

Invertebrate assemblage responses and the dual roles of resistance and resilience to drying in intermittent rivers

Catherine Leigh^{1,2} · Núria Bonada³ · Andrew J. Boulton⁴ · Bernard Hugueny⁵ · Scott T. Larned⁶ · Ross Vander Vorste¹ · Thibault Datry^{1,5}

Received: 30 January 2015 / Accepted: 3 September 2015
© Springer Basel 2015

Abstract Intermittent rivers are naturally dynamic ecosystems in which flow cessation and riverbed drying cause temporal fluctuations in aquatic biodiversity. We analysed datasets from intermittent rivers in different climate zones across the world to examine responses of aquatic macroinvertebrate assemblages to drying, in relation to both taxonomic composition and traits of resistance and resilience. First, we compared the differences in taxonomic richness and turnover and in trait diversity, richness and redundancy before and after intermittent sites dried with the differences in concurrently sampled perennial sites. We found such high levels of variation in the before-after differences at intermittent and perennial sites

that we could not detect statistical differences between them. Second, we examined the effects of climate (arid, Mediterranean, temperate) and durations of dry and post-dry (flowing) periods on responses to drying at intermittent sites. Only climate had a detectable effect; the proportion of taxa at intermittent sites that persisted through drying-rewetting phases was greatest in arid-zone rivers. Regardless of climate, the invertebrates that persisted at intermittent sites were dominated by taxa resistant to drying. By contrast, taxa that persisted at perennial sites had fewer traits conferring resistance but more conferring resilience. The contributions of resistance and resilience combined with the presence of both intermittent and perennial reaches likely supports the long-term stability and persistence of communities in intermittent rivers, despite the inherently high variation in short-term responses to drying.

Electronic supplementary material The online version of this article (doi:[10.1007/s00027-015-0427-2](https://doi.org/10.1007/s00027-015-0427-2)) contains supplementary material, which is available to authorized users.

✉ Catherine Leigh
catherine.leigh@irstea.fr

¹ Irstea, UR MALY, Centre de Lyon-Villeurbanne, 5 rue de la Doua-CS 70077, 69626 Villeurbanne Cedex, France

² CESAB-RB Immeuble Henri Poincaré, Aix-en-Provence Cedex 3, France

³ Grup de Recerca Freshwater Ecology and Management (FEM), Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona (UB), Diagonal 643, 08028 Barcelona, Catalonia, Spain

⁴ Ecosystem Management, School of Environmental and Rural Science, University of New England, Armidale 2350, NSW, Australia

⁵ UMR "BOREA" CNRS 7208/IRD 207/MNHN/UPMC, DMPA, Museum National d'Histoire Naturelle, 43 rue Cuvier, 75231 Paris Cedex, France

⁶ National Institute of Water and Atmospheric Research, 10 Kyle Street, Riccarton, Christchurch, New Zealand

Keywords Climate · Disturbance · Invertebrate community · Traits · Persistence · Temporary river

Introduction

Flooding and drying are disturbances that govern the composition of most aquatic invertebrate communities (Resh et al. 1988; Death 2010; Sponseller et al. 2013), causing marked spatial and temporal fluctuations in diversity and community structure. Nonetheless, high levels of resistance and resilience to these disturbances mean that post-event recovery can be swift (e.g., within weeks; Grimm and Fisher 1989; Fritz and Dodds 2004). Intermittent rivers (IRs) are naturally dynamic ecosystems typified by flow cessation and absence of surface water (Datry et al. 2014a). They are common worldwide and support diverse communities of aquatic invertebrates,

including many taxa that survive in dry riverbeds and/or rapidly recolonise when water returns (Stubbington and Datry 2013; Boersma et al. 2014; Datry et al. 2014b). Yet we know far less about invertebrate community responses to drying than to flooding, particularly in terms of temporal fluctuations (Lake 2000; Leigh et al. 2015). A deeper understanding of the temporal changes that occur in IR communities in response to drying is essential not only to detect and predict future changes in structure and function but also to improve monitoring and management (Cottingham et al. 2001; Datry et al. 2014a).

Although drying is a defining feature of IRs, attributing temporal changes in invertebrate community structure and function to drying is difficult because all river communities vary temporally (Resh and Rosenberg 1989; Palmer and Poff 1997; Bêche and Resh 2007). Many invertebrate communities of IRs are characterized by a lack of temporal stability in abundances and/or a lack of persistence in presences and absences (e.g., Bêche and Resh 2007; Blanchette and Pearson 2013). Alternations between wet and dry phases in IRs, coupled with variation in antecedent flow conditions, contribute to variation in temporal changes in invertebrate communities (e.g., Sponseller et al. 2010; Datry 2012; Leigh 2013). Our understanding of these temporal changes has been hindered by the restricted nature of river-invertebrate survey designs, most of which examine assemblages within individual reaches, river systems or climate zones, not between or across them (although see, e.g., Boulton 2003; Leigh et al. 2013; Datry et al. 2014b).

In this paper, we explore effects of discrete drying events involving surface water loss on macroinvertebrate assemblages of IRs found across multiple climate zones, particularly in relation to traits associated with resistance and resilience to drying, to better understand the mechanisms driving community variation and persistence. Our analysis included intermittent (I) sites, in which flow ceased and surface water disappeared, and perennially flowing (P) sites. We used data collected concurrently from I and P sites within individual rivers before the I sites dried and after flow recommenced at the same sites to assess the temporal changes that occurred in taxonomic and trait composition. Overall, we hypothesized that if flow cessation and stream drying act as structuring forces on invertebrate communities of IRs, then assemblages at I and P sites in IRs will comprise different taxa with different compositions of traits of resistance and resilience to drying. As a result, temporal changes in the assemblages at I and P sites will differ and variation in drying-event characteristics (e.g. among sites, rivers or climate zones) will further influence the temporal changes occurring at I sites. Expanding on our general hypothesis, we posed the following questions:

- Q1 Do temporal changes at I sites differ from those at P sites?
- Q2 Do the durations of dry or post-dry (i.e. post-flow resumption) periods affect temporal changes at I sites?
- Q3 Are there differences in temporal changes at I sites among climate zones?
- Q4 Can resistance and resilience traits of taxa at I and P sites help to explain community persistence in IRs?

In relation to Q1, we hypothesized that flow intermittence and surface water loss would create a disturbance that (i) filters out taxa unable to cope with drying thus leading to more stable, persistent assemblages (less temporal change) at I sites than at P sites or (ii) leads to greater temporal changes at I sites, as assemblages respond to and recover from water loss, than at P sites (Chase 2007). For Q2, we hypothesized that the magnitudes of temporal changes at I sites would increase as the durations of the dry period increased and the post-dry period (following flow resumption) decreased because extended dry periods would act as press or ramp disturbances eliciting ramp responses (e.g., progressive loss of taxa) and short post-dry periods would limit opportunities for recolonisation (Paltridge et al. 1997; Lake 2000). For Q3, we hypothesized that biogeographic distinction in the richness and composition of river taxa and traits (e.g., Bonada et al. 2007; Leigh et al. 2013) would elicit differences in the temporal responses of assemblages to drying among climate zones. Finally, we hypothesized that assemblages at I and P sites would be distinguished by different trait-based patterns of resistance and resilience to drying (Q4).

Methods

International dataset

We gathered data on aquatic macroinvertebrate assemblages from published and unpublished studies of IRs across the world that fulfilled the following selection criteria: within rivers (i) invertebrates must have been sampled from at least one I site and preferably from at least one P site; (ii) samples must have been collected on two occasions from all sites while flowing, i.e., before the I sites dried (=T1) and after flow resumed at the same sites (=T2) and (iii) all T1 samples and all T2 samples must have each been collected concurrently. These criteria generated the largest possible subset of temporal data collected from IRs in a consistent fashion. The dataset was compiled from studies covering 47 sites in total across ten IRs, spanning six countries and three major climate zones (arid, Mediterranean, temperate; Table 1), with raw data

Table 1 Datasets used to explore temporal variation in invertebrate assemblages of intermittent rivers

Climate	River (country)	No. I sites ^a	No. P sites ^a	No. T1 (season, year) ^b	T2 (season, year) ^b	TimeBetween (days) ^c	DryDur (months) ^d	FlowDur (months) ^d	AntiFP (%) ^e	References
Temperate	Albarine River (France)	5	5	Spring, 2010	Autumn, 2010	138	3.5	1	63–94	Datry (2012)
	East Glen River (England)	1	1	Summer, 2008	Summer, 2008	31	0.5	1	100	Stubbington (2011); Stubbington et al. (2011)
	Little Stour River (England)	4	2	Autumn, 1996	Summer, 1998	727	6	9	100	Wood and Armitage (2004)
	Orari River (New Zealand)	5	3	Spring, 2007	Summer, 2008	118	3	1	55–72	Datry et al. (2014b)
	Selwyn River (New Zealand)	2	4	Spring, 2003	Spring, 2004	335	10	1	na	Arscott et al. (2010)
Mediterranean	Asse River (France)	2	4	Spring, 2009	Autumn, 2009	210	5.5	5.5	83–96	Datry et al. (2014b)
	Fuerosos (Spain)	1	0	Summer, 2001	Autumn, 2001	122	3	1	78	Acuña et al. (2005)
Arid	Nahr-el-Kahb (Lebanon)	2	2	Summer, 1979	Autumn, 1979	153	2	2	na	Khalaf and Lahoud (1983)
	Sycamore Creek (USA)	1	0	Spring, 1986	Spring, 1987	350	5	5	79	Grimm et al. (2007); USGS (2007)
	West Stronghold Canyon (USA)	3	0	Spring, 2004	Spring, 2005	343	7	2.5	19	Bogan and Lytle (2007)

T1 Sampling time one, T2 sampling time two, I intermittent, P perennial. Intermittent sites dried for a period between T1 and T2, perennial sites flowed continuously

^a There are 26 I sites (including 5 from rivers with no P sites sampled) and 21 P sites in total. For analyses comparing I and P sites, we only used data from rivers with samples from both I and P sites (42 samples in total). For analyses only using I sites, data from all 26 I sites were included. See Supplementary Material 1 for more detail on site and sample selection

^b Seasons are defined meteorologically

^c TimeBetween is the time elapsed, in days, between the first (T1) and second (T2) sample

^d Relevant to I sites only. DryDur is the duration of the dry period, which spans between when the site dried sometime after T1 and when flow resumed. FlowDur is the duration of the post-dry (flowing) period, which spans between the end of the dry period and T2. Duration was estimated based on information in published studies (e.g. hydrographs or descriptive text), from local river discharge data (gauged or modelled) and/or personal communications with studies' authors. Values are rounded to the nearest 0.5 month. See Supplementary Material 1 for more detail

^e AntiFP reflects the flow permanence of I sites in the 12 month period antecedent to T1 (values for all P sites = 100). Values are the minimum and maximum flow permanence (percentage of time flowing) of the I sites sampled in each river (unless there was only one site per river, in which case only one AntiFP value is given). Values were sourced from local river discharge data (gauged or modelled) and/or personal communications with studies' authors. na not available

provided by the studies' authors when not available directly from the publications. Data to quantify antecedent flow conditions (prior to T1) were unavailable for all sites and rivers in our study (see Table 1), but conditions probably varied. For instance, the East Glen and Selwyn rivers both experienced peak events ($c. 20\text{--}100 \times$ base-flow) 1–2 months prior to T1 (hydrographs in Arscott et al. 2010 and Stubbington 2011) but in the Little Stour, T1 was preceded by an extended low-flow period of $c. 9$ months (hydrograph in Wood and Armitage 2004). Furthermore, while some I sites did not experience a dry phase in the 12 months antecedent to T1 (East Glen and Little Stour sites), flow permanence data indicates others were dry for several months (e.g. on the Orari and Albarine; Table 1). Further details on sample and site selection are given in Supplementary Material 1.

Invertebrates were collected by core, Surber, Hess or kick-net samplers using mesh sizes between 0.2 and 1 mm; these different methods and mesh sizes have been shown previously to produce comparable datasets (Bonada et al. 2007; Statzner et al. 2007; Datry et al. 2014b; see Supplementary Material 1 for more detail). We used abundance data from riffles and runs but not pools because pool habitats were poorly represented across the studies. To standardise sampling effort across all samples and reduce potential sample size-induced bias (Walker et al. 2008), we generated one randomly rarefied dataset of standard sample size (74 individuals per sample, the smallest number of individuals in any one sample across the international dataset). Random rarefaction was made without replacement using function *rrarefy* in the R package *vegan* (Oksanen et al. 2015). We then converted the resampled abundance data to presence/absence data because our questions concerned persistence, with subsequent analyses exploring changes in richness and compositional similarity based on presence/absence rather than abundance data (see Data analysis). The resolution of taxonomic identification within major groups of taxa was standardised to the finest level consistent across individual studies and consistent with the trait assignments used in our study, which was primarily family level (see Data analysis and Supplementary Materials 1 and 2). There were 73 taxa in total across all 47 sites at this level of resolution; 60 of these taxa were identified at the family or superfamily level, the remaining 13 at the order, class or phylum level (Supplementary Material 1).

For Q1 and Q4, we used data only from rivers in which both I and P sites were sampled (Albarine, Asse, East Glen, Little Stour, Narl-el-Kahb, Orari and Selwyn; Table 1). The number of I and P sites across these seven rivers was balanced: 21 I sites and 21 P sites, each sampled twice. For Q2 and Q3, we used data from I sites only (26 sites in total,

each sampled twice), with all ten rivers (the seven above plus Fuirosos River, Sycamore Creek and West Stronghold Canyon) and three climate zones included (Table 1). Sixty-seven taxa were present across the balanced set of 42 I and P sites, and 59 taxa were present across the 26 I sites.

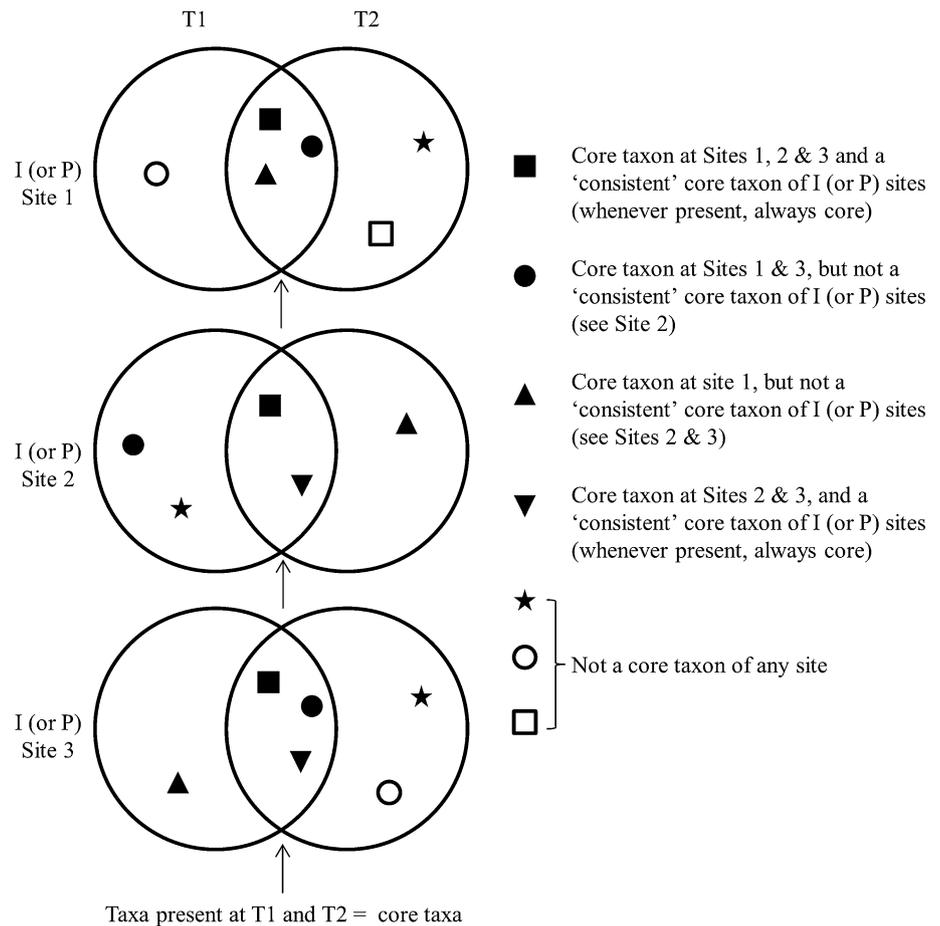
Variables describing temporal changes between T1 and T2

For each river, we calculated the total taxonomic richness across all sites and samples (i.e., the river-level richness). For each site, we then calculated the difference in taxonomic richness between T1 and T2 and determined the ratio of this site-level richness difference to the respective river-level richness. For example, if the difference in richness between T1 and T2 at one site of a river was 2, and the total richness across all sites and samples for that river was 20, the resulting ratio would be $2/20 = 0.10$. This procedure produced a variable (*RichDiff*) standardised by river-level richness and comparable across the dataset (Podani and Schmera 2011). Negative values indicated T2 sample richness was lower than T1.

We described compositional differences between T1 and T2 at each site using Simpson's index of dissimilarity, which represents the taxonomic replacement or turnover component of dissimilarity in composition between two samples (in this case, T1 and T2). More specifically, Simpson's index is a measure of beta diversity reflecting taxonomic gain and loss (Koleff et al. 2003), with higher values indicating greater turnover between samples. Simpson's index is calculated using the number of taxa common to both samples (herein 'core taxa'; Fig. 1) and the number found exclusively in each sample. We included richness of core taxa as an additional variable in our analysis to provide another measure of temporal persistence in IRs. As with *RichDiff*, for each site we calculated the ratio of the site-level richness of core taxa to the relevant river-level richness, terming the resultant variable *Core*.

We then calculated the functional diversity, richness and redundancy of samples by assigning traits of resistance and resilience to flow intermittence and surface-water loss in rivers to each taxon in our dataset (Datry et al. 2014b; Supplementary Material 2). We included three traits associated with resistance to drying (presence of desiccation-resistance forms; body armouring that limits water loss; and respiration systems that allow air breathing) and four traits associated with resilience to drying (high female dispersal; strong adult-flying ability; common occurrence in drift; and strong swimming ability). All traits were assigned at the family or coarser level of taxonomic resolution, as in Datry et al. (2014b). For four of the 73 taxa in

Fig. 1 Graphical depiction of core taxa, as defined in this study, of I and P sites. A taxon is a core taxon of any one I (or P) site when present at that site at both sampling times T1 and T2, and is a ‘consistent’ core taxon of I (or P) sites when, if present at another I (or P) site at T1, it also is a core taxon of that I (or P) site



our dataset there was insufficient information to assign traits, and these taxa were excluded from all trait-based calculations.

We calculated functional diversity as Rao’s quadratic entropy (Q ; Rao 1982; Botta-Dukát 2005), which described the breadth of resistance and resilience traits present within each sample. Q was computed in the R package FD (Laliberté and Legendre 2010; Laliberté and Shipley 2011) using the list of trait assignments (Supplementary Material 2) and the sample-by-presence/absence matrix. Functional richness (FRic) was calculated as the total number of unique trait combinations within a sample, where each taxon in a sample is described by its combination of resistance and resilience traits. Functional redundancy (FRed) was calculated as the ratio of taxonomic richness to functional richness within a sample (cf. Schmera et al. 2014). FRed values greater than one indicate an assemblage has a degree of functional redundancy (i.e., two or more taxa have the same trait combinations), potentially insuring against loss of functional richness if taxa are extirpated. For each site, we then calculated $Qdiff$, $FRicDiff$ and $FRedDiff$ as the differences between T1 and T2 in Q , FRic and FRed, respectively.

Data analysis

Scatterplots of all possible pairs of response variables described above indicated low skew and no obvious outliers in the distributions of their values, for either I or P sites. Boxplots were used to compare the distributions of values for each response variable among rivers, I and P sites and climates; the plots highlighted differences in variation among rivers. These preliminary analyses indicated that our questions would best be explored using mixed-effects models, which we built for each response variable ($RichDiff$, $Core$, Simpson’s index, $Qdiff$, $FRicDiff$, $FRedDiff$) following the protocol outlined by Zuur et al. (2009). Models were built first for question 1 (Q1), which concerned I and P sites, and then for questions two and three combined (Q2–3), which concerned I sites only. For Q1, site (I vs. P) was included as a fixed factor along with a covariate describing the time elapsed between T1 and T2 ($TimeBetween$, d; Table 1). For Q2–3, climate (arid, Mediterranean, temperate) was included as a fixed factor along with two covariates: duration of dry period ($DryDur$, months; Table 1) and duration of the subsequent post-dry period between the end of the dry period when sites

recommended flowing and T2 (*FlowDur*, months; Table 1). *TimeBetween* was used as the covariate for Q1, not *DryDur* or *FlowDur*, because *TimeBetween* applies equally to I and P sites, whereas the latter two variables specifically apply to I sites. All covariates were squareroot transformed prior to analysis.

For each response variable, we selected the optimal model based on the change in Akaike's Information Criterion, corrected for finite sample sizes (AICc; Burnham et al. 2011), between each of the following full models: the relevant above-described model as dependent on the question being explored (Q1 or Q2–3) with (i) no random components, (ii) a random intercept, (iii) a random intercept and slope and (iv) a random variance structure. The selected optimal models either had random intercepts (for *Qdiff* in Q1 and *Core* in Q2–3) or no random components. We used the nlme package within R to run the models (Pinheiro et al. 2012) and only report the statistical significance (*P* values) associated with effects from optimal models. To complement and improve interpretation of results from these models, we calculated standardised effect sizes (Hedge's *d*) and their confidence intervals (CIs) using the means, standard deviations and sample sizes associated with each response variable and pairwise comparison of the levels of fixed, categorical factors included each model (Nakagawa and Cuthill 2007; Supplementary Material 3).

Finally, for the fourth question (Q4) on resistance and resilience to drying, we calculated the proportions of trait combinations ('strategies') conferring resistance and resilience to the core taxa found consistently at I and P sites. A taxon was classed as a 'consistent' core taxon of an I (or P) site when, if present at another I (or P) site at T1, it also was a core taxon of that I (or P) site (Fig. 1; Supplementary Material 2). Taxa with one or more resistance traits but no resilience traits were assigned to a resistance-only strategy (*RT-only*); taxa with one or more resilience traits but no resistance traits were assigned to a resilience-only strategy (*RL-only*) (see Supplementary Material 2 for more details). Taxa with both resistance and resilience traits were not exclusively resistant or resilient to drying, and taxa with neither resistance nor resilience traits were likely to be sensitive to drying. *RT-only* and *RL-only* strategies can be interpreted specifically in relation to resistance or resilience, respectively. We calculated proportions by counting the number of 'consistent' core taxa in each of the four strategies (*RT-only*, *RL-only*, both, neither) across all I and all P sites and then dividing each count by the total number of 'consistent' core taxa (regardless of strategy) across all I and all P sites, respectively. Comparisons of proportions were made within and between I and P sites.

Results

Do temporal changes at I sites differ from those at P sites (Q1)?

Differences in temporal changes, as reflected by the response variables, were not detected between I and P sites. The I-versus-P factor and the *TimeBetween* covariate had no detectable effects on *RichDiff*, *Core*, Simpson's index, *Qdiff*, *FRedDiff* or *FRicDiff*. *P*-values associated with the explanatory variables were all >0.05 , effect sizes were 'small' (mean absolute value = 0.25) and confidence intervals all included zero (Table 2; Supplementary Material 3). Magnitudes of the response variables and directions of the temporal changes they reflected were not consistent within or between rivers or flow regimes (I vs. P), and the variables typically had high standard deviations around their means (Supplementary Material 4).

At I sites, do the durations of dry or post-dry periods affect temporal changes and are there differences in temporal changes among climate zones (Q2–3)?

No significant effects of *DryDur* or *FlowDur* were detected on any variables of temporal change at I sites. Confidence intervals of effect sizes for pairwise climate comparisons all included zero and the effect sizes themselves were not, on average, 'large' (mean absolute value = 0.52; Supplementary Material 3), except for the climate comparisons associated with *Core* (Table 2). *Core* was highest in arid (0.61 ± 0.22) then temperate (0.27 ± 0.22) and Mediterranean (0.16 ± 0.10 ; mean ± 1 SD) climates, indicating that the number of taxa present both before and after the I sites dried (relative to river-level richness) was highest in the arid-zone rivers (Fig. 2).

Can resistance and resilience traits of taxa at I and P sites help explain community persistence (Q4)?

Fifteen taxa were consistently present at I sites, and 20 at P sites (see Supplementary Material 2 for full lists; Fig. 3). At I sites, these consistent core taxa were proportionally dominated by *RT-only* strategies (53 %), and had proportionally more taxa with *RT-only* strategies than those at P sites (30 %). The consistent core taxa at I sites also had proportionally fewer taxa with *RL-only* strategies (13 %) than those at P sites (35 %). Furthermore, the consistent core taxa at P sites had proportionally fewer 'drying-sensitive' taxa (having neither a resistance nor resilience strategy) than those at I sites, which had proportionally more taxa with a combination of both resistance and resilience strategies (Fig. 3). These differences between I and

Table 2 Statistical significance of effects within optimal models exploring temporal changes in invertebrate assemblages of intermittent rivers, with effect sizes (Hedge's *d*) and confidence intervals (CIs) associated with pairwise comparisons of levels of the fixed, categorical factors within the models

Data source	Response variable	Fixed, categorical explanatory factor	Comparison	Statistical significance ^a	Hedge's <i>d</i> ^b	95 % CI
I and P	<i>RichDiff</i>	Site	I vs. P	NS	0.16	−0.45 to 0.77
	<i>Core</i>	Site	I vs. P	NS	−0.35	−0.96 to 0.26
	Simpson's	Site	I vs. P	NS	−0.34	−0.95 to 0.27
	<i>Qdiff</i>	Site	I vs. P	NS	0.27	−0.34 to 0.88
	<i>FRedDiff</i>	Site	I vs. P	NS	0.21	−0.40 to 0.82
	<i>FRicDiff</i>	Site	I vs. P	NS	−0.15	−0.72 to 0.46
I only	<i>RichDiff</i>	Climate	M vs. A	NS	−0.21	−2.22 to 1.80
			T vs. M	NS	0.20	−1.78 to 2.18
			T vs. A	NS	−0.07	−1.91 to 2.05
	<i>Core</i>	Climate	M vs. A	0.04	−2.47	0.46 to 4.48
			T vs. M	NS	0.53	−1.45 to 2.51
			T vs. A	NS	−1.87	−3.85 to 0.11
	Simpson's	Climate	M vs. A	NS	0.73	−1.28 to 2.74
			T vs. M	NS	0.01	−1.97 to 1.99
			T vs. A	NS	0.81	−1.17 to 2.79
	<i>Qdiff</i>	Climate	M vs. A	NS	−0.53	−2.54 to 1.48
			T vs. M	NS	0.45	−1.53 to 2.43
			T vs. A	NS	−0.31	−2.29 to 1.67
	<i>FRedDiff</i>	Climate	M vs. A	NS	−0.12	−2.13 to 1.89
			T vs. M	NS	0.19	−1.79 to 2.17
			T vs. A	NS	0.18	−1.80 to 12.16
	<i>FRicDiff</i>	Climate	M vs. A	NS	0.42	−1.59 to 2.43
			T vs. M	NS	−0.13	−2.11 to 1.85
			T vs. A	NS	0.17	−2.15 to 1.81

I Intermittent sites, P perennial sites, A arid climate, M Mediterranean climate, T temperate climate

^a *P* values associated with the relevant fixed, categorical explanatory variable included in each model. NS non-significant (*P* > 0.05)

^b See Supplementary Material 3 for details on interpretation of the direction (negative or positive sign) of effect sizes

P sites in the strategies represented within their consistent core taxa were equally apparent when only considering the consistent core taxa at I sites that were not also consistent core taxa at P sites, and vice versa (Fig. 3; Supplementary Table S2).

Discussion

Temporal changes in IRs: comparing I and P sites

Variation in temporal changes in taxonomic richness, turnover and functional diversity, richness and redundancy (in traits of resistance and resilience to drying) of the studied assemblages was high at both I and P sites. A scarcity of detectable between-group differences can be due to small true differences between groups, high within-group variability or both. In this study, both factors likely affected the comparisons; all of our response variables

were highly variable within the groups of I and P sites and temporal changes in the response variables were not consistent within groups in either their magnitudes or directions. However, the magnitudes of between-group differences were small (Hedges $d \leq |0.35|$; Table 2).

Metacommunity dynamics (Leibold et al. 2004; Larned et al. 2010) such as dispersal and exchange of taxa among the IR assemblages at I and P sites may have rapidly neutralized any between-group differences in temporal changes in richness and composition that were initially caused by flow cessation and drying at the I sites, contributing to the small between-group differences. Alternatively, a similar type of hydrological disturbance (e.g., habitat contraction or flooding) may have occurred at all sites and rivers between the two sampling times. However, hydrographs and modelled flows for the studied rivers between T1 and T2 (available for five out of the seven rivers with I and P sites; Khalaf and Lahoud 1983; Wood and Armitage 2004; Stubbington 2011; Arscott et al. 2010;

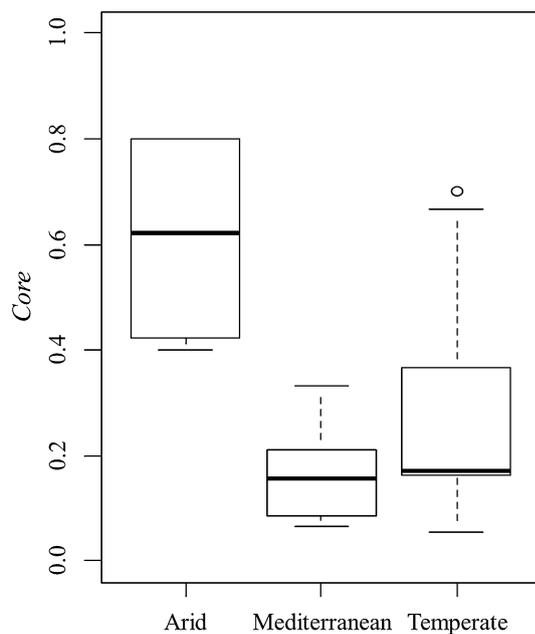


Fig. 2 Core (richness of core taxa at a site proportional to the relevant river-level richness) for I sites within different climate zones (means + 1SD), based on samples collected before and after the sites dried. See [Methods](#) and [Fig. 1](#) for more detail on this variable

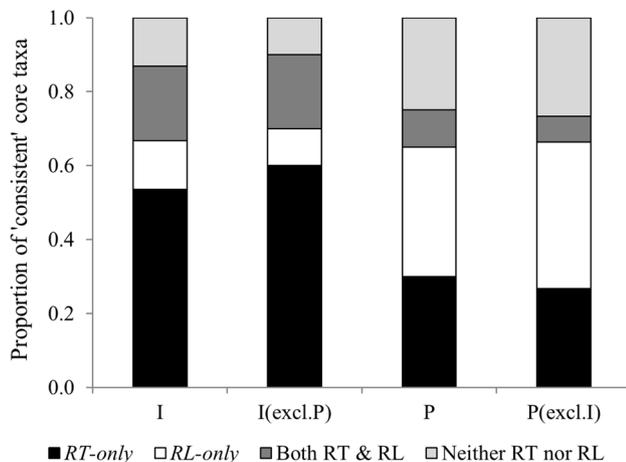


Fig. 3 Proportions of resistance (RT) and resilience (RL) strategies within the 'consistent' core taxa of I or P sites of seven rivers (the Albarine, Asse, Little Stour, Nahr-el-Kahb, Orari, Selwyn and West Glen). Here, 'consistent' core taxa are those present at T1 and T2 within at least one I (or P) but never lost at T2 from any I (or P) site. I(excl.P) includes core taxa of I sites only (excludes any taxon also a core taxon of P sites); P(excl.I) includes core taxa of P sites only (excludes any taxon also a core taxon of I sites)

Larned et al. 2011) refute this possibility; flow reduction did not occur consistently or comparably among P sites between T1 and T2 during which I sites ceased to flow and dried, nor did a comparable peak event occur across I and P sites. In contrast, variation in flow conditions, including

those antecedent to T1, probably contributed to high within-group variability. Antecedent flow conditions can alter invertebrate community composition (Greenwood and Booker 2015), potentially influencing subsequent changes in community structure (Ledger et al. 2006; Chase 2007; McCluney and Sabo 2014). Variation in antecedent flow characteristics, such as in the timing and magnitude of flood peaks (e.g., Leigh 2013) or the durations of dry and/or flow periods (e.g., Larned et al. 2007; Arscott et al. 2010; Datry 2012), which occurred among at least some of our study sites and rivers (see [Methods](#)), may therefore have contributed to the variation in the magnitude and direction of changes post-T1.

Temporal changes at I sites: effects of dry- and post-dry durations and climate

We hypothesized that as dry periods lengthened and post-dry periods shortened at I sites, the magnitudes of temporal changes in invertebrate assemblages would increase. Although such relationships have been observed in some of the rivers in our analysis (Datry 2012; Arscott et al. 2010) we did not detect across-river relationships between temporal changes in invertebrate assemblages and the durations of dry or post-dry periods. Detecting these relationships across broad spatial scales and climate zones may be hampered because responses to drying and flow resumption are strongly influenced by site- and river-specific long-term and antecedent flow conditions, the taxa present prior to disturbance and the spatial arrangement of habitats within each river (Chester and Robson 2011; Bogan and Lytle 2011; Datry et al. 2014b).

Persistence through drying coupled with fast recovery following flow resumption may also explain the lack of detected relationships found between temporal changes in the studied assemblages and durations of dry or post-dry periods. First, resistance to drying strongly characterized the traits of core taxa at I sites, there being four times as many core taxa with *RT-only* as *RL-only* strategies at these sites. This suggests that resistant core taxa persisted in situ throughout the dry periods, at least over the time periods and conditions examined here. Second, the durations of post-dry periods represented in our dataset ranged from 1 to 9 months (Table 1). Some studies indicate that invertebrate communities can recover from flow cessation and/or surface water loss within a month of flow resumption (e.g., Fowler 2004; Vander Vorste et al. 2015). Hence, it is possible that the post-dry sampling of I sites across some of the studies analysed here may have occurred well after the assemblages had recovered from streambed drying. Furthermore, if communities of the studied IRs function as metacommunities (Larned et al. 2010), then dispersal of taxa from P sites to nearby rewetted I sites (i.e., mass

effects; Heino 2013) may have masked the effects of drying.

We found little evidence for differences among climate zones in the temporal responses of I-site assemblages to drying, except in the case of taxa present both before and after dry periods (i.e., core taxa). Our results indicated that the proportion of taxa persisting throughout drying-rewetting phases at I sites was greatest in arid-zone rivers. This was likely driven by a high degree of resistance to drying, which is known to exist in the invertebrate communities of some arid-zone systems (Boersma et al. 2014). If the majority of taxa in such communities are resistant, then they are likely to be buffered against disturbance-induced destabilization (Tilman and Downing 1994; Hughes et al. 2007). However, the numbers of aquatic life stages remaining present and viable within dry riverbeds declines as the severity of drying and time exposed to desiccation increases (Jenkins & Boulton 2007; Stubbington & Datry 2013). Long-term persistence of IR communities may therefore be compromised under abnormally long periods of surface-water loss (e.g. Bêche et al. 2009), even in arid-zone rivers (Bogan et al. 2013), particularly if the availability of sources of recolonising taxa (e.g., nearby P sites) is limited.

Core taxa, resistance and resilience, intermittence and perenniality

Taxa consistently present across I sites before and after drying had proportionally more resistance traits than those consistently present across P sites, but fewer resilience traits. These I-site taxa were dominated by Diptera (e.g. Ceratopogonidae and Tipulidae) and characterised by traits associated with desiccation resistance (Supplementary Material 2). Evidence from studies conducted across multiple continents and climate zones confirms our assessment of these taxa as highly resistant to stream drying. For example, both Ceratopogonidae and Tipulidae persisted in experimentally and repeatedly dried stream mesocosms (Ledger et al. 2012), emerged from rewetted dry sediment collected from a temperate IR in Europe (Datry et al. 2012) and aestivate in the dry sediments of a tropical IR in northern Australia (Paltridge et al. 1997).

Our findings suggest that resistance traits are important in maintaining the core taxa of assemblages at I sites, and that P sites are an important source of taxa with resilience to stream drying that potentially (re)colonise I sites when flow returns. As such, the contributions of resistance and resilience, combined with the presence of both I and P reaches, likely support the persistence of invertebrate communities in IRs. Overall, our multiple-river analysis builds on previous work highlighting the relative importance of resistance (Boersma et al. 2014; McCluney and

Sabo 2014) or resilience (Stanley et al. 1994; Fritz and Dodds 2004; Datry et al. 2014b) in explaining persistence of invertebrate communities in IRs by emphasising the importance of both mechanisms, as suggested by Bogan et al. (2014), in buffering against the environmental variation present in these systems.

Conclusions

Our study is the first large-scale analysis of aquatic invertebrate assemblage data collected before and after drying events of quantified duration in multiple IRs, and from I and P sites sampled concurrently. We were unable to attribute the variation in temporal changes in assemblage attributes to flow cessation and surface water loss, or to the durations of dry- and post-dry periods. However, our analysis suggests that both resistance and resilience traits are important for the persistence of communities in IRs with I and P reaches, despite the substantial degree of within- and among-river variation in short-term responses to drying. Our findings need validation using studies designed explicitly for purpose (compared with our analysis of datasets originally collected for other research questions), encompassing greater numbers of concurrently sampled rivers and sites to increase statistical power. Further, these future studies could: (i) incorporate hydrological data in formal analyses to better account for antecedent flow conditions; (ii) develop and apply a trait classification at a finer level of taxonomic resolution than family and with more traits that are directly linked to desiccation resistance and resilience; (iii) seek to improve knowledge of dispersal capacities of taxa and incorporate information on controls on dispersal such as barriers and overland and down-river distances between sites to assess metacommunity processes; and (iv) increase documentation of temporal changes during drying and the early stages of succession post-flow resumption, at frequent and short intervals (daily-weekly), to describe the drying response and recolonization dynamics more precisely. Such information and data coverage will help to partition out the effects of intermittence, climate and drying-event characteristics on temporal changes in the structure and function of IR communities in response to drying.

Acknowledgments We thank Vicenç Acuña, Michael Bogan, Nancy Grimm, Rachel Stubbington, Paul Wood and their research teams for supplying data and answering our many questions; Rob Rolls for discussions on statistical analyses; and two anonymous reviewers for their comments and suggestions which improved the manuscript. Data from Lebanon and Spain were originally provided to NB for a project supported by the ‘Secretaría de Estado de Educación y Universidades’ (Spain) and co-funded by the European Social Fund (see Bonada et al. 2007; Statzner et al. 2007). CL was funded by IRBAS (Intermittent River Biodiversity Analysis and Synthesis

working group; www.irbas.fr), led by TD and supported by the Centre for Synthesis and Analysis of Biodiversity (CESAB), and funded jointly by the French Foundation for Research and Biodiversity (FRB) and the French National Agency for Water and Aquatic Environments (ONEMA). CL, NB, AB, BH, SL and TD are IRBAS participants. RV was funded by IRSTEA.

References

- Acuña V, Muñoz I, Giorgi A, Omella M, Sabater F, Sabater S (2005) Drought and postdrought recovery cycles in an intermittent Mediterranean stream: structural and functional aspects. *J N Am Benthol Soc* 24:919–933
- Arcsott DB, Larned S, Scarsbrook MR, Lambert P (2010) Aquatic invertebrate community structure along an intermittence gradient: Selwyn River, New Zealand. *J N Am Benthol Soc* 29:530–545
- Bêche LA, Resh VH (2007) Short-term climatic trends affect the temporal variability of macroinvertebrates in California ‘Mediterranean’ streams. *Freshw Biol* 52:2317–2339
- Bêche LA, Connors PG, Resh VH, Merenlender AM (2009) Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography* 32:778–788
- Blanchette ML, Pearson RG (2013) Dynamics of habitats and macroinvertebrate assemblages in rivers of the Australian dry tropics. *Freshw Biol* 58:742–757
- Boersma KS, Bogan MT, Henrichs BA, Lytle DA (2014) Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. *Freshw Biol* 59:491–501
- Bogan MT, Lytle DA (2007) Seasonal flow variation allows ‘time-sharing’ by disparate aquatic insect communities in montane desert streams. *Freshw Biol* 52:290–304
- Bogan MT, Lytle DA (2011) Severe drought drives novel community trajectories in desert stream pools. *Freshw Biol* 56:2070–2081
- Bogan MT, Boersma KS, Lytle DA (2013) Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. *Freshw Biol* 58:1016–1028
- Bogan MT, Boersma KS, Lytle DA (2014) Resistance and resilience of invertebrate communities to seasonal and suprasedonal drought in arid-land headwater streams. *Freshw Biol*. doi:10.1111/fwb.12522
- 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. *Glob Change Biol* 13:1658–1671
- Botta-Dukát Z (2005) Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. *J Veg Sci* 16:533–540
- Boulton AJ (2003) Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshw Biol* 48:1173–1185
- Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav Ecol Sociobiol* 65:23–35
- Chase JM (2007) Drought mediates the importance of stochastic community assembly. *Proc Natl Acad Sci* 104:17430–17434
- Chester ET, Robson BJ (2011) Drought refuges, spatial scale and recolonisation by invertebrates in non-perennial streams. *Freshw Biol* 56:2094–2104
- Cottingham KL, Brown BL, Lennon JT (2001) Biodiversity may regulate the temporal variability of ecological systems. *Ecol Letters* 4:72–85
- Datry T (2012) Benthic and hyporheic invertebrate assemblages along a flow intermittence gradient: effects of duration of dry events. *Freshw Biol* 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. *Freshw Biol* 57:716–727
- Datry T, Larned ST, Fritz KM, Bogan MT, Wood PJ, Meyer EI, Santos AN (2014a) Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. *Ecography* 37:94–104
- Datry T, Larned ST, Tockner K (2014b) Intermittent rivers: a challenge for freshwater ecology. *Bioscience* 64:229–235
- Death RG (2010) Disturbance and riverine benthic communities: what has it contributed to general ecological theory? *Riv Res Appl* 26:15–25
- Fowler RT (2004) The recovery of benthic invertebrate communities following dewatering in two braided rivers. *Hydrobiologia* 523:17–28
- Fritz KM, Dodds WK (2004) Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tallgrass prairie stream system. *Hydrobiologia* 527:99–112
- Greenwood MJ, Booker DJ (2015) The influence of antecedent floods on aquatic invertebrate diversity, abundance and community composition. *Ecology* 8:188–203
- Grimm NB, Fisher SG (1989) Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *J N Am Benthol Soc* 8:293–307
- Grimm N, Fisher S, Bessler J, Bills R, Blaine T, Boulton A, Cetin J, Clinton S, Colella T, Corbett A, Dent L, Donovan K, Downs L, Drake N, Dudley T, Edmonds J, Ford S, Fredrickson C, Freeman J, Gavin J, Goettl A, Gómez R, Greene D, Grove K, Harper B, Henry J, Holland S, Holmes B, Hunter J, Jackson A, Jones J, Kochert C, Main T, Mallett M, Martí E, Millan A, Murphy M, Myers M, Naegeli M, Peralta R, Peterson B, Peterson C, Petrone K, Rector S, Roach J, Schade J, Schrot A, Seddon J, Sponseller R, Stanley E, Stinchfield K, Tseng M, Valett M, Velasco J, Welter J, Wood D, Zachary J, Zhu W (2007) Sycamore Creek macroinvertebrate collections after flooding event. Data catalogue ID 375. Central Arizona-Phoenix Long-Term Ecological Research project. Arizona State University, Tempe, Arizona. <http://caplter.asu.edu/>. Accessed 28 Oct 2013
- Heino J (2013) The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biol Rev* 88:166–178
- Hughes AR, Byrnes JE, Kimbro DL, Stachowicz JJ (2007) Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecol Lett* 10:849–864
- Jenkins KM, Boulton AJ (2007) Detecting impacts and setting restoration targets in arid-zone rivers: aquatic micro-invertebrate responses to reduced floodplain inundation. *J Appl Ecol* 44:823–832
- Khalaf G, Lahoud M (1983) Contribution a l’etude ecologique des fleuves cotiers du Liban, 1: Le Nahr-el-Kalb. *Bull Mens Soc Linn Lyon* 52:21–32
- Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence-absence data. *J Anim Ecol* 72:367–382
- Lake PS (2000) Disturbance, patchiness, and diversity in streams. *J N Am Benthol Soc* 19:573–592
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305

- Laliberté E, Shipley B (2011) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-11
- Larned ST, Detry T, Robinson CT (2007) Invertebrate and microbial responses to inundation in an ephemeral river reach in New Zealand: effects of preceding dry periods. *Aquat Sci* 69:554–567
- Larned ST, Detry T, Arscott DB, Tockner K (2010) Emerging concepts in temporary-river ecology. *Freshw Biol* 55:717–738
- Larned ST, Schmidt J, Detry T, Konrad CP, Dumas JK, Dietrich JC (2011) Longitudinal river ecohydrology: flow variation down the lengths of alluvial rivers. *Ecohydrology* 4:532–548
- Ledger ME, Harris RML, Milner AM, Armitage PD (2006) Disturbance, biological legacies and community development in stream mesocosms. *Oecologia* 148:682–691
- Ledger ME, Harris RM, Armitage PD, Milner AM (2012) Climate change impacts on community resilience: evidence from a drought disturbance experiment. *Adv Ecol Res* 46:211–258
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- Leigh C (2013) Dry season changes in macroinvertebrate assemblages of highly seasonal rivers: responses to low flow, no flow and antecedent hydrology. *Hydrobiologia* 703:95–112
- Leigh C, Stubbington R, Sheldon F, Boulton AJ (2013) Hyporheic invertebrates as bioindicators of ecological health in temporary rivers: a meta-analysis. *Ecol Indic* 32:62–73
- Leigh C, Boulton AJ, Courtwright JL, Fritz K, May CL, Walker RH, Detry T (2015) Ecological research and management of intermittent rivers: an historical review and future directions. *Freshw Biol*. doi:10.1111/fwb.12646
- McCluney KE, Sabo JL (2014) Sensitivity and tolerance of riparian arthropod communities to altered water resources along a drying river. *PLoS ONE* 9:e109276
- Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol Rev* 82:591–605
- Oksanen J, Guillaume Blanchet F, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2015) vegan: Community Ecology Package. R package version 2.2-1. <http://CRAN.R-project.org/package=vegan>
- Palmer MA, Poff NL (1997) The influence of environmental heterogeneity on patterns and processes in streams. *J N Am Benthol Soc* 16:169–173
- Paltridge RM, Dostine PL, Humphrey CL, Boulton AJ (1997) Macroinvertebrate recolonization after re-wetting of a tropical seasonally-flowing stream (Magela Creek, Northern Territory, Australia). *Mar Freshw Res* 48:633–645
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2012) nlme: linear and nonlinear mixed effects models. R package version 3.1-105
- Podani J, Schmera D (2011) A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. *Oikos* 120:1625–1638
- Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. *Theor Popul Biol* 21:24–43
- Resh VH, Rosenberg DM (1989) Spatial-temporal variability and the study of aquatic insects. *Can Entomol* 121:941–963
- Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissmar RC (1988) The role of disturbance in stream ecology. *J N Am Benthol Soc* 7:433–455
- Schmera D, Podani J, Erős T, Heino J (2014) Combining taxon-by-trait and taxon-by-site matrices for analysing trait patterns of macroinvertebrate communities: a rejoinder to Monaghan & Soares (2014). *Freshw Biol* 59:1551–1557
- Sponseller RA, Grimm NB, Boulton AJ, Sabo JL (2010) Responses of macroinvertebrate communities to long-term flow variability in a Sonoran Desert stream. *Glob Change Biol* 16:2891–2900
- Sponseller RA, Heffernan JB, Fisher SG (2013) On the multiple ecological roles of water in river networks. *Ecosphere* 4:17
- Stanley EH, Buschman DL, Boulton AJ, Grimm NB, Fisher SG (1994) Invertebrate resistance and resilience to intermittency in a desert stream. *Am Midl Nat* 131:288–300
- Statzner B, Bonada N, Dolédec S (2007) Conservation of taxonomic and biological trait diversity of European stream macroinvertebrate communities: a case for a collective public database. *Biodivers Conserv* 16:3609–3632
- Stubbington R (2011) The hyporheic zone as a refugium for benthic invertebrates in groundwater-dominated streams. PhD thesis, Loughborough University, Loughborough, UK
- Stubbington R, Detry T (2013) The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones. *Freshw Biol* 58:1202–1220
- Stubbington R, Wood P, Reid I (2011) Spatial variability in the hyporheic zone refugium of temporary streams. *Aquat Sci* 73:499–511
- Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. *Nature* 367:363–365
- US Geologic Survey (USGS) (2007) Discharge data from USGS gage near Sycamore Creek research site. <https://caplter.asu.edu/data/data-catalog/?id=391>. Accessed 28 Oct 2013
- Vander Vorste R, Corti R, Sagouis A, Detry T (2015) Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence. *Freshw Sci*. doi:10.1086/683274
- Walker SC, Poos MS, Jackson DA (2008) Functional rarefaction: estimating functional diversity from field data. *Oikos* 117:286–296
- Wood PJ, Armitage PD (2004) The response of the macroinvertebrate community to low-flow variability and supra-seasonal drought within a groundwater dominated stream. *Arch Hydrobiol* 161:1–20
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York