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## Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence

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Temporary rivers are increasingly common freshwater ecosystems, but there have been no global syntheses of their community patterns. In this study, we examined the responses of aquatic invertebrate communities to flow intermittence in 14 rivers from multiple biogeographic regions covering a wide range of flow intermittence and spatial arrangements of perennial and temporary reaches. Hydrological data were used to describe flow intermittence (FI, the proportion of the year without surface water) gradients. Linear mixed-effects models were used to examine the relationships between FI and community structure and composition. We also tested if communities at the most temporary sites were nested subsets of communities at the least temporary and perennial sites. Taxon richness decreased as FI increased and invertebrate communities became dominated by ubiquitous taxa. The number of resilient taxa (with high dispersal capacities) decreased with increased FI, whereas the number of resistant taxa (with adaptations to desiccation) was not related to FI. River-specific and river-averaged model comparisons indicated most FI-community relationships did not differ statistically among rivers. Community nestedness along FI gradients was detected in most rivers and there was little or no influence of the spatial arrangement of perennial and temporary reaches. These results indicate that FI is a primary driver of aquatic communities in temporary rivers, regardless of the biogeographic species pool. Community responses are largely due to resilience rather than resistance mechanisms. However, contrary to our expectations, resilience was not strongly influenced by spatial fragmentation patterns, suggesting that colonist sources other than adjacent perennial reaches were important.

Identifying general relationships between environmental drivers and community responses is a perennial goal in ecology. Common environment–community relationships are represented by linear or curvilinear relationships that are congruent in direction (increasing or decreasing) and magnitude (slope or inflection) for geographically separated and/or phylogenetically distinct communities. For example, the shapes of relationships between water availability and primary productivity (drivers) and the diversity of bat, amphibian, and bird communities (responses) are remarkably similar over wide biogeographic ranges (Mittelbach et al. 2001, McCain 2007). These observations suggest that some environmental factors are ‘master variables’ with strong direct or indirect effects on most communities in a given taxonomic group or habitat type (Menéndez et al. 2007). Other environmental factors are subsidiary: their effects on community structure are weak or localized. General relationships between environmental drivers and community structure can provide mechanistic explanations for widely observed spatial patterns, including latitudinal and altitudinal gradients in community diversity (McCain 2007), regional beta-diversity

patterns (Melo et al. 2009), species–area relationships (Öckinger et al. 2010) and intercontinental community convergence (Lamouroux et al. 2002).

Although temporary rivers drain all terrestrial biomes and represent the dominant freshwater ecosystems in many areas, they have only recently been considered by ecologists (Larned et al. 2010, Datry et al. 2011, Steward et al. 2012). As a result, the organisation of aquatic communities in these systems has never been analysed across different biogeographic regions. The periodic loss of surface water (hereafter ‘flow intermittence’) is a fundamental challenge for aquatic organisms and may be a major driver of aquatic community diversity and composition. Alteration of aquatic communities caused by flow intermittence may also have cascading effects on biotic communities in adjacent ecosystems, such as riparian and floodplain areas (McCluney and Sabo 2012) or hyporheic zones (Datry et al. 2007). There are some indications that aquatic invertebrate communities in geographically distant river systems display similar responses to variation in flow intermittence. For example, invertebrate taxon richness in temporary rivers of France, New Zealand and the United States of America

(USA) decreased linearly as the severity of flow intermittence increased (Fritz and Dodds 2004, Arscott et al. 2010, Detry 2012). Partial and complete overlap in taxonomic composition has also been reported for invertebrate communities from adjacent temporary and perennial reaches (del Rosario and Resh 2000, Chester and Robson 2011). These observations suggest that intermittence-specialist taxa are rare. However, previous studies of aquatic invertebrates in temporary rivers have been site- or river-specific and differed in aims and methods, preventing the identification of general community patterns and mechanisms.

Aquatic communities of temporary rivers persist through disturbances using both resistance and resilience mechanisms (Fritz and Dodds 2004, Bêche et al. 2009). Resistance reflects the capacity of communities to persist unchanged through periods without surface water and involves a range of physiological adaptations allowing organisms to survive within dry riverbed sediments or remnant pools (Lytle and Poff 2004, Williams 2006). For example, species from several invertebrate groups (e.g. oligochaetes, copepods, dipterans) can persist for years in dry river sediments as cysts and cocoons, or in a state of diapause as larvae or adults (Williams 2006). Resistance can be viewed as a form of temporal dispersal and many freshwater studies have reported more geographically complex patterns than one would expect based on frequent spatial dispersal alone (Bohonak and Jenkins 2003). Resilience reflects the ability of communities to return to their pre-drying state soon after flow resumes. Resilient responses to flow intermittence may be related to dispersal capacity, which governs the rate at which taxa return to a rewetted river channel from aquatic refuges (Stanley et al. 1994, Chester and Robson 2011). The respective roles of resistance and resilience mechanisms in structuring diversity patterns in temporary rivers are unclear. A global analysis of diversity patterns across temporary rivers might help disentangle the roles of resistance and resilience mechanisms. If resistance is the principal persistence mechanism for invertebrates in temporary rivers, relationships between flow intermittence and invertebrate taxon richness should be weak or nonexistent (Fig. 1A). The composition of temporary-reach communities should differ widely from those in perennial reaches because of a progressive taxa replacement along flow intermittence gradients, particularly if there is a cost associated with desiccation-resistance adaptations (Fig. 1B). In contrast, if resilience is the principal persistence mechanism, the progressive colonization of previously-dry reaches by taxa from perennial reaches should result in negative relationships between flow intermittence and taxon richness, and these relationships should be congruent across rivers (Fig. 1A). In addition, taxa-poor communities at the most temporary reaches are expected to be nested-subsets of taxa-rich communities found at the least temporary and perennial reaches (Fig. 1B).

Flow intermittence in river networks can lead to different spatial arrangements of perennial and temporary reaches and thus different patterns of habitat fragmentation (Lake 2003). In many river networks, temporary reaches are concentrated in the upper, middle or lower reaches of rivers (Fig. 1C). These large-scale drying patterns can influence the

effects of fragmentation on dispersal and create mismatches in the geometries of dispersal and disturbance (drying phase) (Fagan 2002). Downstream transport is a dominant feature in lotic ecosystems and overland dispersal is not a general trait across aquatic invertebrate taxa (Bohonak and Jenkins 2003). Therefore, the accessibility of refuges for aquatic invertebrates during dry periods, and dispersal pathways from these refuges following rewetting may differ due to the variable spatial arrangement of temporary and perennial reaches. The overall responses of aquatic organisms to flow intermittence should thus vary with the pattern of habitat fragmentation, particularly if dispersal is an overriding mechanism for explaining community persistence in temporary rivers.

In this study, we investigated the responses of aquatic invertebrate communities to flow intermittence in multiple biogeographic regions. We hypothesized that the persistence of communities in temporary rivers is primarily associated with resilience mechanisms, not resistance mechanisms. Based on the attributes of resilience-structured invertebrate communities described above and in Fig. 1, we predicted that invertebrate communities in temporary rivers would be characterized by negative taxon richness-flow intermittence relationships, and by community nestedness along flow intermittence gradients. We expected these patterns to vary with the spatial arrangement of temporary reaches within river systems. To test our predictions, we used data from 128 sites in 14 temporary rivers across Europe, North America, and New Zealand. The datasets encompassed a wide range of flow intermittence and spatial arrangements of perennial and temporary reaches.

## Method

### Data sets

We compiled datasets from aquatic invertebrate studies of 14 temporary rivers in Europe (seven rivers), North America (five rivers), and New Zealand (two rivers). The datasets consisted of matrices of invertebrate taxa, abundances and sampling dates at multiple sites within temporary and perennial river reaches. The average number of days between two consecutive sampling events on a given site was 146.5 (range: 75–218; median = 155), whereas the average distance between sites was 3.1 km (range: 0.8–10.9; median = 2.2). At each site, invertebrates were collected from riffle habitats using standardized and comparable sampling methods (Surber, Hess, and kick-net samplers with mesh sizes ranging from 250 to 500  $\mu\text{m}$ ) from at least three sites per river (Table 1). The datasets were classified by the spatial arrangement of perennial and temporary reaches (upper, middle and lower reach drying, Table 1). For further information on the individual studies, see the references in Table 1, and details about methods and sites in Supplementary material Appendix 1.

### Quantification of flow intermittence

For each data set, annual flow intermittence (FI, in %), defined as the proportion of the year without surface water,

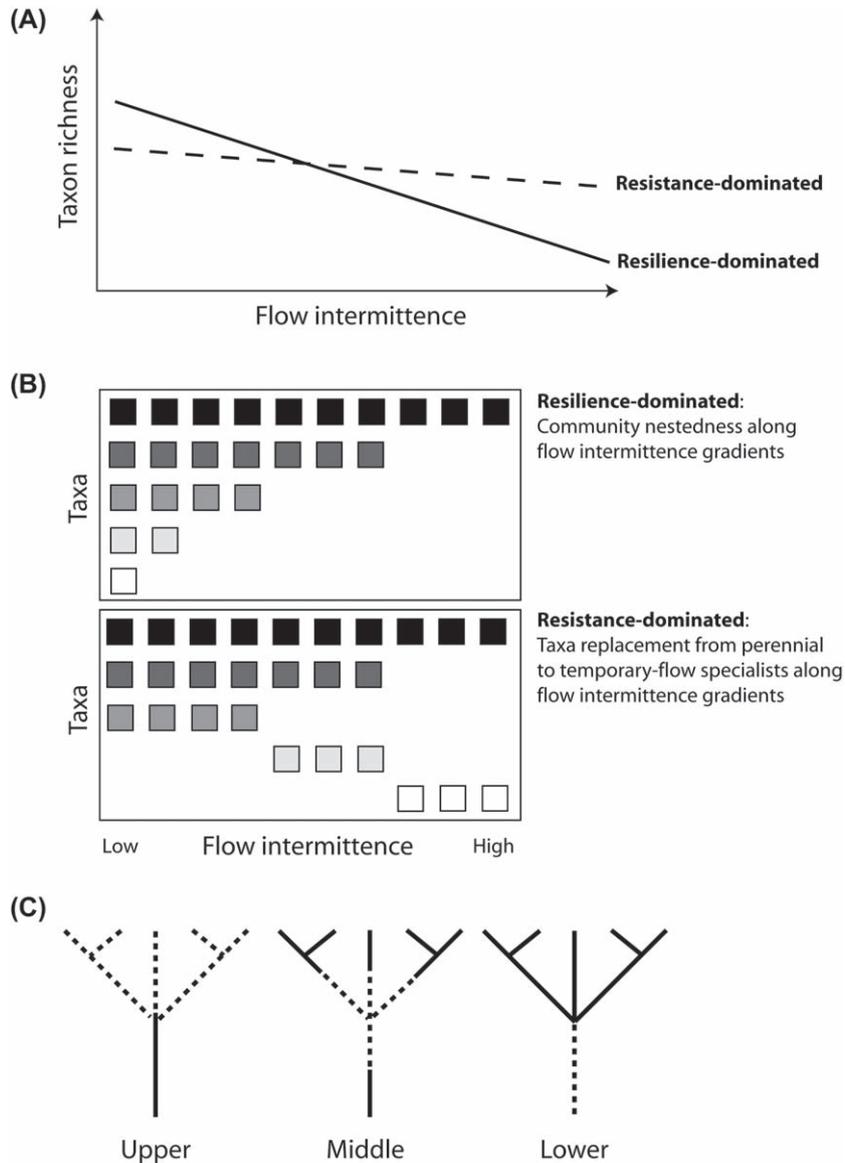


Figure 1. Conceptual diagrams for temporary rivers. (A) Predicted invertebrate taxon richness patterns along flow intermittence gradients. (B) Predicted changes in invertebrate community composition along flow intermittence gradients. (C) Spatial drying patterns in river networks (after Lake 2003). In (B), greyscale boxes represent taxa present at different points along a flow intermittence gradient. Communities structured by resilience are completely nested, because taxa-poor communities at the most temporary reaches are subsets of taxa-rich communities from the least temporary and perennial reaches. Communities structured by resistance are only partially nested and have high rates of taxa replacement by temporary-flow specialists along the flow intermittence gradient. In (C), solid and dashed lines represent perennial and temporary reaches, respectively.

was calculated for each sampling site. One of three procedures outlined below was used to calculate FI values for the sampling points in each river, reflecting the type of flow measurement and quantity of discharge data available in each study. River discharge was standardized to  $l s^{-1}$ .

#### Hydrological modelling

For five datasets (Albarine, Asse, Little Stour, Orari, Selwyn), mean daily flow (including zero-flow) at sampling sites were estimated using the statistical model ELMOD (Larned et al. 2011). For each river, the input data consisted of manual measurements of discharge at sampling sites on  $\geq$  nine dates, and continuous discharge from at least two permanent recorders that bounded the study reaches. The discharge

time-series from each recorder was  $\geq 10$  yr long, and included the study period during which invertebrate samples were collected. Modelled mean daily discharge was used to calculate FI for each site each year.

#### Direct measurement

For four datasets (Garden, Huachuca, Little Lusk, Sycamore), water-state loggers were used to record the presence or absence of water during the invertebrate sampling period (Fritz et al. 2006, Jaeger and Olden 2012). FI was calculated for each sampling site from the logged time-series. Estimates of FI based on ELMOD and water-state loggers at sampling sites along the Albarine River were highly correlated ( $r = 0.93$ ,  $p < 0.001$ ,  $n = 9$ ).

Table 1. Summary of location, climate, catchment characteristics, spatial drying pattern, flow intermittence (FI) and invertebrate sampling details of the 14 temporary rivers used in this study. More details are available in Supplementary material Appendix 1. Unpubl.: unpublished data.

Country	State/Region	River names	Climate type	Catchment area (km <sup>2</sup> )	Spatial drying pattern	FI range (%)	Sampling method	Duration (yr)	No. dates	No. sites	Sample size	References
France	Provence	Asse	Mediterranean	657	Middle	0–20	Hess	3	5	13	49	unpubl.
France	Rhône-Alpes	Albarine	Temperate	313	Lower	0–90	Hess	3	5	18	76	Datry 2012
Germany	East Westphalia	Alme	Temperate	763	Middle	0–35	Kick-net	3	3	7	21	unpubl.
Germany	East Westphalia	Ellerbach	Temperate	91	Lower	0–77	Surber	1	4	3	12	unpubl.
Germany	East Westphalia	Menne	Temperate	8	Lower	0–40	Surber	1	2	3	6	Meyer et al. 2003
Germany	East Westphalia	Sauer	Temperate	109	Lower	0–60	Kick-net	5	2 to 4	14	36	unpubl.
New Zealand	Canterbury	Orari	Temperate	850	Middle	0–80	Hess	2	2	11	22	unpubl.
New Zealand	Canterbury	Selwyn	Temperate	975	Middle	0–92	Hess	5	2 to 10	16	73	Arscott et al. 2010
UK	Kent	Little Stour	Temperate	213	Middle	0–20	Kick-net	9	8	9	72	Wood and Armitage 2004
US	Massachusetts	Fish Garden	Temperate	47	Upper	0–30	Surber	2	3	8	24	Santos and Stevenson 2011
US	Arizona	Garden	Arid	34	Lower	0–95	Kick-net	1	1	9	9	Bogan et al. 2013.
US	Arizona	Huachuca	Arid	25	Lower	0–90	Kick-net	1	1	9	9	Bogan et al. 2013.
US	Illinois	Little Lusk	Temperate	43	Upper	0–82	Hess	2	2	4	7	unpubl.
US	Indiana	Sycamore Branch	Temperate	3	Upper	0–65	Hess	2	2	4	7	unpubl.

## Direct observations

For five datasets (Alme, Ellerbach, Fish Brook, Menne, Sauer) FI was estimated at sampling sites using weekly to bi-monthly observations of flow state (flowing or dry, defined here as the complete absence of surface water) for three to 12 months. Point gauging data and discharge data from adjacent gauging stations were then used to assess flow-state patterns between consecutive observations (Meyer et al. 2003).

## Invertebrate variables

For each sample in the invertebrate datasets, taxon richness (TR) was calculated as the number of taxa per sample. To account for differences in taxonomic resolution among datasets, TR was calculated at three levels of resolution: fine (TR1), medium (TR2), and coarse (TR3). The degree of taxonomic consistency among datasets increases and taxonomic precision decreases from TR1 to TR3. The taxonomic groups used at each level of resolution are shown in Table 2.

Table 2. Number of taxa (No.) and corresponding proportion (%) across species, genera, families and other taxonomic units for the different levels of taxonomic resolution used in the study (TR1, 2 and 3). The taxonomic resolution for each group of taxa is also detailed. Ph: phylum, c: class, sc: sub-class, f: family, o: order, sf: sub-family, g: genus, s: species. EPT: Ephemeroptera, Plecoptera and Trichoptera.

	TR1		TR2		TR3	
	No.	%	No.	%	No.	%
Species	249	42.6	0	0.0	0	0.0
Genera	234	40.0	256	71.5	0	0.0
Families	85	14.5	85	23.7	118	94.4
Others	17	2.9	17	4.7	7	5.6
Total	585	100	358	100	125	100
Taxonomic resolution						
Plecoptera	f, g, s		f, g		f	
Trichoptera	f, g, s		f, g		f	
Ephemeroptera	f, g, s		f, g		f	
Coleoptera	f, g, s		f, g		f	
Diptera*	f, sf, g, s		f, sf, g		f	
Odonata	f, g, s		f, g		f	
Megaloptera	f, g, s		f, g		f	
Hemiptera	f, g, s		f, g		f	
Heteroptera	f, g, s		f, g		f	
Amphipoda	f, g, s		f, g		f	
Decapoda	f, g, s		f, g		f	
Isopoda	f, g, s		f, g		f	
Copepoda	sc		sc		sc	
Ostracoda	c		c		c	
Cladocera	o		o		o	
Mollusca	f, g, s		f, g		f	
Oligochaeta	sc, f, s		sc, f		sc	
Hirudinae	sc, f		sc, f		sc	
Platyhelminth	ph, f		ph, f		ph, f	
Nemathelminthes	ph		ph		ph	
Nematomopha	ph, f		ph, f		ph, f	
Acari	sc		sc		sc	
Hydrozoa	c		c		c	

\*\*Chironomidae subfamilies (Diamesinae, Orthocladinae, Podonominae, and Tanypodinae) and tribes (Chironomini and Tanytarsini) were used across TR1, TR2, and TR3.

To describe the communities in each dataset in terms of taxonomic composition and resistance-resilience traits, the relative abundances of Coleoptera, Diptera, Oligochaeta, and the sum of Ephemeroptera, Plecoptera and Trichoptera (hereafter 'EPT') were calculated in each sample. In addition, each taxon in each dataset was classified into one of four classes using life-history and biological traits: resistant, resilient, resistant and resilient, or neither resistant nor resilient. Although it reduced our ability to detect fine-scale patterns, this classification was undertaken at the coarsest taxonomic level (TR3) to maximize consistency across datasets. We considered the following trait states as resilience traits: long adult lifespan, high female dispersal, strong adult flying ability, common occurrence in drift, and strong swimming ability. We considered the following trait states as resistance traits: presence of desiccation-resistance forms (e.g. cysts, cocoons, diapause stages), body armouring limiting water loss (including the use of external cases), plastron/spiracle respiration, and low rheophily. We used published (Tachet et al. 2002, Poff et al. 2006, Bonada and Doledec 2011) and unpublished (V. Archambault pers. comm.) trait state information to classify each taxon (Supplementary material Appendix 2). Given the coarse taxonomic resolution used (TR 3), we assigned to each taxon the trait states which were dominant across the constituent families, genera or species. Presence of trait states was weighted equally when assigning taxa to trait classes. When a dominance of resistance trait states was found in a taxon, it was classified as resistant ( $n = 41$  taxa). When a dominance of resilience trait states was found in a taxon, it was classified as resilient ( $n = 41$  taxa). If an equal number of resistance and resilience trait states were assigned to a taxon, it was classified as resistant and resilient ( $n = 17$  taxa). When no traits was assigned to a taxon, it was classified as neither resistant nor resilient ( $n = 26$  taxa). For 12 out of 125 taxa, there was no information available regarding resistance and resilience trait states, and classification was based on closely related taxa for which there was some information and author's knowledge.

## Statistical analyses

The invertebrate community variables described above were used as dependant variables in linear mixed-effects models with Gaussian error distributions. Analyses were undertaken using the lme4 package for R (R Development Core Team). For each dependent variable, we tested for effects of FI and then tested if these effects differed between rivers and spatial drying patterns. We compared three nested mixed-effects models that progressively increased in complexity. The first model (null) was a null model with a random intercept. The second model (average) was an average model with a fixed effect of FI across all rivers. The third model (river-specific) was a model with a random effect of FI, which was allowed to vary among rivers (Bolker et al. 2009). River was a random effect in each model. When slopes differed among rivers, we fitted additional models adding longitudinal drying pattern as a fixed effect to test for possible systematic effects of the spatial arrangement of perennial and temporary reaches.

The statistical significance levels for the fixed and random effects in the best-fitting models were determined using likelihood-ratio tests on models with and without each effect (Bolker et al. 2009). To select the most parsimonious models, we used the minimum Akaike's information criterion (AIC). We checked for normality and homogeneity by visual inspections of plots of residuals against fitted values. When average models were selected, we used individual linear regressions to analyse how much individual rivers contributed to the average model.

Nestedness analyses were used to determine whether invertebrate communities at the most temporary sites were nested subsets of communities found at the least temporary and perennial sites. Such patterns would indicate a selective loss of taxa susceptible to drying rather than a replacement of perennial-flow specialists with intermittent-flow specialists along flow intermittence gradients. We tested for community nestedness of both taxa incidence and composition along the flow intermittence gradient at each river and at each taxonomic level (TR1, 2 and 3) using the Brualdi and Sanderson discrepancy index, which provides a conservative test for nestedness (Ulrich and Gotelli 2007). The significance of nestedness was then tested against constrained null models (showing the same marginal totals as the original data) using the 'quasiswap' method (Miklós and Podani 2004).

## Results

### Taxon richness and flow intermittence

Taxon richness decreased for all taxonomic resolutions with increasing FI (likelihood ratio tests between null and average models,  $\chi^2 = 232.59$ , 248.33, and 179.78 for TR1, TR2 and TR3, respectively;  $p < 0.001$ ; Fig. 2). The slopes of the taxon richness–FI relationships did not differ statistically among rivers as indicated by the comparisons between average and river-specific models ( $\chi^2 = 1.08$ , 1.07, and 1.76;  $p = 0.582$ , 0.586 and 0.414, for TR1, TR2 and TR3, respectively, Fig. 2). On average, a 10% increase in FI resulted in the loss of two taxa at the fine taxonomic level (TR1: slope =  $-0.20$ , 95% CI:  $-[0.22:0.18]$ ), one and a half taxa at the medium taxonomic level (TR2: slope =  $-0.16$ , 95% CI:  $-[0.18:0.15]$ ), and one taxon at the coarse taxonomic level (TR3: slope =  $-0.12$ , 95% CI:  $-[0.13:0.10]$ ) (Fig. 2).

### Resistance and resilience traits, community composition and flow intermittence

The significant negative relationships between FI and taxon richness were maintained when resilient taxa and neither resistant nor resilient taxa were considered separately (likelihood ratio tests between null and average models,  $\chi^2 = 125.93$  and 136.03, respectively;  $p < 0.001$ ), but were not significant for resistant taxa or those both resistant and resilient ( $\chi^2 = 13.61$  and 4.77,  $p = 0.1611$  and 0.8622, respectively). For resilient taxa and neither resistant nor resilient taxa, the slopes of the taxon richness–FI relationships differed statistically among rivers as indicated by the

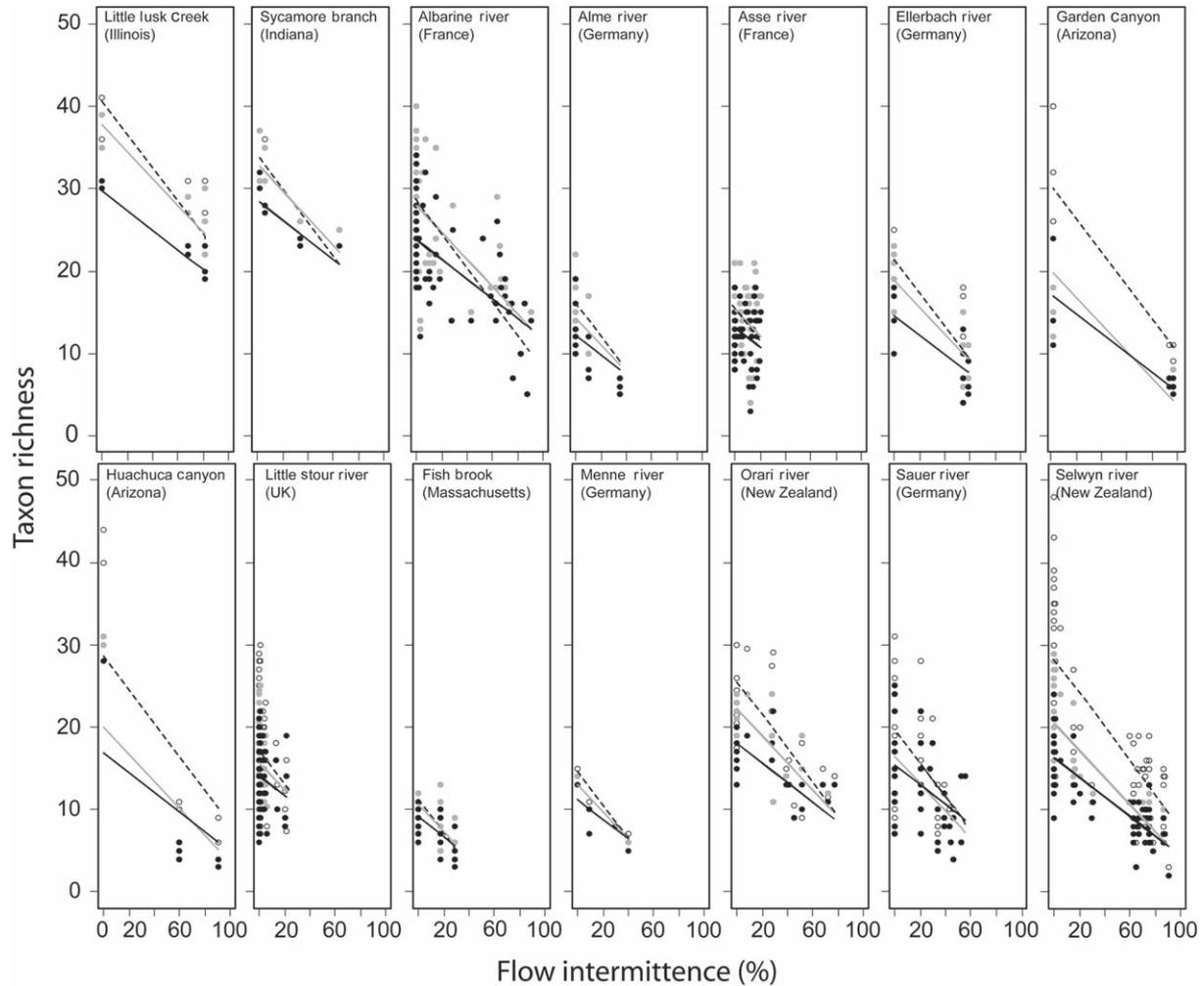


Figure 2. Average mixed-effects models for the 14 data sets of TR1 (white circles, dotted lines), TR2 (grey circles, plain gray line) and TR3 (black circles, plain black line) and FI as a fixed slope, showing a congruent decrease in the number of taxa with increasing FI, regardless of the taxonomic resolution. Linear regressions performed on each dataset individually indicated significant relationships between taxon richness and FI in 11, 10 and 9 rivers out of 14, when considering TR1, 2 and 3, respectively.

comparisons between average and river-specific models ( $\chi^2 = 15.09$ , and  $41.61$ , respectively;  $p < 0.001$ ). However, these relationships did not differ with respect to the spatial arrangement of perennial and temporary reaches (likelihood ratio test,  $\chi^2 = 1.87$  and  $3.11$ ;  $p = 0.7596$  and  $0.5384$ , respectively).

The relative abundances of EPT and Coleoptera decreased, and the relative abundance of Diptera increased among rivers as FI increased (likelihood ratio tests between null and average models,  $\chi^2 = 72.89$ ,  $19.26$ , and  $73.44$ , respectively;  $p < 0.001$ , Fig. 3 and 4). The slopes of these relationships did not differ statistically among rivers (likelihood ratio tests between average and river-specific models,  $\chi^2 = 0.27$ ,  $5.19$ , and  $6.46$ ;  $p = 0.871$ ,  $0.078$ , and  $0.065$ , respectively, Fig. 3 and 4). On average, for every 10% increase of FI, there was a 4% reduction in the relative abundance of EPT taxa (slope =  $-0.37$ , 95% CI:  $-[0.45:0.28]$ ), a 0.5% reduction in the relative abundance of Coleoptera (slope =  $-0.06$ , 95% CI:  $-[0.09:0.04]$ ) and a 4% increase in the relative abundance of Diptera (slope =  $0.38$ , 95% CI:  $[0.30:0.47]$ ). There were no detectable relationships

between the relative abundance of Oligochaeta and FI (likelihood ratio tests between null and average models,  $\chi^2 = 4.79$ ;  $p = 0.092$ ).

### Community nestedness along flow intermittence gradients

At the fine taxonomic level, invertebrate communities at the most temporary sites were nested subsets of communities at the least temporary and perennial sites in 10 of the 14 rivers (Table 3). At medium and coarse levels of taxonomic resolution, nestedness tended to occur primarily in rivers with downstream drying patterns (Table 3).

### Discussion

We demonstrated general and significant effects of FI on invertebrate taxon richness across 14 rivers in Europe, North America and New Zealand. Where FI increased, invertebrate

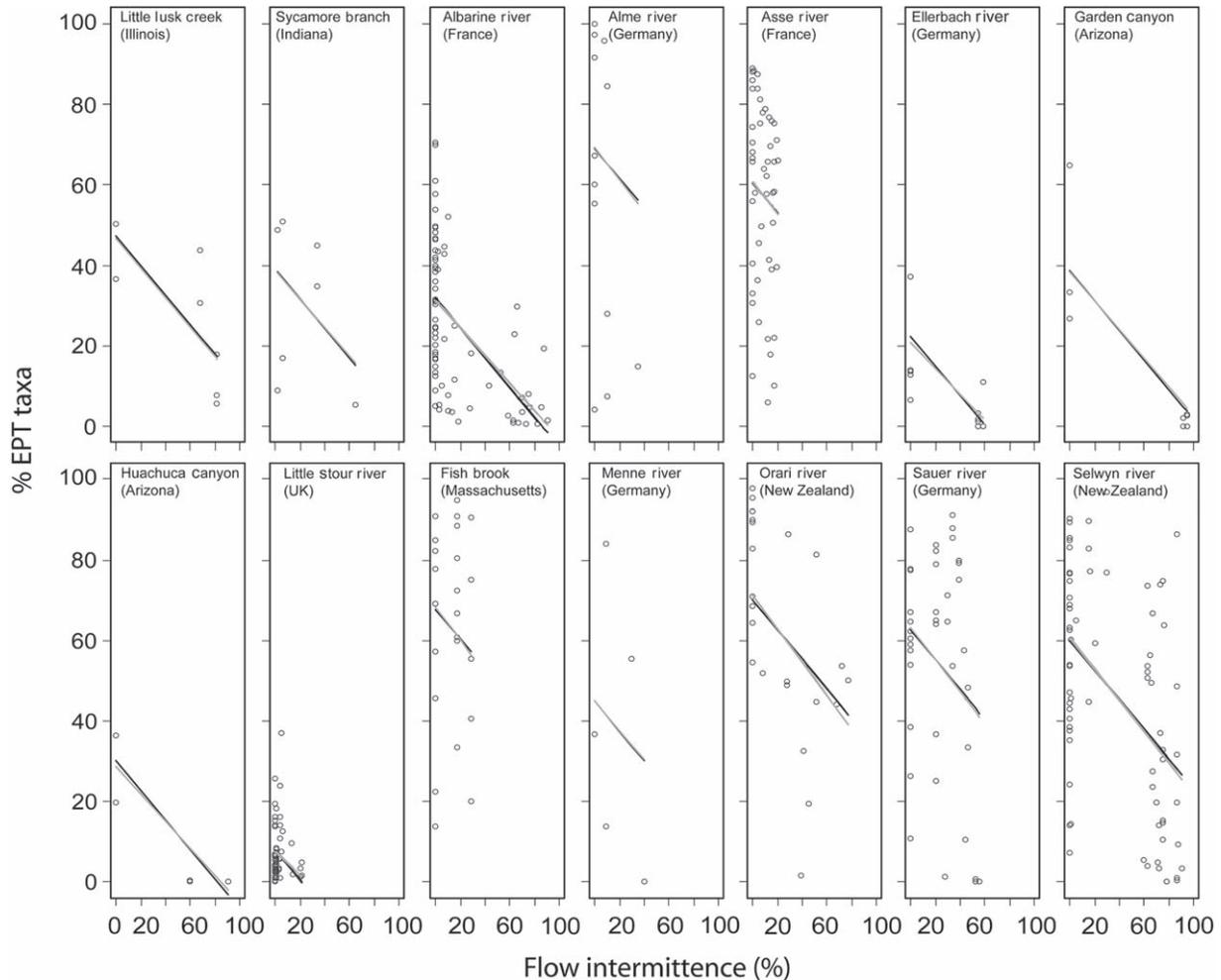


Figure 3. Average (black) and river-specific (grey) mixed-effects models for the 14 data sets of the relative abundance of EPT (Ephemeroptera, Plecoptera and Trichoptera) taxa in communities and FI. Linear regressions performed on each dataset individually indicated significant relationships in 6 rivers out of 14.

communities in these rivers became increasingly taxa-poor. More importantly, the rate of decline in the number of taxa along gradients of FI was not statistically different among the 14 rivers tested for each of the three different levels of taxonomic resolution, despite these rivers representing a wide range of climatic and biogeographic conditions and differing markedly in size and spatial drying patterns. Therefore, our results demonstrate a wide-spread congruence in the responses of invertebrates to FI and suggest that FI is a master variable driving river community structure and composition. Given the increasing intensity and spatial extent of FI in rivers due to anthropogenic water abstraction and climate change (Meybeck 2003, Larned et al. 2010), our findings indicate the potential for widespread declines in river biodiversity.

Our analysis of diversity patterns helps to disentangle the respective roles of resistance and resilience mechanisms in structuring invertebrate communities in temporary rivers. There are three ways in which our results indicate that, as we hypothesized, invertebrate community patterns along FI gradients are primarily a function of resilience rather than resistance. First, the relationships between taxon richness

and FI held across rivers for resilient taxa and for taxa without resistant nor resilient trait states, when coded at the family level. In contrast, no relationships were detected between FI and resistant taxa or taxa with both resistant and resilient trait states. Second, the relative abundances of groups such as EPT and Coleoptera decreased with FI; many species in these groups are susceptible to desiccation (Williams 2006, Datry et al. 2012) and have resilient trait states that facilitate recolonization, such as long life-span or strong flying abilities (Petersen et al. 1999, Bohonak and Jenkins 2003). In contrast, the relative abundance of dipteran taxa increased with FI and desiccation-resistant traits, such as diapause and anhydrobiosis occurs in many dipteran families (Frouz et al. 2003). Desiccation-resistant traits are not likely to be uniform across the Diptera as a group, however, and do not constrain their persistence in perennial habitats. Many dipterans thrive in perennial sites, with an average relative abundance > 25% in the perennial reaches of our 14 study rivers. Third, a significant level of community nestedness occurred along most of the FI gradients in this study, which indicates that taxa-poor communities in the most temporary sites were nested-subsets of

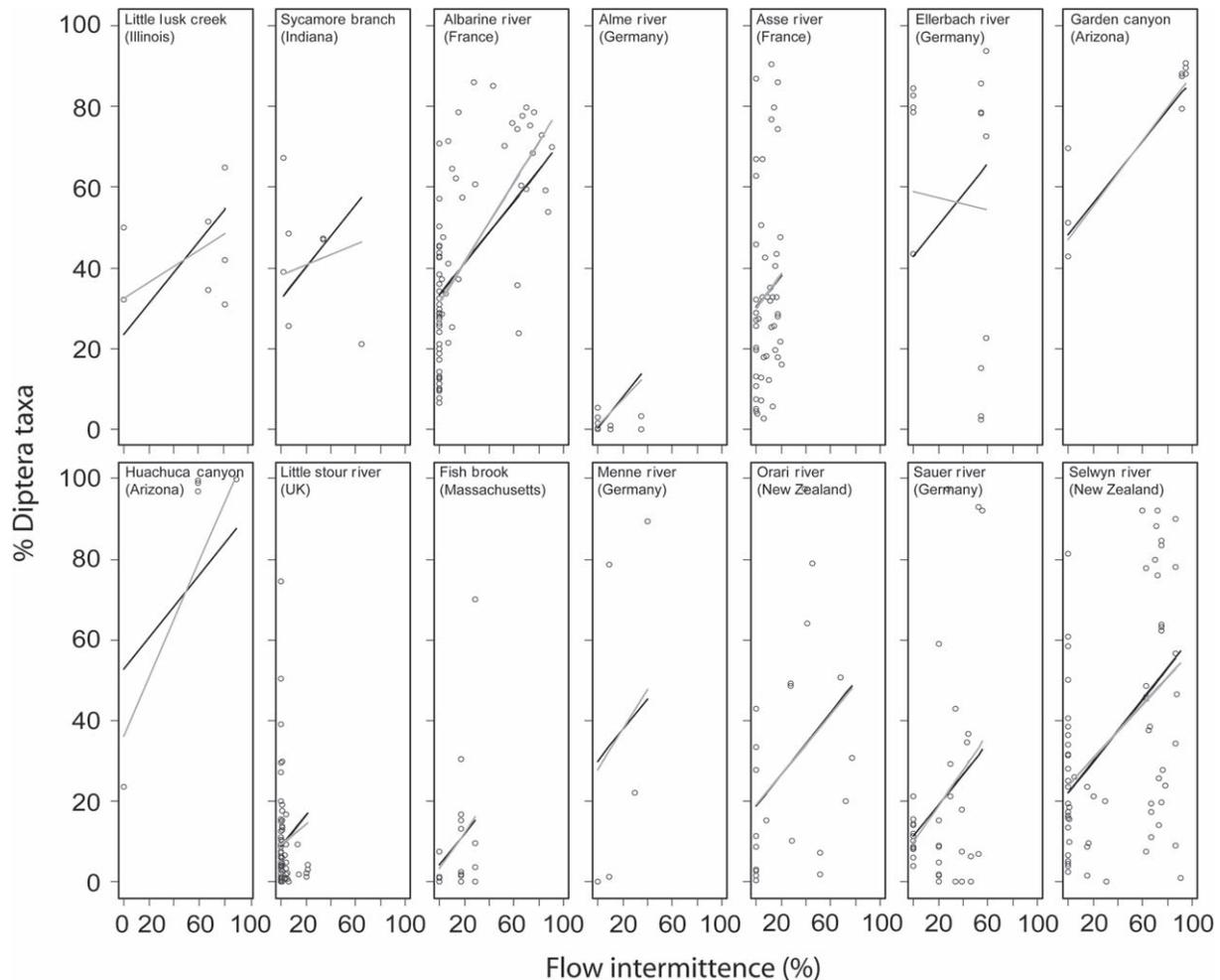


Figure 4. Average (black) and river-specific (grey) mixed-effects models for the 14 data sets of the relative abundance of Diptera in communities and FI. Linear regressions performed on each dataset individually indicated significant relationships in 8 rivers out of 14.

taxa-rich communities in the least temporary and perennial sites. Community nestedness was probably the result of both limited dispersal from source communities in perennial reaches and local extinction along FI gradients (McAbendroth et al. 2005). This suggests that the distribution of aquatic refuges across river landscapes, combined with taxa-specific differences in dispersal abilities may explain much of the colonization and succession dynamics in temporary rivers.

Although dispersal appears to be an overriding mechanism for explaining community persistence in temporary rivers, there was very little evidence that the pattern of habitat fragmentation (i.e. different spatial arrangements of perennial and temporary reaches) had a strong influence on the responses of invertebrate communities to FI. Contrary to our prediction, the FI–taxonomic richness relationships did not vary among spatial arrangements of perennial and temporary reaches. Confounding factors may obscure the effect of spatial fragmentation patterns on aquatic invertebrate communities. It is likely that the magnitude and dynamics of drying and rewetting alter the effects of spatial drying patterns on the responses of invertebrate communities to FI. Complete riverbed drying can occur within a few hours, or disconnected pools can persist for several weeks

in otherwise dry riverbeds. Rewetting may be gradual (e.g. expanding pools driven by groundwater upwelling) or rapid (e.g. flash-flood bores driven by runoff). These variable transitions between wet and dry periods are likely to influence the ability of invertebrates to disperse to and from refuges (Corti and Datry 2012, Bogan et al. 2013). Last, refuges adjacent to (parafluvial ponds, lakes, springs) and beneath (hyporheic zone) river channels were not included in this study, and could play significant roles in maintaining communities in temporary rivers (Boulton et al. 1998, Williams 2006).

Invertebrate communities in reaches with the highest FI were consistently dominated by generalist and ubiquitous taxa, rather than by temporary-habitat specialists. Even in the three rivers where chironomids (Huachuca and Garden) or coleopterans (Little Stour) were identified to the species level, there was still little evidence of temporary-specialist taxa. Because rivers with natural flow regimes are characterized by large variations in discharge, including drought periods (Lake 2003, Lytle and Poff 2004), drying may not be an evolutionary force restricted to temporary rivers as previously thought (cf. Williams 2006, Steward et al. 2012). The absence of apparent temporary-specialist taxa in these

Table 3. Community nestedness for different taxonomic levels (TR1, 2 and 3, see Table 2). Values shown are the discrepancy indexes and the associated p-values from testing indexes against constrained null models. Italics indicate significant p-values.

Taxonomic level	Upper reach drying			Middle reach drying					Lower reach drying					
	Fish Brook	Sycamore Branch	Little Lusk	Asse	Orari	Selwyn	Little Stour	Alme	Albarine	Huachuca	Garden	Ellerbach	Menne	Sauer
TR1	53; 0.01	30; 0.21	24; 0.03	29; 0.55	81; 0.01	123; 0.01	75; 0.15	93; 0.01	73; 0.01	7; 0.01	8; 0.01	75; 0.01	18; 0.49	257; 0.01
TR2	39; 0.07	28; 0.13	28; 0.05	29; 0.51	54; 0.01	69; 0.09	51; 0.45	75; 0.01	60; 0.01	3; 0.01	3; 0.01	57; 0.01	16; 0.59	217; 0.01
TR3	49; 0.98	17; 0.33	22; 0.49	24; 0.35	38; 0.23	45; 0.39	42; 0.31	57; 0.01	87; 0.01	1; 0.01	1; 0.01	33; 0.01	10; 0.37	147; 0.01

rivers contrasts with community patterns in temporary lentic habitats, such as ponds or wetlands, where taxa replacements along decreasing hydroperiod gradients from perennial to temporary-specialists are common (Wellborn et al. 1996). Such patterns are thought to be driven by trade-offs between traits that facilitate survival in temporary environments (e.g. dormancy stages, desiccation-resistant eggs) and traits that reduce vulnerability to predators (e.g. low activity rates, antipredator morphology) (Skelly 1995, Wellborn et al. 1996). Alike temporary wetlands, top aquatic predators (invertebrates, fish) often occur in temporary river reaches due to their connectivity with perennial reaches (Labbe and Faush 2000), and perhaps such trade-offs do not occur along FI gradients in rivers. However, biotic interactions, including competition and predation, have not been as thoroughly examined in temporary rivers compared to temporary lentic habitats (Skelly 1995, Wellborn et al. 1996, Spencer et al. 1999), and empirical data to support this hypothesis are currently lacking. If FI increases in extent and severity in the future, we anticipate an increased biotic homogenization of riverine communities, which will in turn modify the functioning and resilience of river ecosystems (McKinney and Lockwood 1999, Spencer et al. 1999).

We demonstrated that invertebrate communities have congruent responses to FI gradients across a range of river sizes in multiple biogeographic regions, and that the spatial arrangement of perennial and temporary reaches had very little influence on these responses. This suggests that FI is a primary driver of aquatic communities in temporary rivers around the world. Resilience explained invertebrate diversity patterns along FI gradients to a greater degree than resistance. However, invertebrate colonization following the resumption of flow remains a poorly-known process and many questions remain (Chester and Robson 2011). For instance, we do not know to what degree successional patterns are predictable, and what abiotic (e.g. distances to refuges, distribution of refuges across landscapes) or biotic drivers (e.g. predation, competition) control succession. Metacommunity and metapopulation dynamics deserve more attention in temporary rivers and more manipulative experiments are needed to improve our understanding of their effects on diversity patterns. In the context of a worldwide biodiversity crisis, whose severity in freshwater ecosystems has been carefully documented (Dudgeon et al. 2006), the general relationships generated in this study may help water managers mitigate the effects of dams, flow diversion, and water abstraction, and help scientists predict future changes in river biodiversity.

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## References

- Arscott, D. B. et al. 2010. Aquatic invertebrate community structure along an intermittence gradient: Selwyn River, New Zealand. – *J. N. Am. Benthol. Soc.* 29: 530–545.
- Bêche, L. A. et al. 2009. Resilience of fishes and invertebrates to prolonged drought in two California streams. – *Ecography* 32: 778–788.
- Bogan, M. T. et al. 2013. Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. – *Freshwater Biol.* doi: 10.1111/fwb.12105
- Bohonak, A. J. and Jenkins, D. G. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. – *Ecol. Lett.* 6: 783–796.
- Bolker, B. M. et al. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. – *Trends Ecol. Evol.* 24: 127–135.
- Bonada, N. and Doledec, S. 2011. Do mediterranean genera not included in Tachet et al. 2002 have mediterranean trait characteristics? – *Limnetica* 30: 129–142.
- Boulton, A. J. et al. 1998. The functional significance of the hyporheic zone in streams and rivers. – *Annu. Rev. Ecol. Syst.* 29: 59–81.
- Chester, E. T. and Robson, B. J. 2011. Drought refuges, spatial scale and recolonisation by invertebrates in non-perennial streams. – *Freshwater Biol.* 56: 2094–2104.
- Corti, R. and Datry, T. 2012. Invertebrate and sestonic matter in an advancing wetted front travelling down a dry riverbed (Albarine, France). – *Freshwater Sci.* 31: 1187–1201.
- Datry, T. 2012. Benthic and hyporheic invertebrate assemblages along a flow intermittence gradient: effects of drying events. – *Freshwater Biol.* 57: 563–574.
- Datry, T. et al. 2007. Responses of hyporheic invertebrate assemblages to large-sclae variation in flow permanence and surface-subsurface exchange. – *Freshwater Biol.* 52: 1452–1462.
- Datry, T. et al. 2011. Recent perspectives on temporary river ecology. – *Aquat. Sci.* 73: 453–457.
- Datry, T. et al. 2012. Spatial and temporal aquatic–terrestrial transitions in the temporary Albarine River, France: responses of invertebrates to experimental rewetting. – *Freshwater Biol.* 57: 716–727.
- del Rosario, R. B. and Resh, V. H. 2000. Invertebrates in intermittent and perennial streams: is the hyporheic zone a refuge from drying? – *J. N. Am. Benthol. Soc.* 19: 680–696.
- Dudgeon, D. et al. 2006. Freshwater biodiversity: importance, threats, status and conservation. – *Biol. Rev.* 81: 163–182.
- Fagan, W. F. 2002. Connectivity, fragmentation and extinction risk in dendritic metapopulations. – *Ecology* 83: 3243–3249.
- Fritz, K. M. and Dodds, W. K. 2004. Resistance and resilience of macroinvertebrate assemblages to drying and flooding in a tallgrass prairie stream. – *Hydrobiologia* 527: 99–112.
- Fritz, K. M. et al. 2006. Field operations manual for assessing the hydrologic permanence and ecological condition of headwater streams. – EPA 600/R-06/126, USEPA Office of Research and Development, National Exposure Research Laboratory, Cincinnati, OH, USA, <www.epa.gov/nerleerd/methods/headwater.html>.
- Frouz, J. et al. 2003. Survival strategies of chironomids (Diptera: Chironomidae) living in temporary habitats: a review. – *Eur. J. Entomol.* 100: 459–465.
- Jaeger, K. L. and Olden, J. D. 2012. Electrical resistance sensor arrays as a means to quantify longitudinal connectivity of rivers. – *River Res. Appl.* 28: 1843–1852.
- Labbe, T. R. and Fausch, K. D. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. – *Ecol. Appl.* 10: 1774–1791.
- Lake, P. S. 2003. Ecological effects of perturbation by drought in flowing waters. – *Freshwater Biol.* 48: 1161–1172.
- Lamouroux, N. et al. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. – *Ecology* 83: 1792–1807.
- Larned, S. T. et al. 2010. Emerging concepts in temporary-river ecology. – *Freshwater Biol.* 55: 717–738.
- Larned, S. T. et al. 2011. Longitudinal river ecohydrology: flow variation down the lengths of alluvial rivers. – *Ecohydrology* 4: 532–548.
- Lytle, D. A. and Poff, N. L. 2004. Adaptation to natural flow regimes. – *Trends Ecol. Evol.* 19: 94–100.
- McAbendroth, L. et al. 2005. Unravelling nestedness and spatial pattern in pond assemblages. – *J. Anim. Ecol.* 74: 41–49.
- McCain, C. M. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. – *Global Ecol. Biogeogr.* 16: 1–13.
- McCluney, K. E. and Sabo, J. L. 2012. River drying lowers the diversity and alters the composition of an assemblage of desert riparian arthropods. – *Freshwater Biol.* 57: 91–103.
- McKinney, M. L. and Lockwood, J. L. 1999. Biotic homogenization: a few winners replace many losers in the next mass extinction. – *Trends Ecol. Evol.* 14: 450–453.
- Melo, A. S. et al. 2009. Environmental drivers of beta-diversity patterns in New-World birds and mammals. – *Ecography* 32: 226–236.
- Menéndez, R. et al. 2007. Direct and indirect effects of climate and habitat factors on butterfly diversity. – *Ecology* 88: 605–611.
- Meybeck, M. 2003. Global analysis of river systems: from Earth system controls to Anthropocene syndromes. – *Phil. Trans. R. Soc. B* 358: 1935–1955.
- Meyer, A. et al. 2003. Lotic communities of two small temporary karstic systems (East Westphalia, Germany) along a longitudinal of hydrological intermittency. – *Limnologia* 33: 271–279.
- Miklós, I. and Podani, J. 2004. Randomization of presence–absence matrices: comments and new algorithms. – *Ecology* 85: 86–92.
- Mittelbach, G. G. et al. 2001. What is the observed relationship between species richness and productivity? – *Ecology* 82: 2381–2396.
- Öckinger, E. et al. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. – *Ecol. Lett.* 13: 969–979.

- Petersen, I. et al. 1999. Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. – *Freshwater Biol.* 42: 401–416.
- Poff, N. L. et al. 2006. Functional trait richness of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. – *J. N. Am. Benthol. Soc.* 25: 730–755.
- Santos, A. N. and Stevenson, R. D. 2011. Comparison of macroinvertebrate diversity and community structure among perennial and non-perennial headwater streams. – *Northeast. Nat.* 18: 7–26.
- Skelly, D. K. 1995. A behaviour trade-off and its consequences for the distribution of pseudacris treefrog larvae. – *Ecology* 76: 150–164.
- Spencer, M. et al. 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools: relationships with habitat size and permanence. – *Ecol. Lett.* 2: 157–166.
- Stanley, E. H. et al. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. – *Am. Midl. Nat.* 131: 288–300.
- Steward, A. L. et al. 2012. When the river runs dry: human and ecological values of dry riverbeds. – *Front. Ecol. Environ.* 10: 202–209.
- Tachet, H. et al. 2002. *Invertébrés d'eau douce (2nd corrected impression)*. – CNRS Editions, Paris, France.
- Ulrich, W. and Gotelli, N.J. 2007. Null model analysis of species nestedness patterns. – *Ecology* 88: 1824–1831.
- Wellborn, G. A. et al. 1996. Mechanisms creating community structure along a freshwater habitat gradient. – *Annu. Rev. Ecol. Syst.* 27: 337–363.
- Williams, D. D. 2006. *The biology of temporary waters*. – Oxford Univ. Press.
- Wood, P. J. and Armitage, P. D. 2004. The response of the macroinvertebrate community to low flow variability and supra-seasonal drought within a groundwater dominated river. – *Archiv Hydrobiol.* 161: 1–20.

Supplementary material (Appendix ECOG-00287 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix 1–2.