Freshwater Biology

Freshwater Biology (2016) **61,** 1276–1292 doi:10.1111/fwb.12658

Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river

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SUMMARY

1. In river systems, aquatic invertebrate communities are surprisingly persistent over time and generally recover quickly from disturbances. Drift has long been viewed as the primary process promoting this resilience, and it plays a important role in predictive models of community composition and concepts in lotic ecology. More recently, other processes such as vertical migration from the hyporheic zone, aerial oviposition from distant refuges and the use of resistance forms (e.g. diapause) have received greater recognition and support for their importance.

2. In this study, the view that drift is the primary process promoting invertebrate community resilience was challenged in an intermittent alluvial river using reach-scale flow manipulations. First, six treatment channels were completely dried for 1 week, while three others were left flowing to be used as controls. Second, flow was re-established in channels and drift was either allowed or blocked for a 4-week period. Third, during this period the resilience of community structure, composition and function was compared between treatments, and the potential for colonisation from the drift, hyporheic zone, aerial oviposition and resistance forms was measured.

3. Communities recovered after only 2 weeks in all of the previously dried channels, and contrary to our hypotheses, invertebrate community structure, composition and functional trait composition were not altered by blocking drift, indicating it was not the primary process promoting resilience in this river.

4. Three lines of evidence suggested colonisation from the hyporheic zone and not aerial oviposition nor resistance forms promoted resilience following rewetting including the following: (i) finding all common benthic taxa in the hyporheic zone during the drying event, (ii) a distinct decrease in invertebrate size upon rewetting in all treatment channels and (iii) a negative correlation between resilience and water table depth.

5. This experiment highlighted the potential importance of the hyporheic zone as a key source of colonisation in alluvial rivers and emphasises the need for a three-dimensional perspective when considering community resilience in rivers. Adaptive management approaches are needed to direct attention to sources (e.g. hyporheic zone) that are essential to promoting community resilience in rivers facing increased pressures due to climate change, water abstraction and flow regime alteration.

Keywords: aerial oviposition, braided river, hyporheic zone, resistance forms, stream drying

Introduction

Rivers are often viewed as disturbance-prone ecosystems due to their naturally high variations in flow (Resh *et al.*, 1988; Poff *et al.*, 1997). However, river communities are generally persistent over time (e.g. Bêche & Resh, 2007) and often recover quickly from disturbance (e.g. Fritz & Dodds, 2004; Bogan, Boersma & Lytle, 2015; Vander Vorste *et al.*, 2015), implying the existence of underlying processes promoting their resilience (i.e. ability to

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recover following disturbance; Stanley *et al.*, 1994). Among these processes, the colonisation of previously disturbed habitats by drift (i.e. the active or passive downstream transport of organisms; Bilton, Freeland & Okamura, 2001) has been studied extensively (e.g. Needham, 1928; Müller, 1954; Townsend & Hildrew, 1976; Bruno, Bottazzi & Rossetti, 2012). Drift is a fundamental process of colonisation in rivers (Brittain & Eikeland, 1988; Mackay, 1992; Bilton *et al.*, 2001) that is driven by the dendritic nature of river networks and the overwhelming, unidirectional movement of water from upstream to downstream (Fagan, 2002; Altermatt, 2013). Today, it logically serves a predominant role in predictive models of community structure (e.g. Grant, 2011) and pervasive concepts in lotic ecology (e.g. Vannote *et al.*, 1980; Townsend, 1989; Poole, 2002).

Over the last two decades, other processes promoting community resilience in rivers have gradually been explored. For example, the vertical migration of organisms into the underlying hyporheic zone during disturbance (e.g. hyporheic refuge hypothesis; Palmer, Bely & Berg, 1992) and colonisation of surface habitats from the hyporheic zone following disturbance are receiving growing interest (e.g. Dole-Olivier, 2011). The hyporheic zone is now viewed as a key component of riverscapes promoting community resilience, despite a paucity of empirical evidence (but see Holomuzki & Biggs, 2007; Kawanishi *et al.*, 2013). Aerial colonisation is another process receiving great attention within lotic ecology following the recognition that community structure and composition are driven not only by local abiotic or biotic ecological processes but also by large-scale dispersal processes (Leibold *et al.*, 2004; Heino, 2013). Many aquatic invertebrates have an aerial stage which can promote colonisation of previously disturbed habitats (Bilton *et al.*, 2001), making the topic of aerial dispersal abilities and its consequences for population and community dynamics a burgeoning field (e.g. Hughes, Schmidt & Finn, 2009; Cañedo-Argüelles *et al.*, 2015). Moreover, other processes, although less studied, can contribute to the resilience of rivers communities, such as the use of resistance forms (e.g. eggs, cysts, diapause; Stubbington & Datry, 2013) to survive during the disturbance, or the ability of some rheophilic organisms to migrate upstream (e.g. Bruno *et al.*, 2012). Together, results from these studies bring into question the paradigm that drift is the most important process promoting community resilience in rivers.

Alluvial rivers are widespread globally and represent ideal systems to explore the processes promoting resilience because they are frequently disturbed, are inhabited by taxonomically rich and resilient communities, and provide multiple sources from which organisms can colonise previously disturbed channels (Arscott, Tockner & Ward, 2005; Tockner *et al.*, 2006). Alluvial rivers are frequently affected by natural flow disturbances, such as flooding (Doering *et al.*, 2007; Tockner *et al.*, 2006) and drying (Datry, 2012; Vander Vorste *et al.*, 2015). Yet alluvial river communities, notably aquatic invertebrates, are very resilient to these disturbances and generally recover in <4 weeks (e.g. Matthaei, Uehlinger & Frutiger, 1997; Fowler, 2004; Vander Vorste *et al.*, 2015). High resilience is facilitated in alluvial rivers by the complex mosaic of habitats which can be used as refuges during disturbances and serve as sources of colonisation afterwards (Arscott *et al.*, 2005; Stanford, Lorang & Hauer, 2005). For example, due to alternating bounded and unbounded sections of alluvial rivers, large-scale areas of upwelling and downwelling alternate longitudinally along the river corridor (e.g. Stanford & Ward, 1993; Capderrey *et al.*, 2013). Downwelling sections are prone to complete channel drying, while upwelling sections generally flow perennially (e.g. Doering *et al.*, 2007; Capderrey *et al.*, 2013), providing an important source of colonists (Malard *et al.*, 2002; Fowler, 2004; Vander Vorste *et al.*, 2015). Vertically, the expansive hyporheic zones found in alluvial rivers can provide more stable environmental conditions during floods and drying (e.g. Malard *et al.*, 2002; Dole-Olivier, 2011) and can harbour diverse invertebrate communities (e.g. Capderrey *et al.*, 2013) which may migrate to colonise the channel surface (e.g. Holomuzki & Biggs, 2007). Laterally, backwaters, riparian ponds and tributaries are also common aquatic habitats that are less prone to disturbance, hence constituting a source of aerial colonisation for previously disturbed channels (Gray & Harding, 2007). The disturbance regimes of alluvial rivers and their mosaic of aquatic habitats provide a unique opportunity to manipulate potential sources of colonisation and identify the primary processes that promote community resilience.

Our understanding of processes promoting community resilience in rivers has essentially been developed using small-scale experiments (e.g. Williams & Hynes, 1976; Palmer *et al.*, 1992), artificial channels and ponds (e.g. Ledger *et al.*, 2012; Boersma *et al.*, 2014) or field surveys (e.g. Fritz & Dodds, 2004; Datry *et al.*, 2014a; Vander Vorste *et al.*, 2015). These previous studies have been criticised for their inherent methodological limitations (Lake, 2000; Englund & Cooper, 2003). For example, the processes studied in small-scale experiments and artificial channels might not be relevant to large-scale flow disturbances, such as floods or drying (Englund & Cooper, 2003). Large-scale (e.g. river reaches) manipulative experiments permit replicability and manipulation at scales relevant to natural processes (Englund & Cooper, 2003); yet, they remain underutilised in lotic ecology (Larned *et al.*, 2010) and virtually all such experiments have focussed on floods (Olden *et al.*, 2014). Therefore, large-scale manipulative experiments are needed to further explore the processes promoting community resilience after drying in rivers.

In this study, the view that drift is the primary process promoting invertebrate community resilience was challenged in an alluvial river using reach-scale flow manipulations. One-week drying disturbances were generated in six channels, while three other channels that remained flowing were used as controls. Invertebrate community resilience was subsequently compared in channels with and without drift for 4 weeks after the drying event. Following the current paradigm in river ecology, we hypothesised that community structure and composition would be more severely affected by drying in the absence of drift. Therefore, we first predicted that blocking drift would lower taxonomic richness, density and evenness, and alter composition because of a dramatic reduction in the number of colonisers. We also hypothesised that communities recovering in channels without drift would differ in functional trait composition compared to those with drift. Thus, we predicted that blocking drift would dramatically lower functional trait richness, diversity and evenness, and alter trait composition because drifting taxa should provide a broad pool of biological traits for the colonisation of previously disturbed channels. Lastly, we predicted that blocking drift would lower invertebrate body size in the channels because colonisers from the hyporheic zone, aerial oviposition and resistant forms tend to exhibit small body size.

Methods

River and study channels

The Eygues River is a main tributary to the Rhône River located in southern France (Fig. 1). It is subject to a Mediterranean climate that induces frequent extreme flow events, including flooding and drying (Piégay *et al.*, 2009). The Eygues River catchment area is 1100 km^2, and it flows 114 km from its headwaters (1757 m a.s.l.) to the confluence with the Rhône near Orange (67 m a.s.l.). The Eygues River has a mean annual discharge of 6.22 $m^3 s^{-1}$ at the Pont-de-la-Tune gauging station (drainage area 473 km^2) based on records from 1906 to 2003. As for most alluvial rivers in the region, it has an abundant bed load, erodible river banks and relatively steep slopes (Piégay *et al.*, 2009; Vander Vorste *et al.*, 2015). Near Nyons (62 km from the source), the Eygues River has an expansive 140-m-wide alluvial floodplain and flows across 3–4 channel braids. In this alluvial floodplain, nine channels with similar physical habitat characteristics (see Physical characteristics, Fig. 1) were selected for the experiment along an 11-km section of the river.

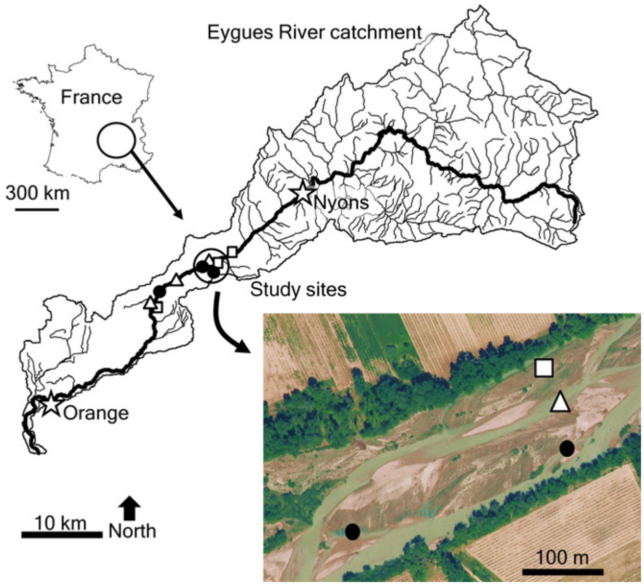

Fig. 1 The Eygues River catchment and nine study channels in south-eastern France with detailed view of four study channels (photograph inset). Symbols represent the three treatment types: *Control* (●), *Drift* (△) and *NoDrift* (□).

The drying disturbance

Drying events (complete loss of surface water along the channel) were generated in six channels (52 ± 12 m length, 356 ± 97 cm wetted width) using dams constructed of plywood, tarpaulin and large boulders which diverted water from channels (Fig. 2a). Dams were fixed across the channel width using steel stakes (1 m length), with care taken to minimise substratum disturbance during their installation (Fig. 2b). After dam installation, channels dried within 24 h and were kept dry for 1 week. Three *Control* channels (44 ± 11 m length, 505 ± 52 cm wetted width) were left undisturbed during the entire experiment.

Drift manipulation

After 1 week of drying, flow was re-established in the dried channels through four open gate valves in each dam (PVC tubes, 11 cm diameter; Fig. 2b). In three of

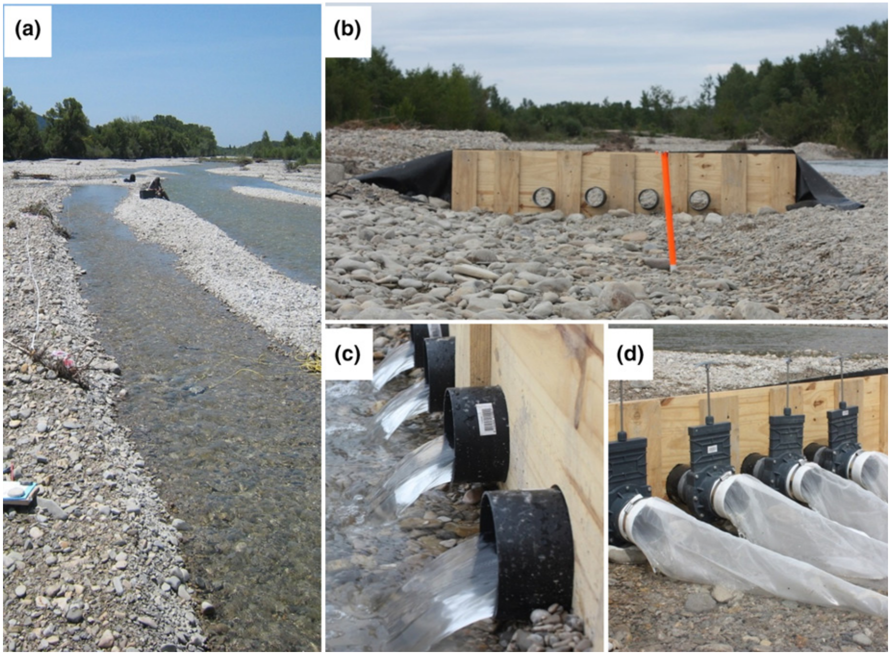

Fig. 2 (a) Alluvial river study channel. (b) Dam used to divert water and create 1-week drying event in *Drift* and *NoDrift* channels. (c) Allowing invertebrate colonisation by drift (*Drift*). (d) Blocking invertebrate colonisation by drift using mesh drift nets (*NoDrift*).

these six channels, drift was allowed through the valves (*Drift* treatment, Fig. 2c). In the other three channels, drift was blocked by filtering water at each dam outlet using mesh drift nets (150 cm length, 250 μm mesh) attached to gate valves (11 cm diameter) fixed onto the PVC tubes (*NoDrift* treatment, Fig. 2d). Invertebrates and organic matter that accumulated in drift nets were removed every 24 h throughout the study period to prevent nets from clogging and to assess the potential contribution of drift (see Sources of colonisation). During this time, individual gate valves were successively closed, while the nets were removed and rinsed.

Sampling of invertebrates and physical characteristics that occurred before drying events is subsequently referred to as date *T0,* whereas sampling that occurred after 1, 2, 3 and 4 weeks of rewetting is distinguished by *T1–4*, respectively. Sampling that occurred on dates during the 1-week drying events is referred to as dates *DryDay3,6,7*, where the numbers distinguish the specific sampling day.

Physical characteristics

Wetted width, water depth and discharge were measured at *T0* and *T1* to ensure similar physical characteristics were maintained in treatment channels following flow manipulations. Wetted width and water depth were measured at 10 locations along the length of each channel (Table 1). Discharge was estimated from depth and flow velocity measurements collected using a Flo-Mate current meter (Marsh McBirney, Loveland, Colorado; Table 1). To assess possible differences among channels that could influence colonisation from the hyporheic zone and resistance forms, the following measurements were made: (i) water table depth measurements were taken on *DryDay7* by driving a stainless steel pipe (2 cm diameter, 14 cm long perforated area, 5 mm perforation diameter) into the riverbed until the water table was reached (Table 1); (ii) following rewetting at *T4*, vertical hydraulic gradient (VHG) and hydraulic conductivity (K) were measured at 10–20 locations each along the length of each channel using methods described by Datry *et al.* (2014b) (Table 1); (iii) median grain size (D_{50}) was estimated by randomly selecting and measuring 200 stones (coarse gravel–boulder, size range = −3.6 to −8.0 φ) from along the length of each channel (Table 1).

Benthic invertebrate communities

Benthic invertebrates (BEN) were sampled from each channel on five sampling dates (*T0–4*). BEN samples were collected from four locations at equally spaced locations (13 ± 3 m apart, mean ± 1 SD) along the length of the channel, using a Hess sampler (250 μm mesh, 0.125 m^2) and preserved in 96% ethanol. Following *T1*, these locations were adjusted either upstream or downstream each week to avoid sampling the same location more than once during the study period.

Table 1 Summary statistics of the physical characteristics measured in *Control*, *Drift* and *NoDrift* channels

	Treatment type		
	Control	Drift	NoDrift
Length (m)			
Mean ± 1 SD	44 ± 11	46 ± 20	58 ± 3
Min–max	60–65	13–60	55–60
Width (cm)			
Mean ± 1 SD	505 ± 72	392 ± 179	319 ± 15
Min–max	392–592	227–659	263–516
Depth (cm)			
Mean ± 1 SD	31 ± 2	12 ± 2	11 ± 5
Min–max	29–34	9–15	8–21
Q ($m^3 s^{-1}$)			
Mean ± 1 SD	0.53 ± 0.25	0.05 ± 0.01	0.02 ± 0.03
Min–max	0.20–0.80	0.01–0.04	0.01–0.10
Water table depth (cm)			
Mean ± 1 SD	–	36 ± 20	19 ± 9
Min–max	–	5–67	5–34
Vertical hydraulic gradient			
Mean ± 1 SD	−8.0 ± 2.6	−18.5 ± 11.9	−13.1 ± 3.9
Min–max	−6.1–11.0	−9.8–31.8	−9.7–17.3
Hydraulic conductivity (K)			
Mean ± 1 SD	$1.45 \times 10^{-5} \pm 6.61 \times 10^{-5}$	$2.59 \times 10^{-4} \pm 2.66 \times 10^{-4}$	$3.42 \times 10^{-4} \pm 9.89 \times 10^{-5}$
Min–max	2.00×10^{-4}–3.23×10^{-4}	8.99×10^{-5}–5.67×10^{-4}	2.81×10^{-4}–4.56×10^{-4}
D50 (phi)			
Mean ± 1 SD	4.6 ± 0.4	4.7 ± 0.3	4.8 ± 0.6
Min–max	4.5–5.0	4.5–5.0	4.5–5.0

Sources of colonisation

The potential contribution of invertebrates in the hyporheic zone, those surviving in dry sediment using desiccation-resistant forms, and those aerially ovipositing was assessed in *Drift* and *NoDrift* channels. Upon collection, all invertebrate samples were preserved in 96% ethanol. Hyporheic invertebrate (HYP) samples were collected at *DryDay7* from three equally spaced locations (16 ± 4 m apart) along the length of each channel using methods detailed in Datry (2012). Briefly, a stainless steel standpipe (2 cm diameter, 14 cm long perforated area, 5 mm perforation diameter) was driven into the riverbed to a depth of 30 cm below the sediment surface with a sledge hammer. Six litres of water was then pumped from the hyporheic zone into a 12-L bucket using a Bou-Rouch pump and sieved through a 250-μm-mesh net to retain invertebrates.

Taxa with desiccation-resistant forms in dry sediment (SED) were sampled at *DryDay7* from three equally spaced locations along each channel, using methods detailed in Datry, Corti & Philippe (2012). At each location, 2.5 L of dry sediment was collected from a 0.25 m² area to a 5 cm depth using a hand-trowel. SED samples were taken to the laboratory ≤24 h after collection, placed into 12-L plastic containers and inundated with 3 L of dechlorinated tap water. SED samples were aerated to maintain dissolved oxygen concentrations in the overlying water column close to saturation. Mesh lids (250 μm) were used to keep emerging and crawling invertebrates from escaping. At *T1*, following 1 week of inundation, invertebrates were collected by intensively stirring sediments by hand and pouring the sediment and water mixture into a mesh sieve (250 μm). The process was repeated five times until sediments had been thoroughly washed free of invertebrates.

Aerially ovipositing taxa (OVP) were sampled using sticky traps (1 m² total surface area) installed 0.5 m above the stream surface at three equally spaced locations along each channel using methods described in Collier & Smith (1995). Sticky traps were coated on both sides (1 m² total surface area) with tree-pest adhesive. Sticky traps were deployed during the first week of rewetting (*T1* until *T2*) to minimise degradation/weathering of captured individuals. A petroleum-based solvent was used to remove invertebrates from the traps.

The potential contribution of drift was not assessed in *Drift* channels to avoid temporarily blocking colonisation by drift. Instead, drifting invertebrates (DFT) were sampled from *NoDrift* channels over two 24-h periods between *T1* and *T2*. The pre-installed drift nets were removed individually, and invertebrates were washed from nets and preserved.

Invertebrates downstream of the dried channels were prevented from colonising by upstream migration (Williams & Hynes, 1976) by scrubbing substratum located 1 2 m downstream by hand for 10 min between 1 and 3 times per day, washing invertebrates further downstream, throughout the study period.

Invertebrate processing and identification

Enumeration and identification of invertebrates was made to the lowest possible taxonomic level depending on their development and condition. Most aquatic insects were identified to genus or species level except for Chironomidae (Diptera), which were identified to subfamily. Most crustaceans, annelids and mites were identified to either the family, class or order. Adult insect taxa collected from OVP samples were counted, identified to family and sexed, and the presence of gravid females was noted.

A total of 61 traits were used to explore community functional trait composition (Tachet *et al.*, 2002; Vander Vorste *et al.*, 2015). Traits comprised maximal size, life-cycle duration, potential number of reproductive cycles per year, aquatic stages, reproduction, dispersal mode and medium, resistance forms, respiration, locomotion and substrate relation, food and feeding style. The trait database used is fuzzy coded (scores 0–5) according to the affinity of each taxon to the particular trait (Tachet *et al.*, 2002). The relative proportion of taxa in a sample with each trait was then calculated by multiplying the proportional trait affinity scores by the $\log_{10}(x + 1)$-transformed density and dividing this value by the total density per sample (Bonada, Dolédec & Statzner, 2007).

From these traits, an *a priori* selection was made to further analyse potential differences in functional trait composition among treatments. *A priori* trait selection was made based on previous studies that found taxa with these traits dominated intermittent alluvial river communities (Bonada *et al.*, 2007; Datry *et al.*, 2014a; Vander Vorste *et al.*, 2015). Selected traits included the following: resistance forms (i.e. eggs, cocoons, desiccation-resistant cells, diapause/dormancy phase), small size ($\leq$9 mm), tegument respiration and burrower substrate relation.

Head capsule size (at the widest point), a surrogate of invertebrate body size (Fairchild & Holomuzki, 2005), was measured for 4794 invertebrates belonging to the genera *Baetis*, *Caenis*, *Leuctra*, *Ecdyonurus* and *Simulini* and to the subfamilies Tanytarsini, Tanypodinae and Orthocladiinae. These eight taxa were the most common taxa in BEN samples, comprising >90% of total density. Measurements were made using an ocular micrometre to the nearest 0.1 mm. From the selected taxa, random subsampling (~10%) was used to select individuals for measurements when there were >100 individuals per sample.

Data analysis

Differences in community structure and composition among treatments. To test our first hypothesis, community structure and composition among treatment types (3 levels: *Control*, *Drift* and *NoDrift*) and sampling dates (5 levels: *T0–4*) were compared using linear mixed-effects (LME) models. These models tested for the effect of each factor and their interaction (i.e. whether the effect of treatment type depended on sampling date) on taxonomic richness, invertebrate density (ind m^{-2}) and Pielou's evenness. A nested, hierarchical approach was used to test for the effect of each factor and their interaction and select the most parsimonious model (Bolker *et al.*, 2009). First, a model was fitted, including treatment type, sampling date and the interaction term as fixed factors (i.e. full model). Second, subsequent models were constructed with a similar structure, removing one of the fixed factors (i.e. simple models). All models included random intercepts to account for random variance in metrics among the nine study channels. Full and simplified models for richness were coded as follows: full model ($n = 166$, d.f. = 17) = richness ~ treatment type + sampling date + treatment type:sampling date + (1 | channel); simple model 1 ($n = 166$, d.f. = 9) = richness ~ treatment type + sampling date + (1 | channel); simple model 2 ($n = 166$, d.f. = 5) = richness ~ treatment type + (1 | channel); and simple model 3 ($n = 166$, d.f. = 7) = richness ~ sampling date + (1 | channel). Models were validated by plotting residuals against fitted values to check for violations of assumed normality and homogeneity. Subsequently, density and Pielou's evenness were $\log_{10}(x + 1)$- and arcsine($\sqrt{x}$)-transformed, respectively, to meet these assumptions. Third, likelihood ratio tests (χ^2) were used to determine the contribution of each fixed factor by comparing the fit (measured as deviance) between models with and without the factor (Bolker *et al.*, 2009). For example, the significance of the interaction term was assessed by comparing the full model to the model without interaction term (i.e. simple model 1). Akaike Information Criteria (AIC) were also used to select the most parsimonious model and improve interpretation of model comparisons beyond likelihood ratio tests (Bolker *et al.*, 2009). The AIC represent a model's goodness of fit and are adjusted based on the number of parameters included in the model (i.e. model complexity); the lower the AIC, the better the model fits the observed data (Bolker *et al.*, 2009). Once the best model was selected, *post hoc* comparisons of pairwise factor combinations were performed to identify differences between treatment types on specific sampling dates. All LME models were constructed and compared using the *lme4* package (Bates *et al.*, 2014) and pairwise *post hoc* comparisons were made using the *phia* package (De Rosario-Martinez, 2015) for R (R Development Core Team, 2011).

Adonis, a permutational multivariate analysis of variance (Anderson, 2001), was used to test the effect of treatment type, sampling date and their interaction on community composition. Adonis returns a R^2 statistic that is a measure of separation among treatment types (0 indicates complete mixing and 1 represents full separation) according to Bray–Curtis dissimilarity values, and a P-value estimated by repeated permutations ($n = 999$) of the data. Bray Curtis dissimilarities were calculated using $\log_{10}(x + 1)$-transformed invertebrate density, averaged within each channel for each sampling date. Non-metric multidimensional scaling (NMDS) was then used to visualise compositional changes in invertebrate communities among treatment types and sampling dates. Similarity percentages (SIMPER) analysis was used to identify taxa that contributed most greatly to the overall Bray–Curtis dissimilarity values. For taxa identified by SIMPER, LME models followed by *post hoc* comparison tests, as described above, were then used to test for the effects of treatment type, sampling date and their interaction on density. Adonis, NMDS and SIMPER analysis were performed with functions in the package *vegan* (Oksanen *et al.*, 2013) for R.

Differences in community functional trait composition among treatments. To test our second hypothesis, community functional trait composition among treatment types and sampling dates was compared using LME models followed by *post hoc* comparison tests. Functional trait richness, diversity and evenness were used as dependent variables in a similar nested, hierarchical approach as presented above. Functional trait richness was measured as the total number of traits present within the community. Functional diversity (i.e. Rao's quadratic entropy) was calculated as an abundance-weighted metric that measured the mean pairwise dissimilarities of randomly selected taxa in a community as a way of describing the breadth of traits present within each community (Rao, 1982; Botta-Dukát, 2005). Functional evenness was measured as the regularity of taxonomic density within the volume of different trait combinations present (Ricotta, Bacaro & Moretti, 2014). To meet model assumptions, functional diversity and evenness were $\log_{10}(x)$- and arcsine($\sqrt{x}$)-transformed, respectively. Functional trait richness, diversity and evenness were calculated using the packages *vegan* and *ade4* (Dray & Dufour, 2007) and the function *FeveR* (Ricotta *et al.*, 2014) for R, respectively.

Principal components analysis (PCA) was used to visualise differences among treatment types and sampling dates in the relative proportion of the four *a priori* selected traits (i.e. resistance forms, small size, tegument respiration and burrower substrate relation). LME models followed by *post hoc* comparison tests were used to test the effect of treatment type, sampling date and their interaction on the relative proportion of individual functional traits. The proportion of taxa in the sample with each functional trait was calculated based on taxon affinity for each trait (i.e. fuzzy coding) using the *ade4* (Dray & Dufour, 2007) for R.

To explore how the depth to the water table during drying events influenced community structural and functional resilience, correlation analyses were performed between water table depth and community resilience. Community resilience in *Drift* and *NoDrift* channels was calculated as the number of weeks of rewetting required before mean values of taxonomic and functional metrics were not different or exceeded those of *Control* channels. This calculation yielded a total of five data points that ranged from 1 to 4 weeks in the time to recover from disturbance. Spearman rho, a non-parametric test for correlation, was then used due to the limited amount of data.

Differences in invertebrate size among treatments. LME models followed by *post hoc* comparison tests were used to test the effect of treatment type, sampling date (only *T0,1,4*) and their interaction on $\log_{10}(x + 1)$-transformed mean head capsule width.

Results

Invertebrate richness and density

A total of 67 327 invertebrates representing 137 taxa were collected in BEN samples ($n = 166$) with a mean density of 7 889 ± 5 845 ind m^{-2} (mean ± 1 SD) from *Control*, *Drift* and *NoDrift* channels (Appendix S1). *Baetis*, *Caenis*, *Leuctra*, *Ecdyonurus* and *Simulini,* and the Chironomidae subfamilies Tanytarsini, Tanypodinae and Orthocladiinae were the

Table 2 Results of linear mixed-effects models used to test the effect of treatment type (3 levels: *Control*, *Drift* and *NoDrift*), sampling date (5 levels: *T0–4* or 3 levels: *T0*, *1*, *4* for individual size) and their interaction on taxonomic structure, community function and individual size

Metric type	Factor	d.f.	ΔAIC	χ^2	*P*-value
Taxonomic structure	Richness				
	Sampling date	12	17.15	41.15	<0.001
	Treatment type	10	7.55	27.55	0.002
	Sampling date × treatment type	8	11.02	27.03	<0.001
	Density				
	Sampling date	12	25.77	49.77	<0.001
	Treatment type	10	−11.00	9.00	0.532
	Sampling date × treatment type	8	−7.12	8.88	0.352
	Evenness				
	Sampling date	12	−23.77	47.77	<0.001
	Treatment type	10	6.19	13.81	0.182
	Sampling date × treatment type	8	3.45	12.55	0.128
Community function	Trait richness				
	Sampling date	12	−23.40	47.39	<0.001
	Treatment type	10	−13.57	33.56	<0.001
	Sampling date × treatment type	8	−10.23	26.23	<0.001
	Diversity				
	Sampling date	12	52.877	76.88	<0.001
	Treatment type	10	6.417	13.59	0.193
	Sampling date × treatment type	8	4.645	11.36	0.182
	Evenness				
	Sampling date	12	8.59	32.59	0.001
	Treatment type	10	−8.51	11.48	0.321
	Sampling date × treatment type	8	−5.01	10.99	0.202
Individual size	Head capsule width				
	Sampling date	6	9.12	21.12	0.002
	Treatment type	6	7.19	19.19	0.004
	Sampling date × treatment type	4	4.38	12.38	0.015

most common BEN taxa. Among the sources of colonisation sampled, HYP samples ($n = 18$) had 37 taxa with mean taxonomic richness of 10 ± 5 taxa and density of 97 ± 101 ind/6L (Appendix S1). SED samples ($n = 18$) had 16 taxa with mean taxonomic richness of 6 ± 2 taxa and density of 12 ± 26 ind m^{-2} (Appendix S1). OVP samples ($n = 18$) had 11 taxa with mean taxonomic richness of 2 ± 1 taxa and density of 4 ± 3 ind m^{-2} (Appendix S1). Gravid adult females comprised <10% of taxa captured in OVP samples. DFT samples ($n = 6$) had 67 taxa with a mean richness of 38 ± 6 taxa and density of 87 ± 63 ind 100 m^{-3} (Appendix S1).

Differences in community structure and composition among treatments

There was a significant interaction between treatment type and sampling date for taxonomic richness (LME treatment × date: χ^2 (8 d.f.) = 27.026, $P < 0.001$), indicating that the temporal variation in taxonomic richness differed among treatments (Table 2, Fig. 3). Before generating the disturbance (*T0*), there were no differences in taxonomic richness among treatments (*post hoc* tests, $P > 0.05$, Fig. 3). After 1 week of rewetting (*T1*), taxonomic richness was higher in *Control* versus *Drift* (*post hoc*: χ^2 (1 d.f.) = 5.65, $P = 0.017$) and *Control* versus *NoDrift* (*post hoc*: χ^2 (1 d.f.) = 4.13, $P = 0.042$), but there was no difference between the *Drift* versus *NoDrift* channels (*post hoc* tests, $P > 0.05$; Fig. 3). After 2 weeks of rewetting (*T2*), taxonomic richness was no longer different among treatments (*post hoc* tests, $P > 0.05$; Fig. 3). Density and Pielou's evenness did not differ among treatments on any sampling date (*post hoc* tests, $P > 0.05$, Fig. 3). For all treatments, density increased during the 2-week period following rewetting (*T1* and *T2)*, before declining at *T3* and *T4* (Table 2, Fig. 3). Pielou's evenness

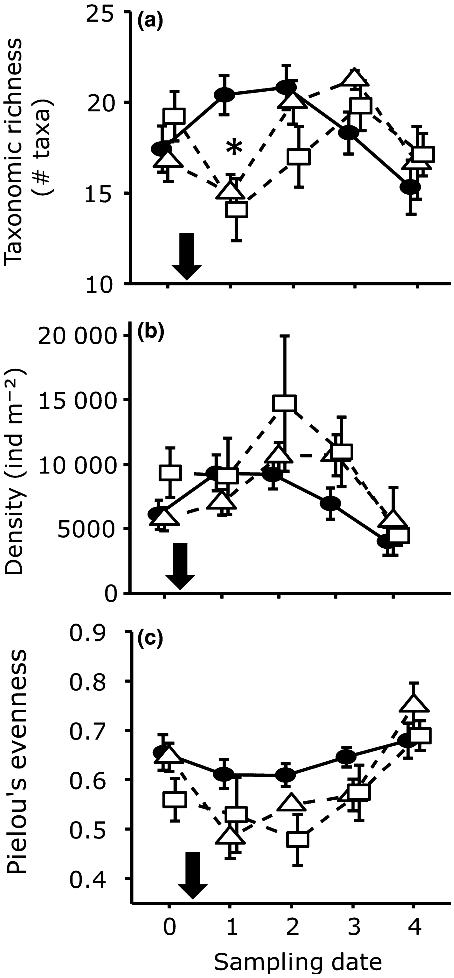

Fig. 3 Differences in taxonomic richness (# of taxa) (a), density (ind m^{-2}) (b) and Pielou's evenness (c) among *Control* (●), *Drift* (△) and *NoDrift* (□) channels over the study period. Arrow indicates a 1-week drying event between *T0* and *T1*. Astrick indicates significant differences between treatment types (*post hoc* tests, $P < 0.05$). Error bars represent ± 1 SE.

Table 3 Results from adonis testing the effect of treatment type (3 levels: *Control*, *Drift* and *NoDrift*), sampling date (5 levels: *T0 4*) and their interaction on community composition using Bray Curtis dissimilarity values

Source	d.f.	*F* statistic	R^2	*P*-value
Sampling date	4	4.606	0.294	<0.001
Treatment type	2	5.093	0.163	<0.001
Sampling date × treatment type	8	0.754	0.096	0.738
Residuals	28		0.447	
Total	42		1.000	

increased gradually following rewetting (LME date: χ^2 (12 d.f.) = 47.77, $P < 0.001$) (Table 2, Fig. 3).

Community composition differed among treatments consistently across all sampling dates (adonis treatment × date: $R^2 = 0.096$, $P = 0.738$; Table 3, Fig. 4). NMDS showed that before the disturbance (*T0*), there was little difference among treatments, but after 1 week of rewetting (*T1*), composition in *Control* differed from that of *Drift* and *NoDrift* channels, but *Drift* and *NoDrift* channels did not differ from each other (Fig. 4). Composition became more similar over the sampling period until *T4*. Dissimilarity in community composition among treatment types was mainly due to densities of *Baetis*, *Caenis* and *Leuctra*. The cumulative contribution of these taxa to dissimilarity was 15% for both *Drift* versus *NoDrift* and *Drift* versus *Control* and 18% for *NoDrift* versus *Control*. For *Baetis*, density increased in *Control* channels from 250 ± 135 ind m^{-2} to 1220 ± 376 ind m^{-2} between *T0* and *T1* compared to *Drift* and *NoDrift* channels (LME treatment × date: χ^2 (8 d.f.) = 29.09, $P < 0.001$); however, at *T2*, densities of *Baetis* were no longer different among treatments (*post hoc* tests, $P > 0.05$).

Differences in community functional trait composition among treatments

There was a significant interaction between treatment type and sampling date for functional trait richness (LME treatment × date: χ^2 (8 d.f.) = 26.23, $P < 0.001$), indicating that the temporal variation in trait richness differed among treatments (Table 2, Fig. 5). Before generating the disturbance (*T0*), there were no differences in trait richness among treatments (*post hoc* tests, $P > 0.05$, Fig. 5). After 1 week of rewetting (*T1*), *Drift* and *NoDrift* differed from *Control* channels (*post hoc*: χ^2 (1 d.f.) = 27.10, $P < 0.001$; χ^2 (1 d.f.) = 16.89, $P < 0.001$, respectively), but not from each other. Trait richness increased in *Control* channels (35.5 ± 2.2 to 38.0 ± 1.3), but remained similar in *Drift* (34.6 ± 1.9 to 33.3 ± 2.6) and *NoDrift* channels (34.3 ± 1.5 to 34.3 ± 2.8) between *T1* and *T2*. All treatments showed similar patterns of functional diversity (LME sampling date: χ^2 (12 d.f.) = 76.88, $P < 0.001$) and functional evenness (LME sampling date: χ^2 (12 d.f.) = 32.59, $P = 0.001$) during the study period (Table 2, Fig. 5).

Communities differed based in their relative proportion of the *a priori* selected traits (Fig. 6). PCA showed that cross sampling dates, treatments were separated along axis 1 (66% of variability), indicating *Drift* and *NoDrift* had a higher proportion of taxa with small body size while *Control* channels had higher proportions of taxa with resistance forms (Fig. 6). Temporal variability was different among treatments for both the proportion of small taxa (LME treatment × date: ΔAIC = 0.20, χ^2 (8 d.f.) = 16.21, $P = 0.040$) and resistance forms (LME treatment × date: ΔAIC = 4.02, χ^2 (8 d.f.) = 2.08, $P = 0.010$).

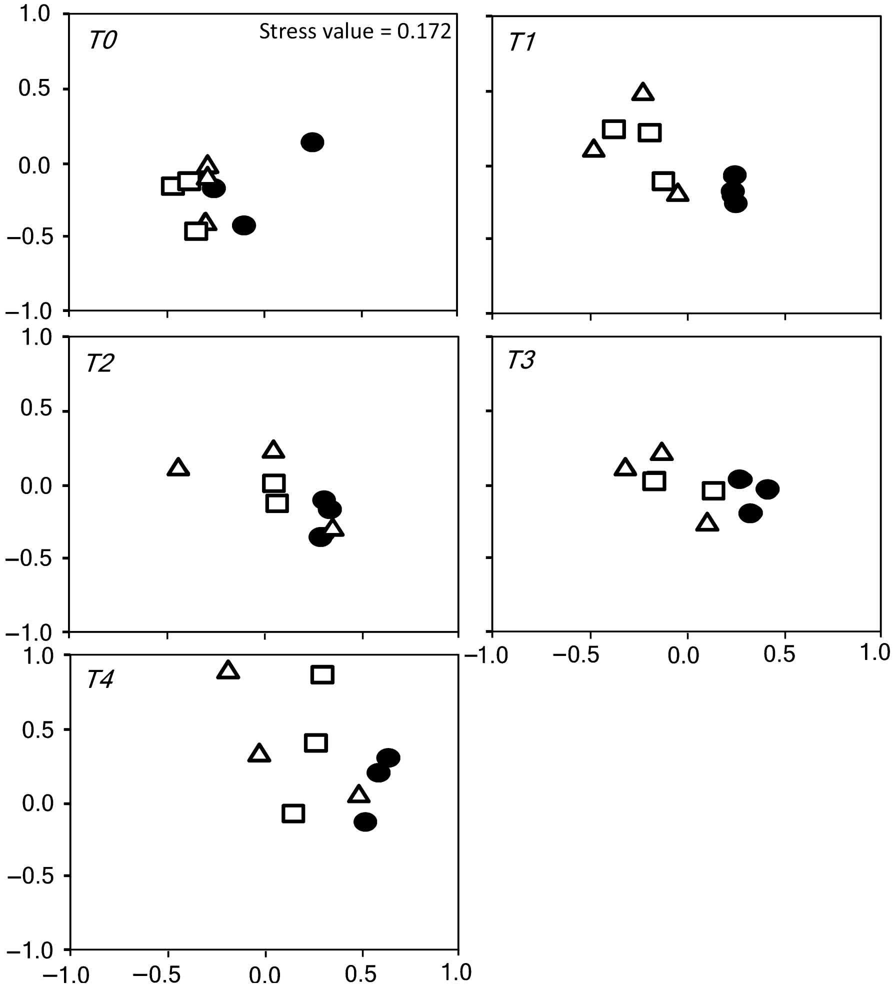

Fig. 4 Non-metric multidimensional scaling (NMDS) plots showing differences in communities among *Control* (●), *Drift* (△) and *NoDrift* (□) channels based on Bray Curtis dissimilarity values over the sampling period. A 1-week drying event occurred between *T0* and *T1*.

At *T0*, the proportion of small taxa was not different for *Drift* versus *NoDrift* (*post hoc* tests: $P > 0.05$), but both treatment types had a significantly higher proportion than *Control* channels (*post hoc*: χ^2 (1 d.f.) = 6.16, $P = 0.013$; χ^2 (1 d.f.) = 5.47, $P = 0.019$, respectively). These differences persisted until *T4* for *Control* versus *Drift* and at *T2* for *Control* versus *NoDrift* (*post hoc* tests, $P > 0.05$).

Resilience of community taxonomic richness (Spearman rho test: $\rho = 0.866$, $P = 0.058$) and functional diversity (Spearman rho test: $\rho = 0.949$, $P = 0.014$) in *Drift* and *NoDrift* was positively correlated with mean depth to the water table during drying events (Fig. 7). Resilience of density, evenness, functional trait richness and evenness were not correlated with water table depth (Spearman rho tests: $P > 0.05$).

Differences in invertebrate size among treatments

There was a significant interaction of treatment type and sampling date on mean head capsule size of the eight most common taxa (LME treatment × date: χ^2 (4 d.f.) = 12.38, $P = 0.015$), indicating that the temporal variation in size differed among treatments (Table 2, Fig. 8). Before the drying event (*T0*), there was no difference in size among treatments (*post hoc* tests, $P > 0.05$). Upon 1 week of rewetting (*T1*), size decreased significantly compared to *Control* in both *Drift* and *NoDrift* channels (*post hoc*: χ^2 (1 d.f.) = 4.99, $P = 0.026$; χ^2 (1 d.f.) = 7.70, $P = 0.006$, respectively) and remained smaller until *T4* (*post hoc*: χ^2 (1 d.f.) = 6.31, $P = 0.012$; χ^2 (1 d.f.) = 9.31, $P = 0.002$, respectively).

Discussion

Drift is not the primary process promoting the resilience of invertebrate communities

In the Eygues River, the view that drift is the primary process of invertebrate colonisation (Brittain & Eikeland, 1988; Mackay, 1992; Bilton *et al.*, 2001; Altermatt, 2013) was challenged. Contradictory to our hypothesis based

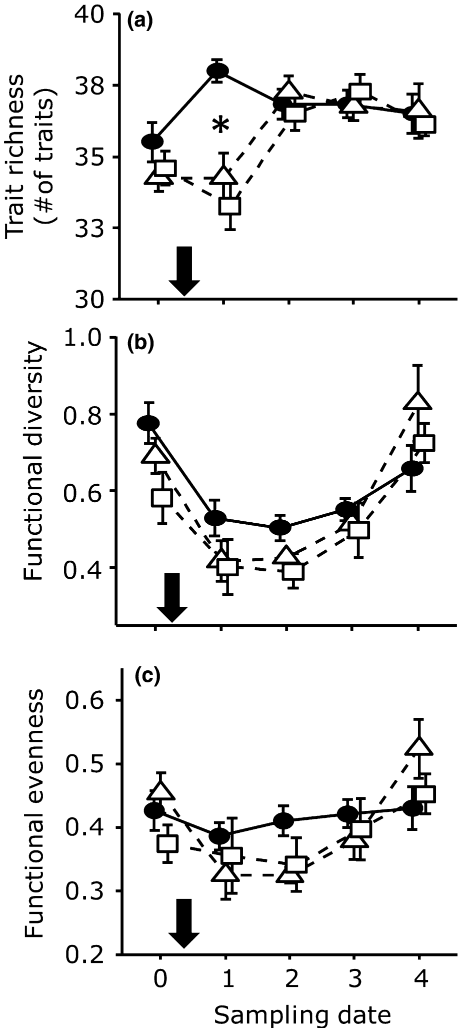

Fig. 5 Differences in functional trait richness (a), diversity (b) and evenness (c) among *Control* (●), *Drift* (△) and *NoDrift* (□) channels over the study period. Arrow indicates a 1-week drying event between *T0* and *T1*. Astrick indicates significant differences between treatment types (*post hoc* tests, $P < 0.05$). Error bars represent ± 1 SE.

on this view, invertebrate communities in *Drift* and *NoDrift* channels were similarly affected by drying. Furthermore, our hypothesis that functional trait composition would be more altered by drying in the absence of drift was unsupported. Against our predictions, taxonomic structure, composition and functional trait richness, diversity and evenness were similar in channels with and without drift, and parallel shifts in invertebrate size following rewetting suggest sources of colonists were similar across dried channels. These results contrast with many previous studies supporting the 'drift paradigm' in small-scale experiments (e.g. Townsend & Hildrew, 1976; Williams & Hynes, 1976; Palmer *et al.*, 1992; Bruno *et al.*, 2012) or observational field studies (e.g. Matthaei *et al.*, 1997) and suggest that drift may not be of overwhelming importance in promoting high community resilience, including the recovery of functional aspects of communities, in intermittent alluvial rivers.

In this alluvial river, invertebrate communities were highly resilient to drying, both structurally and functionally after a 1-week drying event. Taxonomic richness, density and evenness all recovered within 1–2 weeks of rewetting. Previous studies in alluvial rivers in New Zealand, Switzerland and France have also found high community resilience to both floods (e.g. Sagar, 1986; Matthaei *et al.*, 1997) and longer drying events than generated in this study (e.g. Fowler, 2004; Vander Vorste *et al.*, 2015), with recovery generally occurring in <4 weeks following disturbance. Functional diversity was not different in dried channels compared to control channels in this study, despite lower taxonomic and functional trait richness after 1 week of rewetting. This supports the idea that communities in disturbed environments are functionally redundant (i.e. distinct taxa have similar functional traits) because harsh environmental conditions may exclude taxa that are poorly adapted to these conditions, yielding communities comprised of disturbance-resistant and/or resilient taxa (Mouchet *et al.*, 2010; Boersma *et al.*, 2014; Vander Vorste *et al.*, 2015). In the Eygues River, recovery of the eight most common taxa, comprising 90% of total density, within 1–2 weeks of rewetting, was likely the most important reason for high functional resilience. For example, the most common taxa, *Baetis spp.*, reached densities up to 470 ind m^{-2} after 1 week of rewetting. This genus has a small body size and strong swimming ability and can disperse aerially as an adult and, therefore, could potentially colonise previously disturbed channels by drift, vertical migration from the hyporheic zone, aerial oviposition or any combination of these processes.

In alluvial rivers, high resilience of communities can also be explained by the availability of multiple sources of colonisation that are generated through habitat-mosaic dynamics and found vertically, longitudinally and laterally from disturbed channels (Malard *et al.*, 2002; Arscott *et al.*, 2005; Stanford *et al.*, 2005). This three-dimensional matrix of colonisation sources allows organisms to colonise using multiple processes (i.e. pathways *sensu* Grant *et al.*, 2010), increasing community resilience (Fagan, 2002; Grant, 2011). For example, the persistence of modelled river communities facing disturbances was previously shown to be strongly related to the number of colonisation sources and their spatial arrangement on the landscape (e.g. Fagan, 2002; Grant, 2011). In these studies, resilience of communities

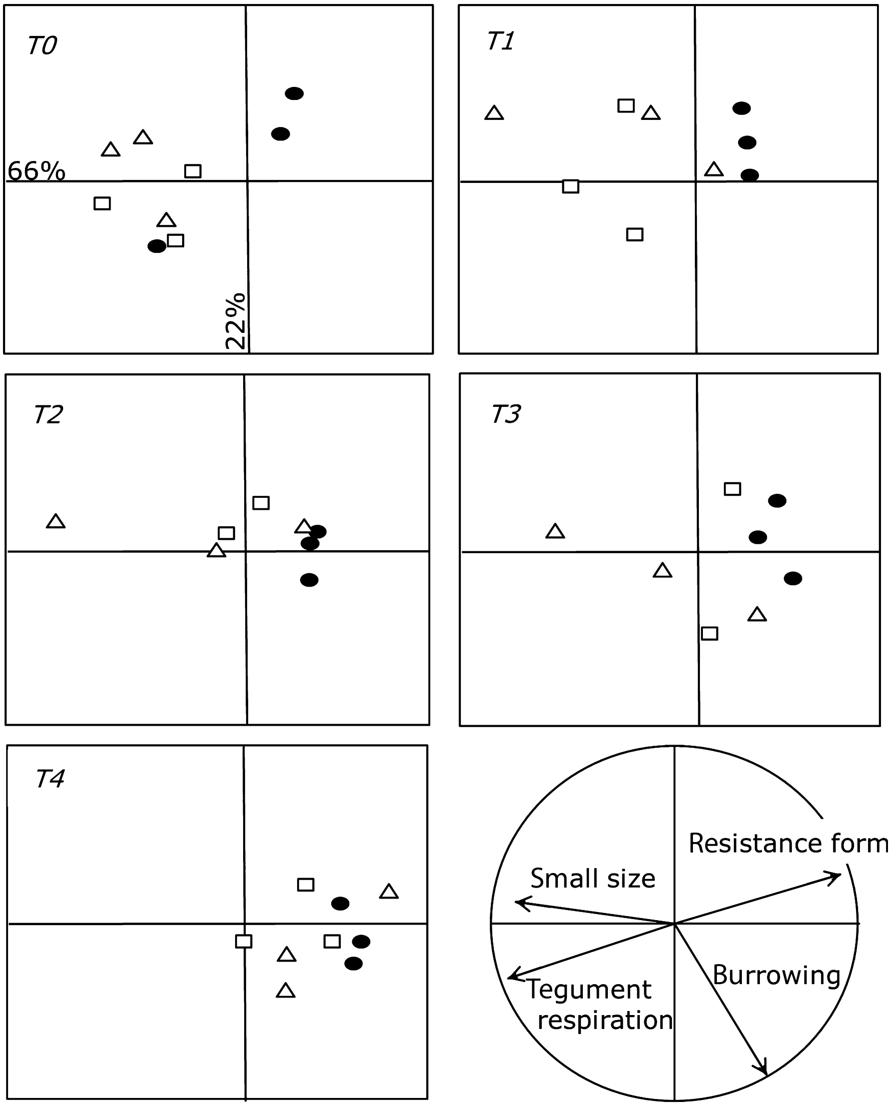

Fig. 6 Principal components analysis (PCA) showing differences among channels in the relative proportion of taxa with small size (≤9 mm), tegument respiration, resistance forms and burrowing habit among *Control* (●), *Drift* (△) and *NoDrift* (□) over the sampling period. A 1-week drying event occurred between *T0* and *T1* sampling dates.

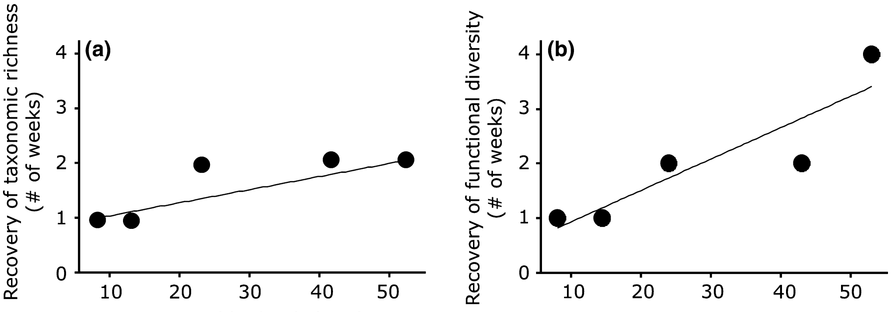

Fig. 7 Relationship between recovery of taxonomic richness and functional diversity and the mean water table depth in channels during drying (cm). Correlation tested with Spearman rho test (ρ = 0.866, *P* = 0.058 for taxonomic richness; ρ = 0.949, *P* = 0.014 for functional diversity).

increased greatly when the number of sources increased and colonisation occurred from multiple pathways. Furthermore, this dimensionality implies that resilience can be maintained despite the loss of a potential colonisation process (e.g. drift), if other colonisation sources remain and taxa have traits that facilitate their use (e.g. vertical migration, aerial oviposition, resistance forms). Identifying and quantifying these sources and processes has been identified as a key challenge facing ecologists aiming to explain patterns in community dynamics (Nathan, 2001), hence the demand for empirical evidence (Grant, 2011).

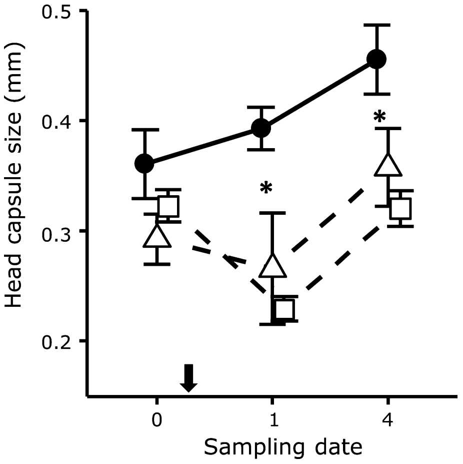

Fig. 8 Mean head capsule size (mm) of the eight most abundant invertebrate taxa among *Control* (●), *Drift* (△) and *NoDrift* (□) channels. Arrow indicates a 1-week drying event between *T0* and *T1*. Astrick indicates significant differences between treatment types (*post hoc* tests, $P < 0.05$). Error bars represent ± 1 SE.

Is vertical migration from the hyporheic zone an essential process promoting invertebrate community resilience?

Three lines of evidence indicate the hyporheic zone was the main source of colonists upon rewetting. First, the hyporheic zone contained, during the drying event, all eight of the most common taxa found in the benthic zone. Second, there was a distinct decrease in head capsule width, a measure of body size, of the eight most common taxa upon rewetting in all treatment channels. This suggests that taxa were coming from the hyporheic zone, where body size is arguably the most important attribute limiting invertebrate colonisation (Gayraud & Philippe, 2001; Bo *et al.*, 2006; Navel *et al.*, 2010; Descloux, Datry & Usseglio-Polatera, 2014). Third, community resilience was negatively correlated with the depth of the water table during drying: the recovery time of both taxonomic richness and functional diversity increased as the water table depth increased. This circumstantial evidence, together with finding that blocking drift had no effect on invertebrate community resilience, indicates most taxa colonising the rewetted channels originated from the hyporheic zone. Previous studies have suggested that the hyporheic zone could be a source of colonists following disturbance in alluvial rivers (e.g. Holomuzki & Biggs, 2007; Kawanishi *et al.*, 2013). For example, Holomuzki & Biggs (2007) found densities of the snail *Potamopyrgus antipodarum* recovered within 12 to 24 h of floods because it used the hyporheic zone as a refuge to escape the strong hydraulic forces. However, further experiments are still needed to deduce direct evidence of the hyporheic refuge hypothesis (i.e. organisms enter the hyporheic zone during disturbance and then return to the surface; Palmer *et al.*, 1992; Stubbington, Wood & Reid, 2011; Dole-Olivier, 2011). In this experiment, it was not possible to distinguish whether organisms collected following rewetting were also in the benthic zone prior to drying, or whether they had already been in the hyporheic zone as eggs or early instars. Future mark–recapture or mesocosm experiments could be used to address this distinction. For example, Kawanishi *et al.* (2013) recaptured individuals of the benthic fish, *Cobitis shikokuensis*, in an intermittent alluvial river after they were marked in isolated pools before the channel dried. Combined with the results from this study, there is mounting evidence that the vertical migration of organisms from the hyporheic zone can be an essential process promoting resilience in alluvial rivers.

Alluvial rivers, such as the Eygues River, are common across most of the Alps and other European mountain ranges including the Apennines and Pyrenees (Piégay *et al.*, 2009; Tockner *et al.*, 2006). These rivers also stretch across large portions of the western United States, Canada, Alaska and New Zealand (Stanford *et al.*, 2005; Gray & Harding, 2007). However, generalising these results across all alluvial rivers or other river types should be performed with caution because the hydrological connections between surface and hyporheic habitats are known to vary spatially along the river corridor (Stanford & Ward, 1993; Malard *et al.*, 2002; Stubbington *et al.*, 2011). For example, in alluvial rivers where the hyporheic zone is unsaturated during dry periods, it is unlikely that its contribution to community resilience would be high (e.g. Datry, 2012). In the Eygues River, channels featured relatively large grain size, high porosity and shallow depth of the water, hence providing an ideal setting to assess the importance of the hyporheic zone as a source of colonisation for surface communities. Yet these channel features are not exclusive to alluvial rivers, and the importance of the hyporheic zone as a refuge and/or source has been evoked across many river types (Williams & Hynes, 1976; Boulton *et al.*, 1992; Stubbington *et al.*, 2015). Therefore, the importance of the hyporheic zone to community resilience may hold true in other river systems as well.

Resistance forms and aerial oviposition may not be as important for promoting community resilience in alluvial rivers as in other systems. In this study, only 7% of benthic taxa were found in dry sediments and density of these taxa was very low (12 ± 26 ind m^{-2}). In contrast, Storey & Quinn (2013) found dry sediments contained 70% of the taxa from nearby flowing headwater streams in New Zealand. Similarly, Datry *et al.* (2012) recovered 65% of the benthic taxa in the Albarine River from dry river sediments. In alluvial rivers, coarse, dry sediments may not maintain the high relative humidity generally associated with invertebrate seedbank viability (Storey & Quinn, 2013; Stubbington & Datry, 2013). Only 10% of benthic taxa were collected from sticky traps in this study, suggesting aerial oviposition was not an important process promoting resilience following rewetting (≤4 weeks) in this river. In contrast, previous studies have shown aerial oviposition can be a key process of colonisation in spatially isolated systems such as headwater (e.g. Hughes *et al.*, 2009) and arid-land streams (e.g. Cañedo-Argüelles *et al.*, 2015), where long distances from colonisation sources are only overcome by taxa with strong flight capabilities.

Despite strong circumstantial evidence, future experiments are needed to demonstrate and quantify the contribution of the hyporheic zone to community resilience. Reach-scale field experiments that manipulate the vertical migration of organisms, using either artificial (e.g. nylon mesh) or natural barriers (e.g. fine sediments), could provide direct evidence of the importance of this process for community resilience. These experiments should be performed across a gradient of stream sizes and types to improve the generality of findings. Clearly, physical habitat characteristics (e.g. % fine sediment, porosity and hydraulic conductivity) affect the vertical migration of organisms (Navel *et al.*, 2010; Descloux *et al.*, 2014; Vadher, Stubbington & Wood, 2015). Yet other abiotic (e.g. water temperature) and biotic (e.g. intraspecific competition) factors could also play an important role (Stubbington *et al.*, 2011).

Considering and managing habitat connectivity in three dimensions

Drift has often been viewed as the primary process promoting the resilience of invertebrate communities in rivers (e.g. Townsend & Hildrew, 1976; Williams & Hynes, 1976; Brittain & Eikeland, 1988; Mackay, 1992; Bilton *et al.*, 2001), and unidirectionality (longitudinal) is a pervasive concept in lotic ecology (Fagan, 2002; Poole, 2002). However, the results of this study indicate that a three-dimensional perspective is more appropriate, at least for alluvial rivers. While the lateral dimension of river ecosystems has long been recognised in basic and applied research, the vertical dimension tends to be overlooked, notably in management practices (Boulton *et al.*, 2010). The hyporheic zone is threatened by many human activities, including agriculture, mining and flow regulation that lead to its clogging with fine sediments (Datry *et al.*, 2014b) and limiting the vertical migration of organisms (Navel *et al.*, 2010; Descloux *et al.*, 2014; Vadher *et al.*, 2015). Furthermore, climate change, water abstraction and flow regime alterations can increase the severity of drying events in rivers (Larned *et al.*, 2010), lowering the water table and preventing the use of the hyporheic zone as a refuge by invertebrates (e.g. Clinton, Grimm & Fisher, 1996). In a context of increasing pressures on river ecosystems, adaptable management approaches are needed to direct attention to sources (e.g. hyporheic zone) that are essential to promoting community resilience (Palmer *et al.*, 2005; Heino, 2013).

Acknowledgments

This project was funded by the Rhône-Méditerranée-Corse Water Agency through the 'Invertebrate community resistance and resilience in intermittent rivers' project, with additional support for RV by IRSTEA. We thank the people who helped dry channels and collect samples in the field including Raphaël Mons, Bertrand Launay, Guillaume Le Goff, Maxence Forcellini, Pascal Roger, Laury Daligualt and Mathieu Cassel. Additionally, we thank associate editor, Richard Johnson, as well as Kate Boersma, Rachel Stubbington and two anonymous referees for their helpful comments.

References

Altermatt F. (2013) Diversity in riverine metacommunities: a network perspective. *Aquatic Ecology*, **47**, 365–377.

Anderson M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.

Arscott D.B., Tockner K. & Ward J.V. (2005) Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river. *Journal of the North American Benthological Society*, **24**, 934–954.

Bates D., Maechler M., Bolker B. & Walker S. (2014) lme4: linear mixed-effects models using Eigen and S4 *R package version 1.1–7* http://cran.r-project.org/package=lme4.

Bêche L.A. & Resh V.H. (2007) Short-term climatic trends affect the temporal variability of macroinvertebrates in California 'Mediterranean' streams. *Freshwater Biology*, **52**, 2317–2339.

Bilton D.T., Freeland J.R. & Okamura B. (2001) Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, **32**, 159–181.

Bo T., Cucco M., Fenoglio S. & Malacarne G. (2006) Colonisation patterns and vertical movements of stream invertebrates in the interstitial zone: a case study in the Apennines, NW Italy. *Hydrobiologia*, **568**, 67–78.

Boersma K.S., Bogan M.T., Henrichs B.A. & Lytle D.A. (2014) Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. *Freshwater Biology*, **59**, 491–501.

Bogan M.T., Boersma K.S. & Lytle D.A. (2015) Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams. *Freshwater Biology*, **60**, 2547–2558.

Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H. *et al.* (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.

Bonada N., Dolédec S. & Statzner B. (2007) Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology*, **13**, 1658–1671.

Botta-Dukát Z. (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, **16**, 533–540.

Boulton A.J., Datry T., Kasahara T., Mutz M. & Stanford J.A. (2010) Ecology and management of the hyporheic zone: stream–groundwater interactions of running waters and their floodplains. *Journal of the North American Benthological Society*, **29**, 26–40.

Boulton A.J., Peterson C.G., Grimm N.B. & Fisher S.G. (1992) Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology*, **73**, 2192–2207.

Brittain J.E. & Eikeland T.J. (1988) Invertebrate drift- a review. *Hydrobiologia*, **166**, 77–93.

Bruno M.C., Bottazzi E. & Rossetti G. (2012) Downward, upstream or downstream? Assessment of meio- and macrofaunal colonization patterns in a gravel-bed stream using artificial substrates. *Annales de Limnologie - International Journal of Limnology*, **48**, 371–381.

Cañedo-Argüelles M., Boersma K.S., Bogan M.T., Olden J.D., Phillipsen I., Schriever T.A. *et al.* (2015) Dispersal strength determines meta-community structure in a dendritic riverine network. *Journal of Biogeography*, **42**, 778–790.

Capderrey C., Datry T., Foulquier A., Claret C. & Malard F. (2013) Invertebrate distribution across nested geomorphic features in braided-river landscapes. *Freshwater Science*, **32**, 1188–1204.

Clinton S.M., Grimm N.B. & Fisher S.G. (1996) Response of a hyporheic invertebrate assemblage to drying disturbance in a desert stream. *Journal of the North American Benthological Society*, **15**, 700–712.

Collier K.J. & Smith B.J. (1995) Sticky trapping of adult mayflies, stoneflies and caddisflies alongside three contrasting streams near Hamilton, New Zealand. *New Zealand Natural Sciences*, **22**, 1–9.

Datry T. (2012) Benthic and hyporheic invertebrate assemblages along a flow intermittence gradient: effects of duration of dry events. *Freshwater Biology*, **57**, 563–574.

Datry T., Corti R. & Philippe M. (2012) Spatial and temporal aquatic–terrestrial transitions in the temporary Albarine River, France: responses of invertebrates to experimental rewetting. *Freshwater Biology*, **57**, 716–727.

Datry T., Lamouroux N., Thivin G., Descloux S. & Baudoin J.M. (2014b) Estimation of sediment hydraulic conductivity in river reaches and its potential use to evaluate streambed clogging. *River Research and Applications*, doi:10.1002/rra.2784.

Datry T., Larned S.T., Fritz K.M., Bogan M.T., Wood P.J., Meyer E.I. *et al.* (2014a) Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. *Ecography*, **37**, 94–104.

De Rosario-Martinez H. (2015) phia: Post-hoc interaction analysis. R package version 0.1?5, http://cran.r-project.org/web/packages/phia/.

Descloux S., Datry T. & Usseglio-Polatera P. (2014) Trait-based structure of invertebrates along a gradient of sediment colmation: benthos versus hyporheos responses. *Science of the Total Environment*, **466–467**, 265–276.

Doering M., Uehlinger U., Rotach A., Schlaepfer D.R. & Tockner K. (2007) Ecosystem expansion and contraction dynamics along a large alpine alluvial corridor (Tagliamento River, Northeast Italy). *Earth Surface Processes and Landforms*, **32**, 1693–1704.

Dole-Olivier M.J. (2011) The hyporheic refuge hypothesis reconsidered: a review of hydrological aspects. *Marine and Freshwater Research*, **62**, 1281–1302.

Dray S. & Dufour A.B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22**, 1–20.

Englund G. & Cooper S.D. (2003) Scale effects and extrapolation in ecological experiments. *Advances in Ecological Research*, **33**, 161–213.

Fagan W.F. (2002) Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, **83**, 3243–3249.

Fairchild M.P. & Holomuzki J.R. (2005) Multiple predator effects on microdistributions, survival, and drift of stream hydropsychid caddisflies. *Journal of the North American Benthological Society*, **24**, 101–112.

Fowler R.T. (2004) The recovery of benthic invertebrate communities following dewatering in two braided rivers. *Hydrobiologia*, **523**, 17–28.

Fritz K.M. & Dodds W.K. (2004) Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tallgrass prairie stream system. *Hydrobiologia*, **527**, 99–112.

Gayraud S. & Philippe M. (2001) Does subsurface interstitial space influence general features and morphological traits of the benthic macroinvertebrate community in streams? *Archiv für Hydrobiologie*, **151**, 667–686.

Grant E.H.C. (2011) Structural complexity, movement bias, and metapopulation extinction risk in dendritic ecological networks. *Journal of the North American Benthological Society*, **30**, 252–258.

Grant E.H.C., Nichols J.D., Lowe W.H. & Fagan W.F. (2010) Use of multiple dispersal pathways facilitates amphibian persistence in stream networks. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 6936–6940.

Gray D. & Harding J.S. (2007) Braided river ecology: a literature review of physical habitats and aquatic invertebrate communities. *Science for Conservation*, **279**, 50.

Heino J. (2013) The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biological Reviews of the Cambridge Philosophical Society*, **88**, 166–178.

Holomuzki J.R. & Biggs B.J. (2007) Physical microhabitat effects on 3-dimensional spatial variability of the hydrobiid snail, Potamopyrgus antipodarum. *New Zealand Journal of Marine and Freshwater Research*, **41**, 357–367.

Hughes J.M., Schmidt D.J. & Finn D.S. (2009) Genes in streams: using DNA to understand the movement of freshwater fauna and their riverine habitat. *BioScience*, **59**, 573–583.

Kawanishi R., Inoue M., Dohi R., Fujii A. & Miyake Y. (2013) The role of the hyporheic zone for a benthic fish in an intermittent river: a refuge, not a graveyard. *Aquatic Sciences*, **75**, 425–431.

Lake P.S. (2000) Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, **19**, 573–592.

Larned S.T., Datry T., Arscott D.B. & Tockner K. (2010) Emerging concepts in temporary-river ecology. *Freshwater Biology*, **55**, 717–738.

Ledger M.E., Harris R.M.L., Armitage P.D. & Milner A.M. (2012) Climate change impacts on community resilience: evidence from a drought disturbance experiment. *Advances in Ecological Research*, **46**, 211–258.

Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J.M., Hoopes M.F. *et al.* (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.

Mackay R.J. (1992) Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 617–628.

Malard F., Tockner K., Dole-Olivier M.J. & Ward J.V. (2002) A landscape perspective of surface–subsurface hydrological exchanges in river corridors. *Freshwater Biology*, **47**, 621–640.

Matthaei C., Uehlinger U.R.S. & Frutiger A. (1997) Response of benthic invertebrates to natural versus experimental disturbance in a Swiss prealpine river. *Freshwater Biology*, **37**, 61–77.

Mouchet M.A., Villéger S., Mason N.W.H. & Mouillot D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**, 867–876.

Müller K. (1954) Investigations on the organic drift in North Swedish streams. *Report Institute Freshwater Research Drottningholm*, **35**, 133–148.

Nathan R. (2001) The challenges of studying dispersal. *Trends in Ecology & Evolution*, **16**, 481–483.

Navel S., Mermillod-Blondin F., Montuelle B., Chauvet E., Simon L., Piscart C. *et al.* (2010) Interactions between fauna and sediment control the breakdown of plant matter in river sediments. *Freshwater Biology*, **55**, 753–766.

Needham P.R. (1928) A net for the capture of stream drift organisms. *Ecology*, **9**, 339–342.

Oksanen J., Guillaume Blanchet F., Kindt R., Legendre P., Minchin P.R., O'hara R.B. *et al.* . (2013) Vegan: community ecology package. *R package version 2.0–9*, http:\\cran.r-project.org\package=vegan.

Olden J.D., Konrad C.P., Melis T.S., Kennard M.J., Freeman M.C., Mims M.C. *et al.* (2014) Are large-scale flow experiments informing the science and management of freshwater ecosystems? *Frontiers in Ecology and the Environment*, **12**, 176–185.

Palmer M., Bernhardt E., Allan J., Lake P., Alexander G., Brooks S. *et al.* (2005) Standards for ecologically successful river restoration. *Journal of Applied Ecology*, **42**, 208–217.

Palmer M.A., Bely A.E. & Berg K.E. (1992) Response of invertebrates to lotic disturbance: a test of the hyporheic refuge hypothesis. *Oecologia*, **89**, 182–194.

Piégay H., Alber A., Slater L. & Bourdin L. (2009) Census and typology of braided rivers in the French Alps. *Aquatic Sciences*, **71**, 371–388.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D. *et al.* (1997) The natural flow regime. *BioScience*, **47**, 769–784.

Poole G.C. (2002) Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology*, **47**, 641–660.

Rao C.R. (1982) Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology*, **21**, 24–43.

Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W. *et al.* (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, **7**, 433–455.

Ricotta C., Bacaro G. & Moretti M. (2014) A new measure of functional evenness and some of its properties. *PLoS ONE*, **9**(8), e104060. doi:10.1371/journal.pone.0104060.

Sagar P.M. (1986) The effects of floods on the invertebrate fauna of a large, unstable braided river. *New Zealand Journal of Marine and Freshwater Research*, **20**, 37–46.

Stanford J., Lorang M. & Hauer F. (2005) The shifting habitat mosaic of river ecosystems. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen*, **29**, 123–136.

Stanford J.A. & Ward J.V. (1993) An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. *Journal of the North American Benthological Society*, **12**, 48–60.

Stanley E.H., Buschman D.L., Boulton A.J., Grimm N.B. & Fisher S.G. (1994) Invertebrate resistance and resilience to intermittency in a desert stream. *American Midland Naturalist*, **131**, 288–300.

Storey R.G. & Quinn J.M. (2013) Survival of aquatic invertebrates in dry bed sediments of intermittent streams: temperature tolerances and implications for riparian management. *Freshwater Science*, **32**, 250–266.

Stubbington R., Boulton A.J., Little S. & Wood P.J. (2015) Changes in invertebrate assemblage composition in benthic and hyporheic zones during a severe supraseasonal drought. *Freshwater Science*, **34**, 344–354.

Stubbington R. & Datry T. (2013) The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones. *Freshwater Biology*, **58**, 1202–1220.

Stubbington R., Wood P.J. & Reid I. (2011) Spatial variability in the hyporheic zone refugium of temporary streams. *Aquatic Sciences*, **73**, 499–511.

Tachet H., Richoux P., Bournaud M. & Usseglio-Polatera P. (2002) *Invertébrés d'eau douce (2nd corrected impression)*. CNRS éditions, Paris, France.

Team R.D.C. (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Tockner K., Paetzold A., Karaus U., Claret C. & Zettel J. (2006) *Ecology of braided rivers, in Braided rivers: process, deposits, ecology and management*. (eds G. H. Sambrook Smith, J. L. Best, C. S. Bristow and G. E. Petts), Blackwell Publishing Ltd., Oxford, UK. doi: 10.1002/9781444304374.ch17

Townsend C.R. (1989) The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*, **8**, 36–50.

Townsend C.R. & Hildrew A.G. (1976) Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *Journal of Animal Ecology*, **45**, 759–772.

Vadher A.N., Stubbington R. & Wood P.J. (2015) Fine sediment reduces vertical migrations of *Gammarus pulex* (Crustacea: Amphipoda) in response to surface water loss. *Hydrobiologia* **753**, 61–71.

Vander Vorste R., Corti R., Sagouis A. & Datry T. (accepted 2015) Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence. *Freshwater Science*, in press.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130–137.

Williams D.D. & Hynes H.B.N. (1976) The recolonization mechanisms of stream benthos. *Oikos*, **27**, 265–272.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Invertebrate taxa collected in benthic invertebrate (BEN), drifting invertebrate (DFT), hyporheic zone invertebrate (HYP), aerially ovipositing invertebrate (OVP), desiccation resistant forms in dry sediment (SED) sampling efforts. Relative abundance (RA) calculated as mean relative abundance per sample.

(Manuscript accepted 14 July 2015)