if these natural disturbances occur at the same magnitude at multiple research sites, the responses may differ according to stream type. In our study, we examined the various responses of functional feeding guilds (FFGs), related to the feeding methods and food types of macroinvertebrates, and habit trait guilds (HTGs), related to the mobility of macroinvertebrates and location of food obtained, to floods and droughts in different stream types (perennial, intermittent, or ephemeral). The stream types were categorised according to the stream flow conditions, flow permanence, and stream connectivity. Perennial streams were those maintaining continuous lotic habitats; intermittent streams were lotic habitats during periods of heavy rain but either connected or isolated pools during dry periods; and ephemeral streams existed only during the rainy season. Among the substrates, cobbles and boulders were highly dominant during heavy rain, especially in the first periods of heavy rain, whereas silt and sand were more often present in high proportions at intermittent stream sites. Across all stream types, highly intense and heavy rain led to a decrease in species richness and abundance, with changes in the composition of both FFGs and HTGs. Organisms characterised as scrapers and/or clingers (e.g., Ecdyonurus dracon, E. levis, and Simuliidae sp.), were highly resistant to high discharge compared to other FFGs or HTGs and were dominant during floods. In dry periods, the composition and richness of FFGs and HTGs were more affected at intermittent streams than at perennial streams. Long-lasting dry periods consistently reduced lotic habitat abundance and diversity and increased the amount of lentic habitats as well as zones with sedimentation, especially at intermittent stream sites, resulting in a decrease in collector-filterer organisms and an increase in burrowers (e.g., Ephemerella strigata). Despite seasonal predictability, however, floods of relatively lower magnitude and intensity provided opportunities for some species, especially clingers (e.g., Epeorus pellucidus) and swimmers (e.g., Baetis fuscatus), to be introduced and/or become established in new habitats downstream in the ephemeral streams. Our research indicated that spatial (i.e., stream type) and temporal (i.e., floods and drying events) heterogeneities are the defining factors that influence functional diversity in benthic macroinvertebrate communities.

Key words: droughts, ephemeral stream, floods, functional feeding guilds, habit trait guilds, intermittent stream, perennial stream
Introduction

Floods and droughts are common natural disturbances in streams that affect the structure and function of benthic macroinvertebrate assemblages (Bonada et al. 2007). They generally reduce habitat suitability for the existing organisms (Cowx et al. 1984, Lake 2000, Brasher 2003), although these disturbances can vary depending on their magnitude, duration, intensity, frequency, predictability, and the rate of change (Lake 2000, 2003, Humphries and Baldwin 2003). Floods enhance hydrological connectivity by increasing discharge, causing benthic macroinvertebrates to drift downstream, passively or actively (Siegfried and Knight 1977, Matthaei et al. 1997, Lake 2003), thus increasing the use of the hyporheic zone (e.g., space among interstitial substrates) as a refuge (Dole-Olivier et al. 1997), as well as scouring the main food sources (e.g., periphyton) for these communities (Grimm and Fisher 1989).

Meanwhile, droughts reduce discharge, wetted width, and water depth of streams (Dahm et al. 2003). At the beginning of a dry period, the diversity of benthic macroinvertebrates may increase because individuals gather and concentrate in a reduced area (Wright and Berrie 1987). During prolonged dry periods, habitat changes and interactions between organisms, such as competition and predation, decrease species diversity (Boulton 2003). Macroinvertebrates that endure regular dry periods, however, have behavioural and physiological adaptations that slow their discharge from the area or help them transition from lotic to lentic habitats (Bonada et al. 2006, Dewson et al. 2007). In contrast, supra-seasonal droughts can severely impact macroinvertebrate survival and their ability to manage unexpected disturbances (Boulton 2003); therefore, their recovery after supra-seasonal droughts can be highly variable, depending on their resistance and resilience to recover from these conditions (Boulton and Lake 2008).

The response of organisms to natural disturbances of the same magnitude can vary greatly, depending on the flow permanence of the stream (e.g., perennial, intermittent, and ephemeral) and taxa (Bogan et al. 2014). For example, benthic macroinvertebrate assemblages in perennial streams are rarely adapted to endure extreme conditions, including intense irregular natural disturbances, and therefore are severely affected by abrupt heavy rain or a cease in stream flow (Caruso 2002, Lake 2007). However, altered macroinvertebrate assemblages in perennial streams rapidly recover from regular flooding, whereas recovery in intermittent streams is delayed due to sequential drying events after floods (Miller and Golladay 1996, Fritz and Dodds 2004, Stubbington et al. 2009b). The recovery of macroinvertebrate assemblages can be difficult in ephemeral streams, however, because the flow of stream water is highly dependent on the amount of precipitation. In intermittent streams, prolonged dry periods can lower stream widths (habitat area), creating isolated pools or few connected pools with a lack of lotic habitat (Chaves et al. 2008).

In addition, the response of organisms to natural disturbances may also depend on life history characteristics, such as functional feeding guilds (FFGs) and habit trait guilds (HTGs), which are differentiated according to their habitat preferences, mode of locomotion, and food type consumed (Cummins and Klug 1979, Cummins et al. 2008). For example, in FFGs during dry periods, collector–filterers such as Hydropsychidae have serious difficulty remaining in their original habitats because their uptake and processing of fine particulate organic matter relies on stream currents (Bond and Downes 2000, Robinson et al. 2003, 2004, Bae and Park 2009, McMullen and Lytle 2012). In HTGs, clingers and swimmers, have some advantages during floods compared to other HTGs because they are mobile and can cling to rocks (Poff et al. 2006, Sueyoshi et al. 2014). Burrowers and sprawlers, however, have limited swimming ability and prefer habitats with high sedimentation rates, which gives them an advantage during dry periods because of increased sediment accumulation rates from reduced water flow during prolonged periods of drought (Sueyoshi et al. 2014).

Although many previous studies have considered the effects of floods and droughts, most were conducted independent of the opposite condition (but see Miller and Golladay 1996, Fritz and Dodds 2004, Stubbington et al. 2009a, 2009b, Bae et al. 2014). Thus, in this study, we investigated changes in macroinvertebrate communities in terms of FFGs and HTGs after floods and droughts across 3 different stream types (i.e., perennial, intermittent, and ephemeral). In particular, we tested 2 hypotheses: (1) the high intensity and amount of rain severely influences the composition of both FFGs and HTGs among benthic macroinvertebrates, and (2) drought events influence changes in the composition of FFGs and HTGs in intermittent streams more than other types of streams.

Materials and methods

Study sites

Macroinvertebrate samples were collected monthly (or twice per month during heavy rain periods) using a Surber net (30 cm × 30 cm) at 6 sampling sites (altitude: 32–78 m) with 3 replicates (Fig. 1) along the Dobong stream, Korea, a tributary of Jungrang stream, from July 2006 to January 2008. Every replicate at each sampling site was
collected at the same or at an adjacent location during each sampling period to account for changes in environmental factors and functional diversity caused by floods and droughts. Sampling sites DBI1, DBP1, and DBI2 are in Bukhansan National Park, and others (i.e., DBE1, DBP2, and DBE2) are near the park (Fig. 1); therefore, the study area has little anthropogenic disturbance (Bae et al. 2014). According to Williams (2006) and Stubbington et al. (2009a), the sampling sites were divided into 3 stream types based on stream flow conditions, flow permanence, and stream connectivity: DBP1 and DBP2 were categorised as perennial (maintaining continuous lotic habitats); DBI1 and DBI2 were categorised as intermittent (lotic habitats were maintained during periods of heavy rain, and the stream area was mainly composed of connected or isolated pools during dry periods); and DBE1 and DBE2 were categorised as ephemeral (streams that exist only during the rainy season; Bonada et al. 2007, Bae and Park 2009, Bae et al. 2014).

Because of monsoons in the study area, >50% of the annual precipitation occurs during summer (Jun–Aug; Jung et al. 2001); after this period, the dry season usually begins in late summer or early autumn and continues until winter. In particular, <4% of annual precipitation occurs during winter (2006: 67.3 mm [4.0%]; 2007: 36.1 mm [3.0%]). During the survey periods, daily precipitation rates were variable, ranging from 0 to 241 mm/d (Fig. 2). Summer precipitation was typically much higher than during other seasons. Analysis of the precipitation data over 30 years from the Korea Meteorological Administration (http://www.kma.go.kr) revealed that the average precipitation was 868.8 mm in summer (July: 376.7 mm) and 66.8 mm in winter. In this study, precipitation during the first summer (2006: 1303.7 mm) was much higher than usual (especially during July: 1014.0 mm), whereas precipitation during the last summer (2007: 566.2 mm) was lower than predicted (especially during July: 274.1 mm; Bae et al. 2014).

**Ecological data**

Macroinvertebrates were mostly identified to species level under microscope. To understand the response of macroinvertebrates to flood and drought conditions, macroinvertebrates were differentiated into 5 FFGs: collector–gatherers (CG), collector–filterers (CF), predators (PR), scrapers (SC), and shredders (SH); and 5 HTGs: clingers (CL), swimmers (SW), burrowers (BU), sprawlers (SP), and climbers (CB), based on a previous study by Merritt and Cummins (2006; Table 1).

Hydrological, physical, and chemical factors were also surveyed at each sampling site, including water temperature (°C), dissolved oxygen (DO, mg/L), electrical conductivity (conductivity, μS/cm), pH, velocity (cm/s), water depth (cm), stream width (cm), and discharge (m³/s; APHA 2005). Substrate composition was also measured at each sampling site and included boulders (substrate size [D] ≥ 256 mm), coarse cobbles (128 ≤ D < 256 mm), fine cobbles (64 ≤ D < 128 mm), pebbles (16 ≤ D < 64 mm), gravel (2 ≤ D < 16 mm), and smaller substrates (D < 2 mm). Precipitation data in the study area were obtained from the Korea Meteorological Administration (http://www.kma.go.kr).
Data analysis

To assess the differences among macroinvertebrate assemblages according to natural disturbances and/or stream types, we used a 3-step analysis. First, rarefied species richness was assessed to construct individual-based species accumulation curves and to compare taxa richness among stream types with varying numbers of individuals (Sanders 1968) because sample size (here, the number of individuals at each site, described later) influenced the collected number of taxa in a sample. Rarefied species richness was computed based on the ability of probability theory to extract the expected species richness for a given size (here, the minimum number of individuals among sites) of a sample (Heck et al. 1975). In addition, we used the cumulated abundance in each category of FFGs and HTGs at each site.

Second, species richness and abundance of FFGs and HTGs were compared among the sampling sites based on the Kruskal-Wallis (K-W; \( P < 0.05 \)) and Dunn’s multiple comparison tests (Zar 1999), which were applied when there was a significant difference among sites. Linear regression analyses were used to evaluate the effects of heavy rain on the abundance (in natural log) of FFGs and HTGs. These statistical tests were conducted using the statistical software STATISTICA 6.0 (StatSoft 2004).

Finally, a principal component analysis (PCA) was used to characterise the effects of natural disturbances on FFGs and HTGs using PC-ORD software 4.25 (McCune and Mefford 1999). We conducted PCA on the correlation matrix of the abundance of FFGs or HTGs to facilitate interpretation and reduce the complexity (i.e., dimensionality) of the raw data, dividing them into small numbers of implicative and “principal” components. We computed the Spearman rank correlation coefficients between PCA axes (axes 1 and 2) and environmental variables to identify the variables influencing the main gradient of PCA axes. The community data and some environmental variables (i.e., precipitation, velocity, depth, width, discharge, and turbidity) characterised by large variation were log-transformed prior to the analyses to reduce variation and assume a normal distribution. Prior to the log-transformation, the number 1 was added to each value to avoid the problem of log 0 (Bae et al. 2011).

Results

Hydrological factors (i.e., velocity, water depth, width and discharge) were highly variable at all study sites during the survey periods (Fig. 3). The effect of these factors increased sharply during the first period of heavy rain (Jul to beginning of Aug 2006) but was lower during other periods. Values of velocity, water depth, and discharge were relatively higher during the first period of heavy rain than during the second period of heavy rain in 2007, even though stream width was similar between those 2 periods.
Heavy rain influenced substrate composition, and the proportion of large substrate particles, including cobbles and boulders, was high at most sampling sites (36.7–63.3% during Jul 2006) in the first period of heavy rain (Jul to beginning of Aug 2006), whereas the proportion of these substrates was relatively lower in other periods (Fig. 4). During the dry periods (autumn and winter), the smaller substrates (silt and sand) tended to increase at intermittent stream sites (up to a 50 and 68.3% increase in smaller substrates was observed at DBI2 and DBI1, respectively).

Across all sampling periods (102 samples total), 168 species and 201,569 individuals (44 families, 10 orders, 3 classes) were identified. Species richness was higher at the perennial streams (DBP1: 30, and DBP2: 31, on average) than at intermittent (DBI1: 23, and DBI2: 22) and ephemeral stream types (DBE1: 15, and DBE2: 14). Abundance values were also higher at the perennial streams (DBP1: 2568, and DBP2: 2758) than other stream types (DBI1: 1339, DBI2: 1116, DBE1: 2302, and DBE2: 1712). The species richness and abundances of FFGs and HTGs were both also significantly higher at perennial
Table 2. Average values in species richness and abundance of functional feeding guilds (FFGs) and habit trait guilds (HTGs) across 3 stream types. Abbreviations for the categories of FFGs and HTGs are given in Table 1. Different letters indicate the statistically significant differences of each functional category among sampling sites, based on the Dunn’s multiple comparison tests ($P < 0.05$). The values in the parenthesis represent standard error.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Category</th>
<th>Perennial stream</th>
<th>Intermittent stream</th>
<th>Ephemeral stream</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>DBP1</td>
<td>DBP2</td>
<td>DBI1</td>
</tr>
<tr>
<td>Functional feeding guilds (FFGs)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species richness</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SC</td>
<td>4 (2)ab</td>
<td>5 (2)a</td>
<td>4 (2)ab</td>
<td>3 (2)bc</td>
</tr>
<tr>
<td>CG</td>
<td>11 (4)ab</td>
<td>14 (5)a</td>
<td>7 (5)b</td>
<td>9 (4)b</td>
</tr>
<tr>
<td>PR</td>
<td>8 (2)c</td>
<td>7 (3)ab</td>
<td>7 (3)b</td>
<td>6 (2)bc</td>
</tr>
<tr>
<td>SH</td>
<td>5 (2)c</td>
<td>3 (2)a</td>
<td>4 (2)a</td>
<td>3 (2)ab</td>
</tr>
<tr>
<td>CF</td>
<td>3 (1)c</td>
<td>2 (1)a</td>
<td>1 (1)b</td>
<td>1 (1)b</td>
</tr>
<tr>
<td>Abundance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SC</td>
<td>74 (98)ab</td>
<td>260 (251)a</td>
<td>123 (157)a</td>
<td>51 (60)b</td>
</tr>
<tr>
<td>CG</td>
<td>1379 (1325)</td>
<td>1289 (1059)</td>
<td>553 (1226)</td>
<td>475 (582)</td>
</tr>
<tr>
<td>PR</td>
<td>557 (429)c</td>
<td>792 (648)a</td>
<td>356 (452)c</td>
<td>375 (253)b</td>
</tr>
<tr>
<td>SH</td>
<td>237 (242)</td>
<td>203 (224)</td>
<td>283 (303)</td>
<td>163 (165)</td>
</tr>
<tr>
<td>CF</td>
<td>321 (466)c</td>
<td>213 (374)a</td>
<td>25 (291)b</td>
<td>51 (73)c</td>
</tr>
<tr>
<td>Habit trait guilds (HTGs)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species richness</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CL</td>
<td>12 (4)a</td>
<td>15 (5)a</td>
<td>7 (6)b</td>
<td>7 (3)b</td>
</tr>
<tr>
<td>SW</td>
<td>2 (1)bc</td>
<td>4 (2)a</td>
<td>1 (2)b</td>
<td>2 (1)b</td>
</tr>
<tr>
<td>BU</td>
<td>5 (2)c</td>
<td>4 (2)a</td>
<td>4 (2)b</td>
<td>4 (2)b</td>
</tr>
<tr>
<td>SP</td>
<td>8 (3)c</td>
<td>7 (3)a</td>
<td>8 (3)a</td>
<td>6 (3)bc</td>
</tr>
<tr>
<td>CB</td>
<td>3 (2)</td>
<td>2 (1)</td>
<td>3 (1)</td>
<td>2 (1)</td>
</tr>
<tr>
<td>Abundance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CL</td>
<td>683 (630)c</td>
<td>890 (780)a</td>
<td>381 (608)c</td>
<td>205 (173)c</td>
</tr>
<tr>
<td>SW</td>
<td>286 (345)c</td>
<td>635 (776)a</td>
<td>101 (636)c</td>
<td>94 (116)b</td>
</tr>
<tr>
<td>BU</td>
<td>105 (77)</td>
<td>112 (106)</td>
<td>159 (226)</td>
<td>99 (76)</td>
</tr>
<tr>
<td>SP</td>
<td>1192 (1530)</td>
<td>913 (823)</td>
<td>500 (1035)</td>
<td>433 (392)</td>
</tr>
<tr>
<td>CB</td>
<td>300 (341)</td>
<td>191 (211)</td>
<td>197 (328)</td>
<td>262 (336)</td>
</tr>
</tbody>
</table>

stream sites (PR species/abundance at DBP1: 8/557 and DBP2: 7/792) than at other stream types (ephemeral species/abundance at DBE1: 3/138, and DBE2: 2/119; Kruskal-Wallis test, $P < 0.05$; Table 2). Species richness (average number of species at DBI1: 4, and DBI2: 3; Kruskal-Wallis test, $P < 0.05$) and abundance of SH, however, were statistically higher at the intermittent stream site (DBII), although abundance values were not statistically significant. The species richness of BU (average species number at DBI1: 4 and DBI2: 4) was also significantly higher at the intermittent stream sites (Kruskal-Wallis test, $P < 0.05$). The rarefaction curves from the individual sites revealed similar patterns at each stream type (Fig. 5). The expected species richness was the highest at perennial sites, followed by intermittent and ephemeral stream sites.

The assessment of FFGs and HTGs provided insight into the changes in stream habitat conditions according to the magnitude of precipitation (Fig. 6 and 7). The proportions (%) of SC (e.g., *Ecdyonurus draco*) and CG (e.g., *Baetis fuscatus*) were relatively higher in summer 2006 (Fig. 6a). For instance, during the first 2 sampling periods, the proportions of SC were 62.5 and 52.9%, respectively at DBI1; however, abrupt changes in the relative proportion of FFGs (e.g., the abrupt increase in the proportion of SC, as had occurred the previous year) were not observed in summer 2007. At DBI2 (intermittent stream), the proportion of PR, including *Conchapelopia unzenalba* and *Sweltsa nikkoensis*, was higher in autumn and winter and accounted for 63.1 to 73.4% of organisms, respectively. At ephemeral streams, the relatively high proportion of CG was consistently observed (maximum proportion during the sampling periods: 99.9% at DBP2 and 96.4% at DBE2), except during the periods immediately before the points at which ephemeral streams were completely dry in the first sampling year (4.5% at DBP2 and 27.1% at DBE2).
Fig. 5. Individual-based rarefaction curves during the study period. DBP1 and DBP2: perennial stream; DBI1 and DBI2: intermittent stream; and DBD1 and DBE2: ephemeral stream.

Fig. 6. The relative ratios of (a) functional feeding guilds (FFGs) and (b) habit trait guilds (HTGs) at 3 different stream types during the study period. Abbreviations for the categories of FFGs and HTGs are given in Table 1.
Fig. 7. Cumulative abundances of each type of (a) functional feeding guilds and (b) habit trait guilds during the study period (perennial stream: DBP1 and DBP2, intermittent stream: DBI1 and DBI2, and ephemeral stream: DBE1 and DBE2).
In July 2006, the ratio of CL, including *Ecdyonurus dracon*, *Ecdyonurus levis*, *Rhyacophila nigrocephala*, and Simuliidae sp., was extremely high at DBP1 (61.9%), DBE1 (50.0%), DB11 (81.9%), and DB12 (84.6%). At DBE2, the proportion of SW, such as *B. fuscatus*, was higher (90.0 and 86.5%) during the first and second survey periods, respectively) than that during the other periods (Fig. 6b). During the dry seasons of autumn and winter, the proportion of BU, such as *Davidius lunatus* and *Ephemera strigata*, increased at the intermittent streams DBI1 and DBI2 (Fig. 6b); however, during July 2007, the proportion of HTGs were similar to that of the previous years, with the exception of DBE1 and DBE2.

Both FFGs and HTGs showed similar relationships with the amount of precipitation (Fig. 8, Appendix Table S1). The abundances of most FFGs and HTGs significantly decreased as a function of the intensity of precipitation at the perennial stream (DBP2): SC (−0.56/0.37 in slope in the linear regression/R²), CG (−0.50/0.37), PR (−0.84/0.63), SH (−0.65/0.39), CF (−0.83/0.44), CL (−0.68/0.55), BU (−0.64/0.43), SP (−0.91/ 0.64), and CL (−0.58/0.17). SW, however, increased along with the level of precipitation at ephemeral streams (DBE1: 1.84/0.36).

The PCA results based on both FFGs and HTGs reflected the intensity of heavy rain, especially during summer 2006 (Fig. 9). The eigenvalues of the first 2 PCA axes were 2.51 (50.2% of the explained variance) and 0.86 (7.3%), respectively, for FFGs, and 2.26 (45.2%) and 1.24 (24.8%) for HTGs. Although the sampling sites were separately ordinated according to stream type (especially those from the ephemeral streams DBE1 and DBE2), the intensity of heavy rain was also influential. For instance, the data from the first 2 sampling periods (106JU to 606AU1) were mainly located on the right (based on FFGs) or lower-right portions (based on HTGs) in PCA ordinations, whereas during the second heavy rain period (2007), no sites were clearly differentiated from the data of other periods. In the PCA ordination based on FFGs, all guilds were negatively correlated with axis 1, indicating abundances in all the categories were notably lower during the first 2 survey periods. In the PCA based on HTGs, axis 2 was positively correlated with all the HTGs except for SW, indicating the abundance of SW was higher during the first heavy rain periods in 2006. Considering the relationships between the PCA axes and environmental factors, the axes from the 2 PCAs showed the highest correlation values with the amount of precipitation (i.e., axis 1 of the FFGs was 0.429, and axes 1 and 2 of the HTGs were 0.347 and −0.576, respectively). Additionally, hydrological variables, such as velocity (−0.522), depth (−0.333), width (−0.375), and discharge (−0.575), were also correlated with axis 2 of the HTGs (Table 3). The Spearman rank correlation coefficients, however, were lower, or not statistically significant, in relation to other parameters (e.g., water quality).

**Discussion**

**General effects of heavy rain**

The extreme intensity, as well as the high amount of “seasonal” heavy rain, significantly reduced the species richness and abundance of benthic macroinvertebrates and abruptly altered the composition of FFGs and HTGs. Discharge or water flows abruptly increased from flooding, with substrate scouring resulting in the removal of surface substrates (Bond and Downes 2003, Gibbins et al. 2005). Substrate composition (Wood and Armitage 2004) and substrate stability (Death 1995) regulate the distribution and abundance of macroinvertebrates at local or broad scales (Rabeni and Minshall 1977); therefore, abrupt changes in substrate composition due to flooding were expected to substantially alter FFGs and HTGs. In addition, increased shear stress may also contribute to the removal of macroinvertebrates (Bond and Downes 2000, 2003).

In our study, species of SC (FFGs) and CL (HTGs), including *Ecdyonurus dracon*, *Ecdyonurus levis*, and *Sweltsa nikkoensis*, as well as organisms in Elmidae and Simuliidae, were relatively abundant during the first heavy rain periods compared with other survey periods. This difference in abundance can be caused by body shape. For instance, *Ecdyonurus dracon* and *E. levis* have a flattened body shape and can easily attach to boulders or cobbles with high resistance from the increased discharge (Bae et al. 2014). By contrast, as scoured and disrupted habitat stabilised and recovered, diverse species with various FFGs and HTGs were observed in high abundance. Streams that harbour various heterogeneous substrates may provide more refuges and colonists (here, perennial streams) during floods, whereas bedrock streams, or streams with homogenous channels, would be more influenced by floods and take more time to recover (Fisher et al. 1982, Angradi 1997, Gjerlov et al. 2003). During summer 2007, when the magnitude of precipitation was less severe than 2006, stable substrates (embedded stones) might have provided macroinvertebrate refuges from flood events despite increased rates of discharge. Additionally, small floods may enhance maintenance of habitat heterogeneity and support macroinvertebrate diversity within patchy streams (Robinson et al. 2003, Lepori and Hjerdt 2006). Furthermore, smaller floods may result in a more rapid subsequent recovery (Lancaster and Belyea 1997, Lake 2000).

In this study, the variability of FFGs and HTGs in response to the magnitude of floods was reflected in the PCA. The data from the first and second survey periods

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Fig. 8. Responses of functional feeding guilds and habit trait guilds to changes in precipitation at 3 different stream types.
Fig. 9. PCA ordination based on (a) functional feeding guilds and (b) habit trait guilds. The values in parenthesis along each axis represent the explained variance and eigenvalues, respectively. Acronyms in the ordination represent the information on the samples. The first number represents the sampling site (1: DBI1, 2: DBP1, 3: DBI2, 4: DBE1, 5: DBP2 and 6: DBE2), and 06 and 07 indicate the year the sample was obtained (2006 and 2007, respectively). The last 1 or 2 letters indicate the sampling month (JA: January, F: February, M: March, MA: May, J: June, JU: July, A: August, S: September, O: October, N: November and D: December).

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(106J to 606A2) were separated from the other sampling periods in the PCA; however, the community recovery was expected to be rapid (e.g., 4 days to 6 weeks), as reported in previous studies (e.g., Death 1996, Matthaei et al. 1996). In our study, the community also largely recovered within 1 month (Robinson et al. 2003), although community recovery after disturbances can be dependent on the magnitude of the flood as well as its predictability and intensity (e.g., Snyder and Johnson 2006). In the PCA, data collected ~4 weeks after the first heavy rain periods in 2006 (106A3 to 606A3) were scattered and close to other sampling dates, which were not greatly affected by heavy rain, indicating they had recovered from the floods.

**Different responses to natural disturbances at various stream types**

Drying events were highly influential on the macroinvertebrate composition in intermittent streams. Post-drought community composition reflected differences in drought types (seasonal vs. supra-seasonal), intensity, duration, availability of refuges, and the condition of the catchment and stream channel (Lake 2003). Because the daily precipitation after August 2006 was extremely low (during the autumn drought), different responses of the components of FFGs and HTGs to dry events were observed. Long-lasting dry periods were more influential on the composition of the macroinvertebrate community based on FFGs and HTGs at the intermittent streams. The riffle zone area was continuously reduced, whereas that of the stagnant pool zone increased; therefore, the increase in species richness and abundance may have occurred because the species were more concentrated in a reduced area at the beginning of the drought period (Wright et al. 2001). Habitat diversity and suitability (Cowx et al. 1984, Cazaubon and Giudicelli 1999), area of the habitat zone (Brasher 2003), and the lateral and longitudinal connectivity (Lake 2000), however, were all continuously reduced with a decrease in discharge. With the habitat changes from lotic to lentic habitats, some species (e.g., *Hydropsyche kozhantschikovi*, Simuliidae sp.) that rely on water currents for their feeding or living (including CF, SW, and/or CL) are not able to compete with other types of FFGs and HTGs. Increased lentic habitats, as well as sedimentation rates, provided opportunities for BU (e.g., *Ephemera strigata*) to out-compete other species (Dewson et al. 2007).

At the perennial stream, high habitat diversity was maintained (e.g., continuous riffle-pool sequences), even though the stream width decreased during the dry periods (Bae et al. 2014). The highest species richness and abundance levels in FFGs and HTGs were therefore maintained during
the dry periods. In particular, CFs that inhabit lotic conditions, such as Hydropsyche kozhantschikovi, H. orientalis, and Cheumatopsyche sp., showed a high abundance at the perennial stream compared with other stream types (i.e., the intermittent stream).

Although seasonal floods generally decrease species richness and abundance, they may provide an opportunity for species to be introduced and established in new habitats, especially for species that inhabit ephemeral streams. During the survey periods in the ephemeral stream, the observed species richness and abundance were extremely low and variable due to harsh and unstable stream conditions. Additionally, many species were unable to survive at those sites during the dry periods because the stream flow was strongly dependent on precipitation. During the heavy rain period in 2006, when precipitation was high, most individuals could not establish and were flushed out of the ephemeral streams. During and after this heavy rain period at the ephemeral streams, CGs, mainly including Chironomidae (e.g., Tanytarsus spp.) and Oligochaeta (e.g., Lumbriculus variegatus), which were expected to easily recover from floods, were observed. During the second heavy rain period of 2007, however, when the amount and magnitude of precipitation was less severe than that of 2006, many individuals passively drifted downstream, especially including CL (Epeorus pellucidus) and SW (B. fuscatus). These species could be maintained at high density at the ephemeral stream after heavy rain but may only persist during periods when stream flow exists.

Conclusions

In this study, we compared changes in functional guilds (FFGs and HTGs) of benthic macroinvertebrates during floods and dry periods at 3 stream types (perennial, intermittent, and ephemeral streams). During the first sampling period, when the magnitude and amount of precipitation was extremely high, the abundance and species richness levels in the FFGs and HTGs were extremely low at all stream types. The changes of community composition in FFGs and HTGs (e.g., the decrease in CFs and SWs along with an increase in BUs) were more heavily influenced at the intermittent streams during the prolonged dry periods because of the continuous decrease in habitat diversity, the change of water flow conditions (from lotic to lentic), and increased sedimentation. The abundance of CLs or SWs was relatively higher during the first heavy rain periods in 2006, and they were rarely collected after the heavy rain. Our results suggest that these 2 natural disturbances strongly contributed to the compositions of FFGs and HTGs, and that the responses to these disturbances are diverse, depending on the stream type.

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References


**Supplementary information**
Appendix Table S1 is available for download via the Inland Waters website, https://www.fba.org.uk/journals/index.php/IW/issue/view/128