Title: Hyporheic invertebrates as bioindicators of ecological health in temporary rivers: a meta-analysis

Short title: Hyporheic bioindicators in temporary rivers

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Abstract

Worldwide, many rivers cease flow and dry either naturally or owing to human activities such as water extraction. However, even when surface water is absent, diverse assemblages of aquatic invertebrates inhabit the saturated sediments below the river bed (hyporheic zone). In the absence of surface water or flow, biota of this zone may be sampled as an alternative to surface water-based ecological assessments. The potential of hyporheic invertebrates as ecological indicators of river health, however, is largely unexplored. We analysed hyporheic taxa lists from the international literature on temporary rivers to assess compositional similarity among broad-scale regions and sampling conditions, including the presence or absence of surface waters and flow, and the regional effect of hydrological phase (dry channel, non-flowing waters, surface flow) on richness. We hypothesized that if consistent patterns were found, then effects of human disturbances in temporary rivers may be assessable using hyporheic bioindicators. Assemblages differed geographically and by climate, but hydrological phase did not have a strong effect at the global scale. However, hyporheic assemblage composition within regions varied along a gradient of higher richness during wetter phases. This indicates that within geographic regions, hyporheic responses to surface drying are predictable and, by extension, hyporheic invertebrates are potentially useful ecological indicators of temporary river health. With many rivers now experiencing, or predicted to experience, lower flows and longer dry phases owing to climate change, the development of ecological assessment methods specific to flow intermittency is a priority. We advocate expanded monitoring of hyporheic zones in temporary rivers and recommend hyporheic invertebrates as potential bioindicators to complement surface water assessments.

Keywords

Ecological assessment; low river flows; aquatic invertebrates; river health; climate change; flow intermittency

Abbreviations

ANOSIM, analysis of similarities; CAP, canonical analysis of principal coordinates; EPT, Ephemeroptera, Plecoptera and Trichoptera; DC, dry channel; NMDS, non-metric multi-dimensional scaling; NSF, no surface flow; SF, surface flow

1. Introduction

Temporary rivers experience varying periods of flow cessation and surface drying (Larned et al., 2010) and are the major inland water component of many regions, including Australia (Kennard et al., 2010), southern Africa (Davies et al., 1995), North America (Poff and Ward, 1989), South America and the Mediterranean basin (Bonada et al., 2008). This widespread occurrence, along with the increase in flow intermittency occurring through climate change across much of the world (Kundzewicz et al., 2008) and the escalating human demand for water (Vörösmarty et al., 2010), makes understanding ecological consequences of intermittency in river systems increasingly important (Datry et al., 2011).

However, flow intermittency challenges our ability to monitor and assess the ecological integrity of temporary rivers. First, variation in the presence and timing of flow creates considerable spatial and temporal variation in these rivers' physical, chemical and biological attributes, such that many conventional indicators of river health may not detect anthropogenic changes (Datry et al., 2011). For example, taxonomic richness is expected to decline in temporary rivers as their waters decline and channels dry (Larned et al., 2010), but this response is not consistent among rivers or through time (Rolls et al., 2012). Therefore, this variation must be incorporated into the assessment process so that variation owing to natural wetting and drying can be distinguished from that caused by human activities (Sheldon, 2005), such as a reduction in taxonomic richness associated with land use change (Boulton et al., 1997). Second, the unpredictable spatio-temporal presence of surface waters means that monitoring programs based on sampling surface waters at specific locations or times of year produce incomplete datasets (Steward et al., 2012), complicating analyses and creating gaps in reporting.

To avoid these problems, monitoring environments other than surface waters in temporary rivers have been suggested, including dry riverbeds (Steward et al., 2011) and the hyporheic zone, defined as the saturated sediments beneath the surface channel and adjacent banks. A major advantage of the hyporheic zone as a monitoring environment in temporary rivers is its persistence. Streams with dry surface channels can have substantial hyporheic zones (Valett et al., 1990; Claret and Boulton, 2003), and hyporheic invertebrates of temporary rivers have been collected from beneath both dry and wet channels, and across multiple seasons (e.g. Boulton et al., 1992a; del Rosario and Resh, 2000; Young et al., 2011). Although water can be lost from the subsurface sediments of some rivers within days of flow cessation (Datry, 2012), aquatic invertebrates often persist beneath surface channels in moist or dry sediments, even during long dry phases (Stubbington et al., 2009). These features suggest that hyporheic fauna are a viable alternative for temporary river bioassessment.

The potential for hyporheic invertebrates to act as indicators of health in temporary rivers has long been recognised (Boulton et al., 1992a), comparable to the use of macroinvertebrate richness and composition in permanent waters as indicators of overall river health (e.g. Barbour et al., 1999 (USA); Davies, 2000 (Australia); Clarke et al., 2003 (UK)). However, only a few attempts have been made to include hyporheic invertebrates in river health assessments (e.g. Nelson and Roline, 2003; Moldovan et al., 2013). This may reflect the cryptic nature of hyporheic fauna (‘out of sight, out of mind’), a reluctance to accept new sampling methods, and a lack of appreciation of the ecological interactions between surface and hyporheic ecosystems in most rivers.

Further, in the context of temporary rivers, there is a need to determine the extent of hyporheic physical, chemical and biological variation attributable to surface flow conditions (Stubbington et al., 2011a). Factors known to affect hyporheic invertebrate distribution and composition, such as sediment characteristics and interstitial flow patterns, and the selectivity of sampling techniques (Fraser and Williams, 1997), also require consideration.

We aimed to assess the potential of hyporheic invertebrates of temporary rivers as ecological indicators of river health. We analysed hyporheic invertebrate data from temporary rivers across the world to determine whether assemblage composition and richness showed consistent patterns of variation that could be attributed to: (a) factors that could be controlled in a survey program, such as geographical location, climate zone and sampling techniques, and (b) factors that vary such as hydrological conditions at the time of sampling (hydrological phase). Our rationale was that if patterns of variation were consistent, and therefore predictable and quantifiable, then hyporheic invertebrates of temporary rivers could be used as bioindicators of variation owing to anthropogenic disturbance. We hypothesized that the broad-scale factors of climate and geographical region would have strong effects on hyporheic assemblage composition and, within these factors, surface water and surface flow conditions would also be important drivers (Fig. 1). In addition, we hypothesized that hyporheic invertebrate richness would be lower when the surface channel was dry or there was no surface water flow, and lower still when the system was also affected by anthropogenic disturbance (Fig. 1).

2. Methods

2.1. Literature search

We searched for relevant studies using the electronic databases Science Citation Index Expanded and Conference Proceedings Citation Index-Science within ISI Web of Science (Thomson Reuters), and the Boolean search statement: Topic = (invertebrate* OR macroinvertebrate*) AND (dry* OR temporar* or ephemeral* or intermitten* or episodic*) AND (stream* OR river*) AND (hyporhe* OR intersti* OR vertical*), where * indicates all possible word endings. This yielded 75 studies, which we examined individually to confirm suitability. Studies were excluded if they were not field-based (i.e. experimental microcosm studies or review papers), were from perennially flowing rivers, did not collect hyporheic invertebrates, only examined certain taxa, and/or taxonomic resolution was coarser than family level for the Insecta. Where taxa lists or detail on collection methods or hydrological conditions were not given, we contacted the authors to access the data. This refined the 75 studies to 14, which we expanded to 21 by including data from two independent, unpublished studies (Leigh, Stubbington) and from five other published studies cited within those from the original search. Four of the 21 studies included rivers within primarily agricultural landscapes (Table 1). All other studies were conducted in areas with minimal anthropogenic impact, confirmed by the studies' authors (pers. comm.) or as inferred from the study-region descriptions (e.g. nature reserves, national parks).

We standardised the invertebrate records to presence-absence data using the lowest levels of within-group taxonomic resolution consistent across studies. Separate taxa lists were created for samples collected during different hydrological phases, classed as: dry channel (DC), flowing (surface flow, SF) and non-flowing waters (no surface flow but surface water present, NSF). When a study's taxa list was drawn from samples taken during multiple hydrological phases including SF, it was allocated to the category 'mix'. Broad-scale geographical region (Antarctica, Australia, Europe, New Zealand and North America), climate zone (arid, mediterranean, polar, subarctic, temperate and tropical), collection method and depth were also used to categorise the data. Collection methods were classed as wells (invertebrates pumped from pipes sunk into the subsurface sediments), cages (invertebrates collected from buried colonisation pots), pits (invertebrates collected from pits in the hyporheic zone) and dug (invertebrates picked from sediments dug from the beneath the channel). Depth was categorised as either ≤ 30 cm or > 30 cm. This yielded 24 taxa lists (termed 'cases') for our meta-analysis (Table 1). We also compiled accompanying information on direction of surface-subsurface flow during sampling (upwelling, downwelling or neutral), mesh size used to screen the invertebrate samples, and substrate composition.

2.2. Meta-analysis

To examine patterns in assemblage composition, we calculated Bray-Curtis similarities between all pairs of cases from the presence-absence data. The resultant similarity matrix formed the basis of all subsequent analyses involving assemblage composition (performed in PRIMER v6 with the PERMANOVA+ add-on; Clarke and Gorley, 2006; Anderson et al., 2008).

We tested the hypotheses that assemblage composition would be significantly associated with climate zone, geographical region, collection method, collection depth and hydrological phase (e.g. Fig. 1A), using separate one-way ANOSIM (analyses of similarities). Data collected from agricultural landscapes were not included in these analyses as these particular hypotheses did not concern the potential effects of anthropogenic impacts. Differences were evaluated based on the ANOSIM *R* statistic (with $R > 0.25$ and, when there were > 1000 possible permutations of cases, P-values < 0.05 indicative of substantial differences between groups (Clarke and Warwick, 2001)). Although multi-factor models and interactions were not analysed owing to limited degrees of freedom, we created a joint climate and geographical region factor to test for differences in composition that were associated with their combination. Patterns of variation in assemblage composition among the cases, as indicated by the ANOSIM analyses, were visualised using non-metric multi-dimensional scaling (NMDS) ordination, based on 100 random starts. The two-dimensional solution was displayed if stress (goodness of fit) was < 0.2 (Clarke and Warwick, 2001).

Canonical analysis of principal coordinates (CAP) was used to explore the relationship between assemblage richness and variation in composition (based on the Bray-Cutis similarity matrix) among cases, excluding those from agricultural landscapes. CAP is a constrained ordination technique designed to visualise multivariate patterns pertaining to specific hypotheses, and can be used as tool for prediction to place new data in ordination space (Anderson and Willis, 2003; Anderson et al., 2008). We used CAP to analyse how well the assemblage composition data could predict the positions of cases along a gradient of richness (as a proxy for river health) and the model's predictive capacity was tested using new cases (the cases from agricultural landscapes).

Under our hypothesis that hyporheic invertebrate richness, if acting as a good indicator of river health, would be lower under dry compared with wet conditions, and lower still under conditions of anthropogenic impact (Fig. 1B), the position of cases from low-impact study regions along the gradient should indicate where ‘healthy’ rivers lie given the hydrological phase at the time of sampling. A decline in these rivers’ health should lower their position, and ‘unhealthy’ rivers disturbed by human activities should be lower on the gradient than ‘healthy’ (relatively undisturbed) rivers with comparable features (e.g. similar flow regimes and matched hydrological phases) (Fig. 1C). CAP model performance was evaluated based on the percentage of variation in the similarity matrix explained by the model, the trace statistic to test the null hypothesis of no difference in composition along the richness gradient, and a ‘leave-one-out’ procedure to check for overparameterisation by choosing the number (*m*) of principal coordinate axes for the analysis that minimises the ‘leave-one-out’ residual sums of squares (Anderson and Robinson, 2003; Anderson et al., 2008).

Patterns in richness data were also examined graphically to evaluate consistencies in the relationship between hydrological phase and richness metrics within climate and geographical regions (Fig. 1B), and to assess overall differences among those regions and among collection methods. Metrics comprised overall (raw absolute) richness and the mean richness and relative richness (proportion of total richness) of the cases’ most taxonomically rich groups (Mollusca, Crustacea, Insecta), including the EPT group (Ephemeroptera, Plecoptera and Trichoptera) within the Insecta. We included EPT metrics because EPT taxa are routinely used as bioindicators in river health assessment (e.g. Barbour et al., 1999) owing to their sensitivity to pollutants and changes in water quality.

All comparisons and analyses involving richness were based on taxa lists as reported by each study. Although sampling effort and taxonomic abundance may affect richness measures (Gotelli and Colwell, 2001), it was not possible to use standardisation techniques (e.g. taxon sampling curves) prior to our analyses because many of the lists on which the richness (presence-absence) data were based were aggregations of taxa identified across samples (i.e. one list of taxa per case rather than separate lists for each sample collected per case) and abundance data were not consistently available. However, when there were enough cases within regions to compare sampling effort and richness, no clear trend was observed (Fig. 2). Therefore, although we acknowledge this limitation of the data, we consider raw taxon richness the best measure available for the purposes of our study.

3. Results

Assemblage composition was significantly associated with climate, both individually (ANOSIM $R = 0.464$, $P = 0.0003$) and in combination with broad geographical region ($R = 0.641$, $P = 0.0001$). Pairwise comparisons between cases grouped by the joint factor of climate and geographical region indicated that differences were present between all groups (pairwise R range: 0.333-1), except temperate New Zealand and Australian groups, Australian arid and temperate zone groups, arid Australian and North American groups, and tropical Australian and arid North American groups (pairwise R all < 0.2; P-values not informative owing to low numbers of possible permutations). In NMDS ordination space, cases from temperate climates tended to align positively along the first axis (Fig. 3A). Cases from the high and low latitudes (tropical, subarctic and polar regions) tended to have lower representation of taxonomic groups than those from elsewhere (Fig. 4A,B). Cases from temperate climates generally had greater richness and/or relative richness of EPT and Insecta than those from other climates (Fig. 4A,B).

Depth of collection and the hydrological phase during sampling were not significantly associated with assemblage composition (ANOSIM $P = 0.4680$ and 0.3940, respectively) at the global scale (i.e. among rather than within climate and geographical regions). However, there was a significant relationship between the method used to collect hyporheic invertebrates (wells, pits, cages, dug) and assemblage composition ($R = 0.351$, $P = 0.0030$). Pairwise comparisons indicated differences between all methods except for pits and cages (for which $R < 0.05$), which could be visualised on the NMDS ordination (Fig. 3B). Pit- and cage-collected cases had lower richness and relative richness of crustacean taxa compared with those collected from wells (Fig. 4C,D). The one 'dug' case was from Antarctica and was taxonomically distinct from all other cases, containing only Rotifera, Nematoda and Tardigrada. Therefore, we repeated the above analyses without this case; results did not change (climate: $R = 0.390$, $P = 0.0009$; climate-geographical region: $R = 0.599$, $P = 0.0003$; method: $R = 0.255$, $P = 0.0015$), and both depth and hydrological phase were non-significant. Further, pairwise R statistics indicated that assemblage compositions were similar ($R < 0.25$) between the same pairs of regions and collection methods listed above.

There was a strong and statistically significant relationship between assemblage richness and variation in composition (CAP, Fig. 5), with the canonical correlation explaining 98.3% of the variation in the similarity matrix of cases from systems classed as undisturbed by agricultural land use ($m = 10$, CAP trace statistic = 0.97, $P = 0.0001$). Assemblages from Europe and from temperate climates tended to have higher richness than those from higher latitudes or from mediterranean or arid climates (Fig. 5A). Within climate and geographical regions, richness was usually higher when flow or surface water was present during sample collection (Figs. 5A, 6). The greatest deviation from this trend involved the ‘mix’ case from arid North America, collected under conditions that included some surface flow. Richness of this case was low compared with the other ‘mix’ and ‘surface-flowing’ cases from the same climate and geographical region (Fig. 5A, 6). However, the invertebrates in this case had been collected from among the deepest hyporheic zones (mean collection depth = 93 cm; Boulton et al., 1992a) of all cases included in the analysis.

Within climate and geographical regions, a similar trend of lower richness in ‘dry-channel’ or ‘non-flowing’ cases (DC or NSF) compared with ‘mix’ or ‘surface-flowing’ cases (mix or SF) was observed for EPT taxa (Fig. 7A). However, when these comparisons were based on relative rather than absolute EPT richness, the differences between DC/NSF and mix/SF cases within regions were generally smaller (Fig. 7B). This suggested that relative EPT richness in the hyporheic zone may, in some instances, vary less in response to changes in surface hydrology than absolute EPT richness. However, comparison of EPT absolute and relative richness between the two anthropogenically disturbed and the two undisturbed cases from temperate Europe (Fig. 7) showed that while absolute richness of the disturbed cases was always lower than the undisturbed cases, relative richness was only lower for one of the disturbed cases.

Total richness for all four of the anthropogenically disturbed cases was predicted successfully by the CAP model. Based on their composition data, the richness of these ‘new’ cases from agricultural landscapes was predicted within ± 5 taxa of the observed values (Figs. 5B, 6; Table 1). The positions of these cases along the gradient were also consistent with patterns among the other cases; European temperate zone cases had higher richness than other cases, and SF cases had higher richness than NSF and DC cases. Further, in support of our hypotheses and consistent with observed values, the new cases were successfully predicted to have lower richness than those from undisturbed locations within the same climate zone (mediterranean) or climate-geographical region (temperate Europe) (Figs. 5B, 6; Table 1).

4. Discussion

4.1. The potential of hyporheic invertebrates as bioindicators of ecological health in temporary rivers

Our meta-analysis of trends in the composition and richness of hyporheic assemblages from across the world suggests that there may be sufficient predictability in the responses of hyporheic invertebrates to surface drying and anthropogenic disturbance to support their use as ecological indicators in temporary rivers. Although assemblages differed between broad-scale climate and geographical regions, there was consistency in the trends observed between richness, hydrological phase and level of anthropogenic disturbance (as indicated by agricultural land use). Within regions, higher richness of hyporheic invertebrates was associated with surface flow presence than absence of surface flow or water, and the richness of cases from agricultural landscapes relative to this pattern was always lower.

Human activities have long been known to affect ecological processes and biotic communities in the hyporheic zone (e.g. Boulton et al., 1997; Trayler and Davis, 1998), and the mechanisms by which these effects occur are manifold. Agriculture, land clearing, urban development and river regulation can all modify sediment transport, promote colmation (clogging of interstices) and interfere with hydrological exchange between the surface and subsurface (Boulton et al., 1998). These processes in turn affect hyporheic metabolism, water quality and invertebrate assemblages (Brunke and Gonser, 1997; Hancock, 2002). However, natural alternation between wet and dry phases in surface waters can also affect the composition of hyporheic assemblages (e.g. Boulton et al., 1992b; Mori et al., 2012). Our meta-analysis has shown that ecological effects of agriculture on temporary rivers, as indicated by changes in hyporheic invertebrate assemblages, can be distinguished from natural wetting and drying cycles, suggesting that this biota is a potential ecological indicator of river health for these systems.

4.2. Hyporheic invertebrate richness and EPT metrics as potential bioindicators

The success of any monitoring or assessment program lies in its ability to detect changes in river health, diagnose the causes of poor health and instigate action to improve health. The choice of indicator(s) plays a major role in determining this success (Bunn et al., 2010). Indicators should be easy to measure, pertinent to the spatiotemporal scale of the assessment, and respond to anthropogenic impacts in a predictable and interpretable way (Boulton, 1999; Boulton et al., 2010).

While our study showed that total invertebrate richness and the richness and relative richness of EPT responded consistently to hydrological phase within broad-scale climate and geographical regions, there was less difference between wet and dry phases in relative than absolute EPT richness. Therefore, the proportion of EPT taxa in a hyporheic assemblage may be more stable as surface hydrology varies than the absolute number of EPT taxa. If this property of proportional richness is found to exist in any one site, system or group of systems targeted for bioassessment, the metric may provide a relatively reliable indication of health in temporary rivers.

However, while absolute EPT richness of anthropogenically-disturbed cases was lower than that of undisturbed cases from the same broad-scale region (temperate Europe), relative EPT richness of one of the disturbed cases was comparable with that of the undisturbed cases. This may reflect a relationship between the ability of hyporheic bioindicators, such as EPT richness, to detect anthropogenic disturbances and the type, severity or combination of the disturbances involved. In a Colorado stream affected by multiple human impacts, hyporheic EPT richness was a poor indicator and could not distinguish between impact types (Nelson and Roline, 2003). Taxonomic composition, however, was indicative of flow regulation effects, and high abundances of one particular taxon (a stonefly) were specifically indicative of mining effects (Nelson and Roline, 2003). Our findings and studies such as Nelson and Roline (2003) highlight the need for further investigation into the potential use of EPT metrics in hyporheic bioassessments, and into the development of hyporheic bioindicators more generally.

4.3 Caveats to and recommendations on the use of hyporheic invertebrates as bioindicators

Hyporheic sampling methods can be selective (Fraser and Williams, 1997; Boulton et al., 1998) and the general influence of sampling methods on ecological assessment outcomes is a well-known caveat of bioassessment (Cao and Hawkins, 2011). Our study indicated that sampling method and assemblage composition were associated. Crustacea, for example, were better represented in cases for which samples had been collected from wells rather than pits or cages. Differences in sampling methods among the cases may even have played a role in structuring the differences observed between regions. First, we included all reported taxa in our analysis, although some studies were primarily interested in macroinvertebrates and the collection and identification of meiofauna was therefore unlikely to be consistent across regions. Second, the mesh size used to screen invertebrates probably influenced sample composition and richness. The absence of Crustacea from temperate North American cases (Fig. 4), for example, may have partially resulted from the relatively large mesh size used (250 µm; Table 1), potentially precluding collection of small invertebrates such as microcrustaceans.

Therefore, while the technical capacity and funding level of any assessment program will dictate the collection methods, sampling effort, taxonomic resolution and other identification protocols implemented (Lindenmayer et al., 2012), the potential effects of these factors on assessment outcomes must be acknowledged. Based on the techniques commonly used by most studies (Table 1) and from our own experiences of sampling hyporheic fauna, we recommend standardized protocols such as sampling from wells inserted 30-60 cm in the streambed and using self-priming hand-pumps to collect 5-6 L, filtered through a maximum mesh size of 125 µm. Consideration of factors beyond the control of the operator that influence the composition and distribution of hyporheic fauna, such as sediment characteristics and direction of vertical hydrological exchange (Brunke and Gonser, 1997; Boulton et al., 1998), will also help to discriminate anthropogenically induced changes in hyporheic bioindicators. Pilot studies and the strategic development of sampling and analytical methods (e.g. Buss et al., 2009; Downes 2010) will be essential to ensure success.

Finally, we suggest that temporary river assessment programs incorporating hyporheic bioindicators will benefit during developmental stages from a conceptual understanding of how surface flow variation mediates changes in those indicators (e.g. Fig. 8), both in disturbed and undisturbed locations. We suggest that in many rivers, particularly 'losing' systems where downwelling water predominates, the loss of surface water may be followed by a gradual reduction in the volume of the saturated hyporheic zone (Fig. 8A, B). As surface-subsurface flow exchange uncouples and the size of the saturated subsurface continues to decrease, changes in hyporheic water quality occur (e.g. reduction in dissolved oxygen; Fig. 8C), followed by potentially substantial change in invertebrate assemblage composition, distribution and diversity (Boulton and Stanley, 1995; Stanley and Boulton, 1995). Our study suggests that this process may manifest as a marked but gradual decline in richness along the drying gradient, with anthropogenic disturbance compounding the ecological response (Fig. 8D). Therefore, initial assessment data must be collected over adequate spatial and temporal scales that span wet, dry and transitional phases in flow intermittency so that the full range of invertebrate responses to surface flow variation can be described, tested against the conceptual understanding and, if possible, modelled for use in future assessments.

5. Conclusion

Our global analysis provides evidence that invertebrate assemblage characteristics within hyporheic zones have the potential to act as ecological health indicators of temporary rivers. While this supports the broader suggestion that patterns and processes within hyporheic zones are important indicators of the health of connected surface- and groundwater ecosystems (Boulton and Stanley, 1996; Boulton, 2000), a lack of baseline data and uptake of protocols to develop, test and use hyporheic indicators will continue to hinder their routine use (Boulton et al., 2010). Increased efforts to compile knowledge and gather data on hyporheic fauna will help to resolve this issue and improve our understanding of hyporheic responses to surface system disturbances (Marmonier et al., 2012; Wood et al., 2012). We advocate expanded monitoring of hyporheic zones in temporary rivers and recommend hyporheic invertebrates as potential bioindicators to complement surface water assessments.

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Table 1: Characteristics of systems used in the meta-analysis of hyporheic invertebrate assemblage composition and richness, separated into twenty-four cases based on climate, geographical location, anthropogenic disturbance[a], hydrological phase during sampling and collection particulars.

Climate	Broad geographical location	River	Anthropogenic disturbance[a]	Maximum flow cessation period (mo y^{-1})[b]	Hydrological phase	Collection method	Collection depth (cm)	Mesh size (µm)	Vertical hydrological exchange direction	Stream bed composition[c]	Number of samples	Total richness[d]	Source[e]
Temperate	Europe (France)	Albarine River	low	6	SF	wells	≤30	90	?	coarse alluvium	100	45	Datry, 2012
Temperate	Europe (UK)	River Lathkill	low	5	SF	wells	≤30	90	D,N	cobble, gravel, sand	167	36	Stubbington et al., 2011a, b
Temperate	Europe (UK)	River Glen	other	5	SF	wells	≤30	90	D	cobble, gravel, sand	120	35 (32)	Stubbington, 2011; Stubbington et al., 2011a
Temperate	Europe (UK)	Little Stour River	other	only dries during supra-seasonal droughts	SF	wells	≤30	90	?	coarse alluvium	99	27 (32)	Stubbington et al., 2009; Wood et al., 2010
Temperate	New Zealand	Selwyn River	low	11	SF	wells	≤30	90	?	coarse alluvium	82	33	Datry et al., 2007
Temperate	Australia (Australian Capital Territory, ACT)	Burke and Condor Creeks	low	1	SF	cages	≤30	n/a	?	?	6	25	Young et al., 2011
Temperate	Australia (ACT)	Burke and Condor Creeks	low	1	DC	cages	≤30	n/a	?	cobble, boulder, gravel, sand	6	11	Young et al., 2011
Temperate	Australia (Victoria)	Lerderderg and Werribee Rivers	low	2	DC	pits	≤30	50	D	gravel, pebble, cobble, boulder	5	8	Boulton et al., 1992b
Temperate	North America (West Virginia)	Two unnamed tributaries of Elklick Run	low	3	SF	cages	≤30	250	?	cobble, boulder, sand	15	22	Griffith and Perry, 1993

Temperate	North America (Massachusetts)	Bigelow Brook tributary	low	12	DC	pits	≤30	n/a	?	cobble, gravel, sand, silt	6	15	Collins et al., 2007
Mediterranean	North America (California)	Cronin Creek	low	5	NSF+DC	wells	>30	63	D	cobble, gravel	82	28	del Rosario and Resh, 2000
Mediterranean	North America (California)	Cronin Creek	low	5	DC	wells	>30	63	N	cobble, gravel	10	18	del Rosario and Resh, 2001
Mediterranean	Australia (South Australia)	Finniss, Light, Marne, Onkaparinga and Wakefield Rivers	other	9	SF	wells	>30	75	mix	sand, silt, gravel, cobble	9	16 (17)	C. Leigh, unpubl. data
Mediterranean	Australia (South Australia)	Angas, Marne and Wakefield Rivers	other	9	NSF	wells	>30	75	mix	sand, silt, gravel, cobble	7	10 (13)	C. Leigh, unpubl. data
Arid	Australia (South Australia)	Brachina Creek	low	9	NSF+DC	wells	>30	50	D,N	cobble, gravel	88	18	Cooling and Boulton, 1993
Arid	North America (Arizona)	Sycamore and Bridle Creeks	low	9	SF	cages	≤30	63	D,U	gravel	80	12	Boulton et al., 1991
Arid	North America (Arizona)	Sycamore and Bridle Creeks	low	9	mix	wells	≤30	50	mix	gravel, sand	17	20	Boulton et al., 1992a
Arid	North America (Arizona)	Sycamore and Bridle Creeks	low	9	mix	wells	>30	50	mix	gravel, sand	17	7	Boulton et al., 1992a
Arid	North America (Arizona)	Sycamore and Bridle Creeks	low	9	DC	wells	>30	50	mix	gravel, sand	17	7	Boulton et al. 1992a
Arid	North America (Arizona)	Sycamore Creek	low	9	DC	pits	?	50	D,U	gravel, pebble, cobble, boulder	10	9	Boulton et al., 1992b

Arid	North America (Arizona)	Rock Creek	low	8	NSF+DC	wells	>30	63	?	sand	209	16	Clinton et al., 1996
Tropical	Australia (Northern Territory)	Magela Creek	low	6	DC	pits	>30	63	D	sand	3	7	Paltridge et al., 1997
Subarctic	North America (Alaska)	Toklat River	low	?	SF	cages	≤30	65	U	cobble, gravel	4	8	Crossman et al., 2012
Polar	Antarctica	Von Guerard Stream and Harnish Creek	low	11	SF	dug	≤30	n/a	?	coarse alluvium	18	3	Treonis et al., 1999

[a] 'low' indicates study areas in nature reserves, national parks, native woodlands, protected national recreation areas, or in areas that have been defined by the studies' authors as under low influence of anthropogenic impact (pers. comm. T. Datry). 'Other' indicates study regions in primarily agricultural landscapes. However, flow losses can be exacerbated in some reaches of the River Lathkill owing to disused mine-drainage soughs, and on the Glen by extractions for human use

[b] approximate, based on information provided in the studies, and applicable only to the study sites used in this study

[c] as defined in each publication or by the studies' authors

[d] based on the taxonomic resolution used in this study. Values in parentheses are the predicted values from canonical analysis of principal coordinates (*see* Results)

[e] unpublished data by Stubbington (2011; PhD thesis) were consolidated with data from Stubbington et al. (2011a) collected from the same river, sites and sampling period (River Glen); as were data from the River Lathkill (Stubbington et al., 2011a, b) and data from the Little Stour River (Stubbington et al., 2009; Wood et al., 2010)

NSF, no surface flow but surface water present

SF, surface flow

DC, dry surface channel

mix, mixture of hydrological phases that includes surface flow, or an unspecified mix of vertical hydrological exchange directions

D, downwelling

N, neutral

U, upwelling

?, data not available

n/a, not applicable

Figure captions

Figure 1: Conceptual diagrams of hypotheses on hyporheic invertebrate assemblages of temporary rivers. **A**: relationships, illustrated as if in two-dimensional ordination space, between assemblages of taxa from different climate and geographical regions (encircled diamonds, triangles and squares) collected under different hydrological phases (open symbols indicate assemblages beneath dry surface channels). **B**: relationships between taxonomic richness and these same factors. **C**: hypothetical gradient of taxonomic richness of assemblages from different climates and regions, showing how dry phases and disturbance by human activities deflect samples down the gradient. Climate ‘A’ is drier than ‘B’. ‘Undisturbed’ and ‘Disturbed’ reflect river systems subject to different levels of anthropogenic impact. ‘Wet’ vs ‘Dry’ refers to surface water flow vs no surface water flow, surface water presence vs absence, or surface water flow vs surface water absence.

Figure 2: Relationship between taxonomic richness versus sampling effort within climate and geographical regions examined in this study that had > 3 taxa lists (‘cases’): temperate Europe and arid North America.

Figure 3: Two-dimensional non-metric multi-dimensional scaling (NMDS) ordination (stress = 0.158) of hyporheic invertebrate assemblages (‘cases’) collected using different methods and from different climate and geographical regions, not including those from agricultural landscapes. **A**: encircled symbols show climate and geographical regions with at least two cases, including at least one dry channel (DC) case. **B**: dashed line encircles cases for which samples were collected from wells, solid line from pits and cages.

Figure 4: Richness and relative richness (mean ± 1 standard deviation) of taxonomic groups identified to higher levels of taxonomic resolution (Mollusca: family, Crustacea: order and family, EPT: family and Insecta: family) by climate and geographical region (**A**, **B**) and by collection method (**C**, **D**). EPT refers to Ephemeroptera, Plecoptera and Trichoptera; relative richness is a unitless measure showing Mollusca, Crustacea and EPT richness proportional to the richness of all invertebrate taxa.

Figure 5: Canonical analysis of principal coordinates (CAP) ordination relating hyporheic assemblages ('cases') to a taxonomic richness gradient. **A**: CAP model based on sampling locations with low anthropogenic disturbance. Ellipses show trend of higher richness for cases sampled during wet phases (solid line) and lower richness during dry phases (dashed line), exceptions include the two high-latitude, low richness cases (subarctic and polar cases) and the deep-zone case from arid North America. **B**: predicted placement of cases from agricultural landscapes ('disturbed' cases) onto the gradient, in comparison with 'undisturbed' cases from similar regions or climates. Hydrological phase during sampling (SF, mix, NSF, DC): *see* Table 1.

Figure 6: Total richness of invertebrates in hyporheic zones sampled in different climate and geographical regions, and in 'undisturbed' and 'disturbed' (primarily agricultural) landscapes. Hydrological phase during sampling: dry channels (DC), non-flowing surface waters (NSF), surface flow (SF and mix): *see* Table 1. Closed, black bars show SF data, unless indicated as mix.

Figure 7: Richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) in hyporheic zones sampled in different climate and geographical regions, and in ‘undisturbed’ and ‘disturbed’ (primarily agricultural) landscapes. **A**: raw EPT richness; **B**: relative richness, a unitless measure of EPT richness proportional to the richness of all invertebrate taxa. Hydrological phase during sampling: dry channels (DC), non-flowing surface waters (NSF), surface flow (SF and mix): *see* Table 1. Closed, black bars show SF data, unless indicated as mix.

Figure 8: Conceptual model of different conditions (A, B, C, D) in the hyporheic zone of a temporary river, unimpacted or impacted by human activities, during a complete surface-flow cycle through time. Consistent subsurface flow is assumed, and variations on this general model will occur in association with differences in climate, geographical location, and both small- and large-scale river characteristics (units of measure are therefore not provided). A: surface flow magnitude; B: hyporheic saturation (depth to water table); C: hyporheic water quality (e.g. dissolved oxygen concentration); D: invertebrate richness in the hyporheic zone.

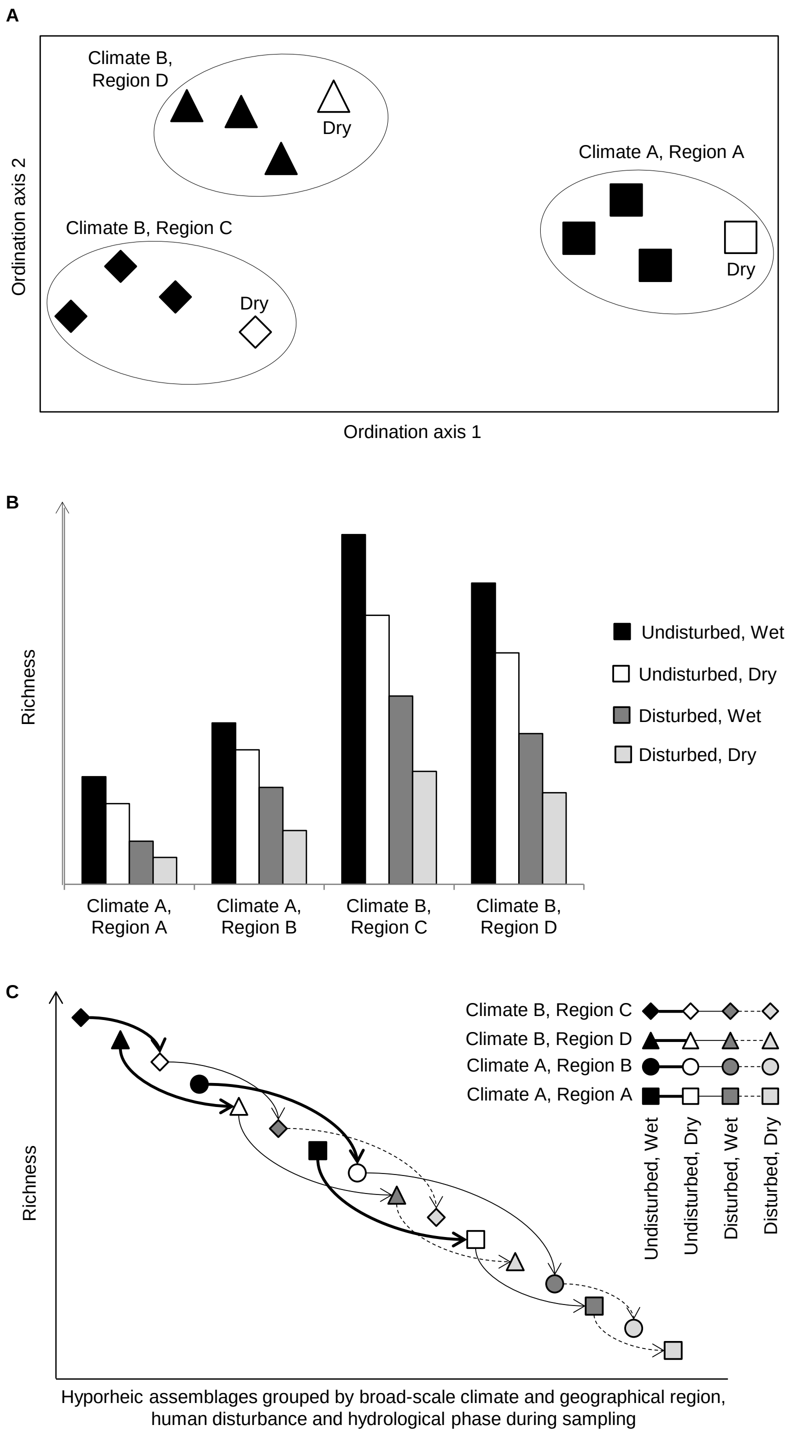
A
Climate B, Region D
Dry
Climate A, Region A
Climate B, Region C
Dry
Dry
Ordination axis 2
Ordination axis 1
B
Richness
Undisturbed, Wet
Undisturbed, Dry
Disturbed, Wet
Disturbed, Dry
Climate A, Region A
Climate A, Region B
Climate B, Region C
Climate B, Region D
C
Richness
Climate B, Region C
Climate B, Region D
Climate A, Region B
Climate A, Region A
Undisturbed, Wet
Undisturbed, Dry
Disturbed, Wet
Disturbed, Dry
Hyporheic assemblages grouped by broad-scale climate and geographical region, human disturbance and hydrological phase during sampling

Figure 1

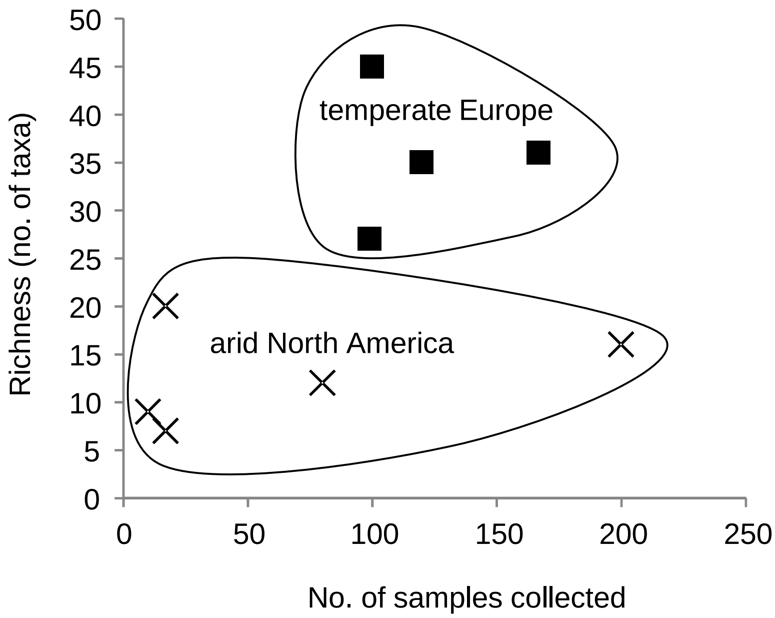
Richness (no. of taxa)
No. of samples collected
temperate Europe
arid North America
0
5
10
15
20
25
30
35
40
45
50
0
50
100
150
200
250

Figure 2

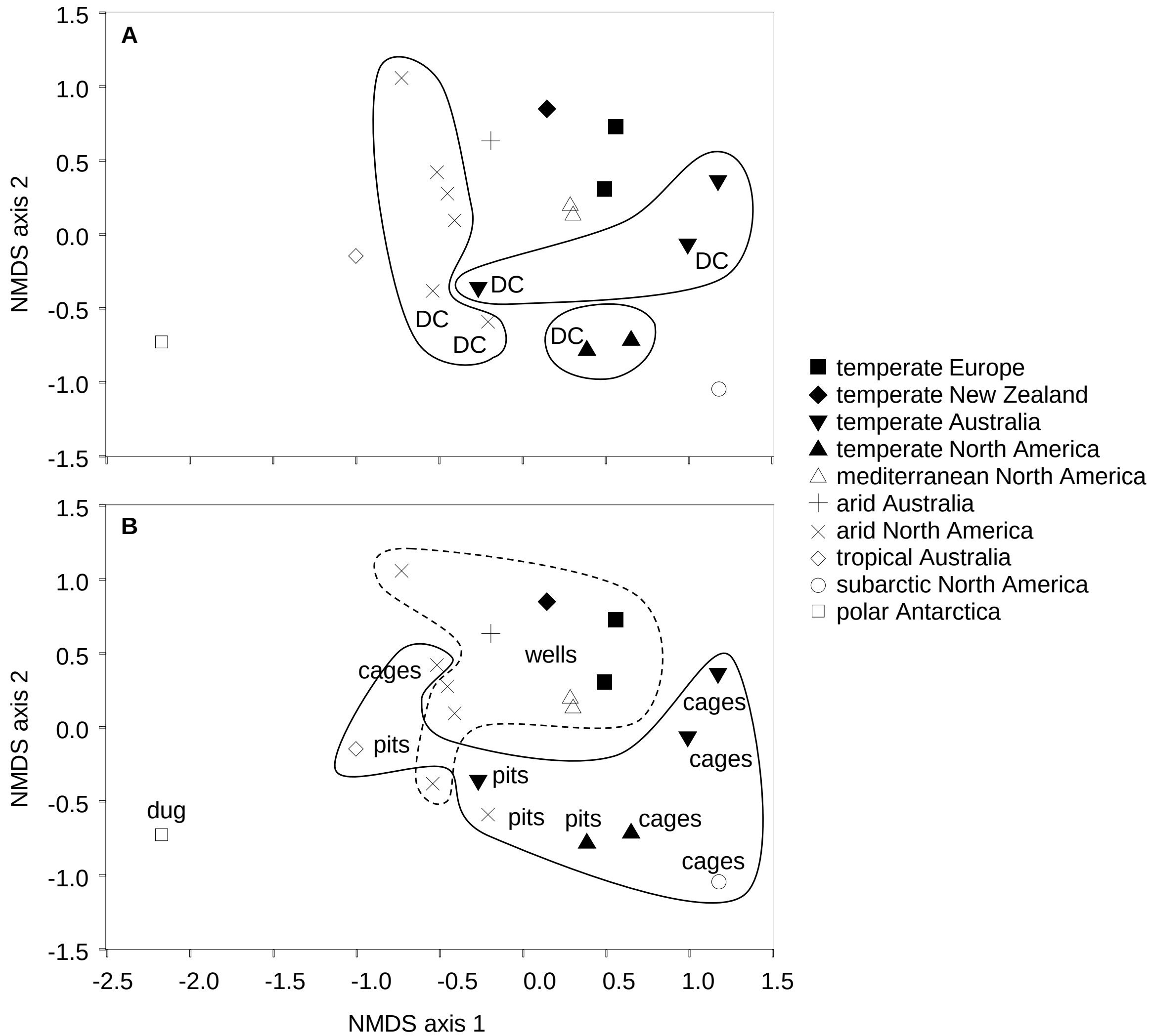
A
B
NMDS axis 1
NMDS axis 2
DC
cages
pits
wells
dug
temperate Europe
temperate New Zealand
temperate Australia
temperate North America
mediterranean North America
arid Australia
arid North America
tropical Australia
subarctic North America
polar Antarctica

Figure 3

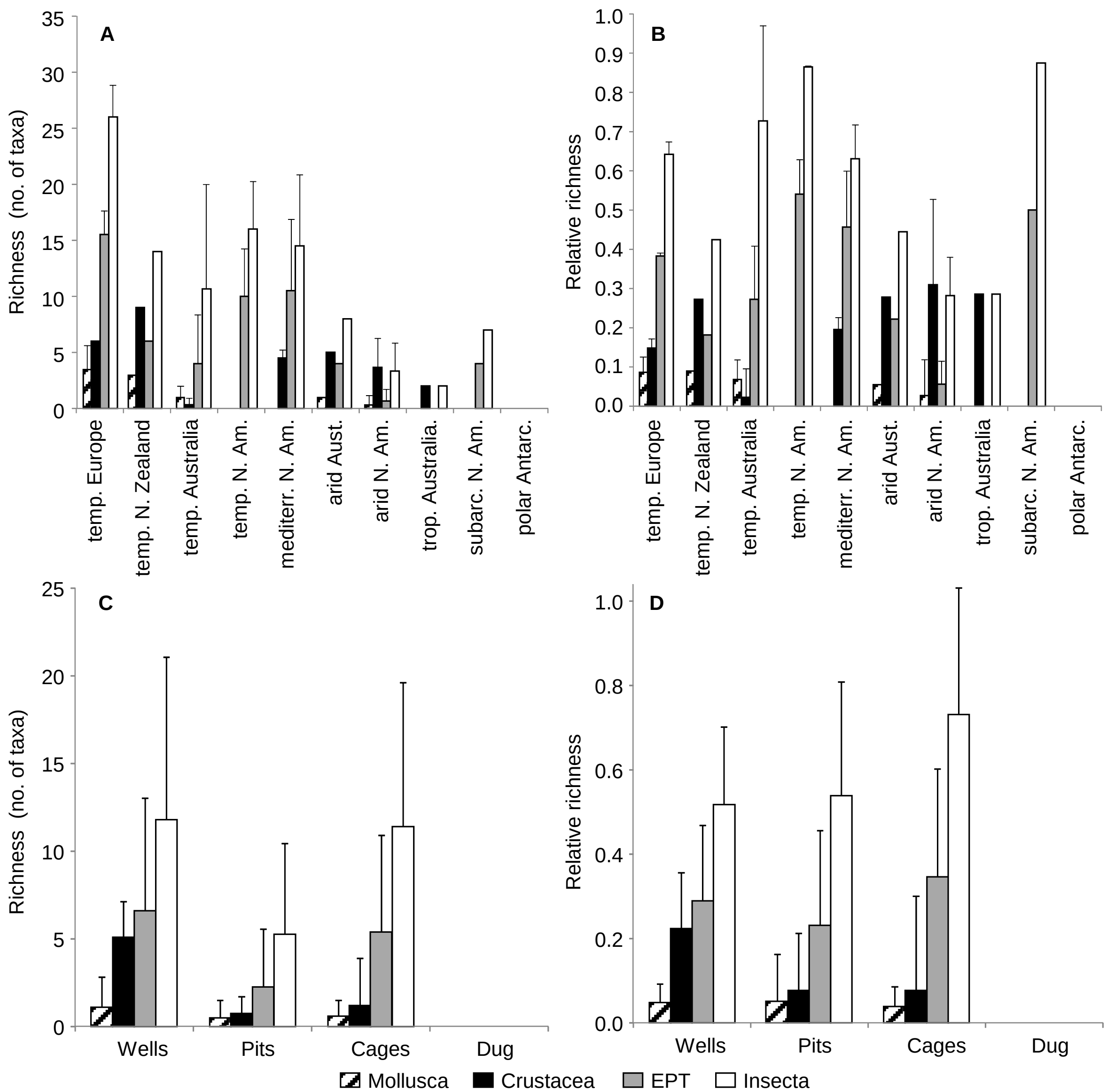
A
Richness (no. of taxa)
0
5
10
15
20
25
30
35
temp. Europe
temp. N. Zealand
temp. Australia
temp. N. Am.
mediterr. N. Am.
arid Aust.
arid N. Am.
trop. Australia.
subarc. N. Am.
polar Antarc.
B
Relative richness
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
temp. Europe
temp. N. Zealand
temp. Australia
temp. N. Am.
mediterr. N. Am.
arid Aust.
arid N. Am.
trop. Australia
subarc. N. Am.
polar Antarc.
C
Richness (no. of taxa)
0
5
10
15
20
25
Wells
Pits
Cages
Dug
D
Relative richness
0.0
0.2
0.4
0.6
0.8
1.0
Wells
Pits
Cages
Dug
Mollusca
Crustacea
EPT
Insecta

Figure 4

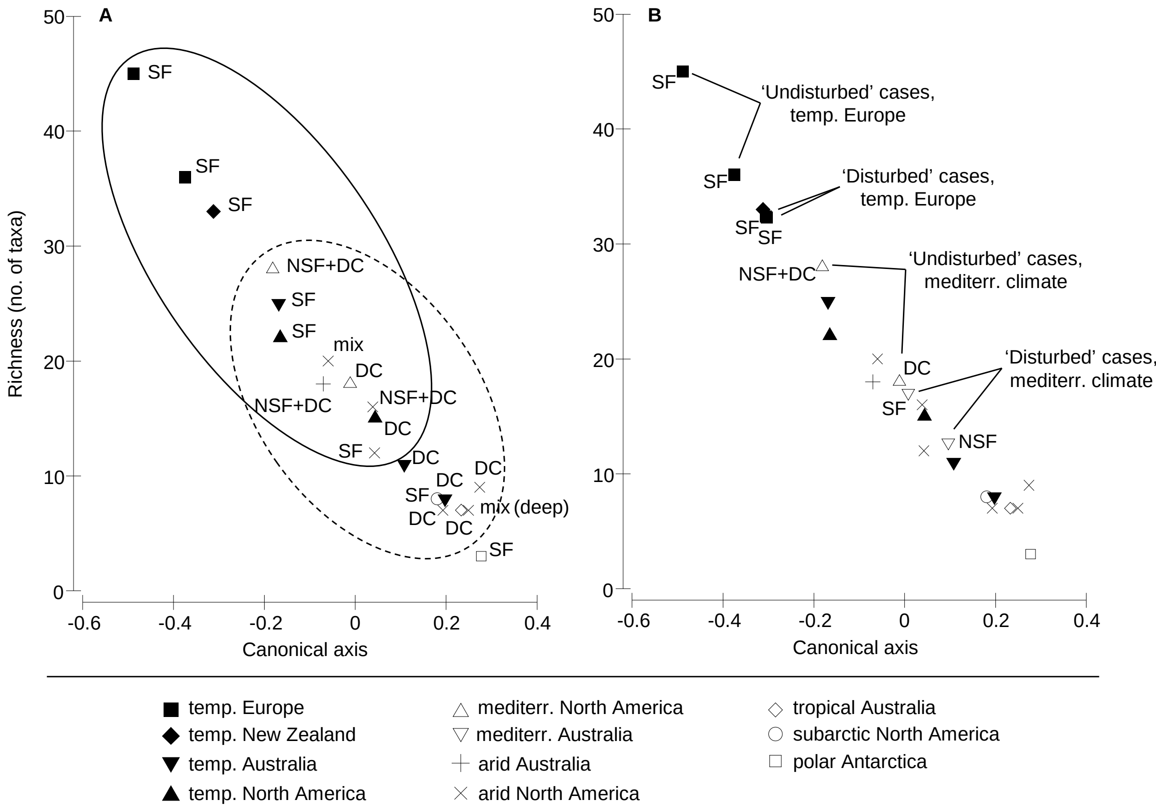
A
B
Richness (no. of taxa)
Canonical axis
Canonical axis
50
40
30
20
10
0
-0.6
-0.4
-0.2
0
0.2
0.4
SF
NSF+DC
mix
DC
NSF+DC
mix (deep)
NSF
‘Undisturbed’ cases, temp. Europe
‘Disturbed’ cases, temp. Europe
‘Undisturbed’ cases, mediterr. climate
‘Disturbed’ cases, mediterr. climate
temp. Europe
temp. New Zealand
temp. Australia
temp. North America
mediterr. North America
mediterr. Australia
arid Australia
arid North America
tropical Australia
subarctic North America
polar Antarctica

Figure 5

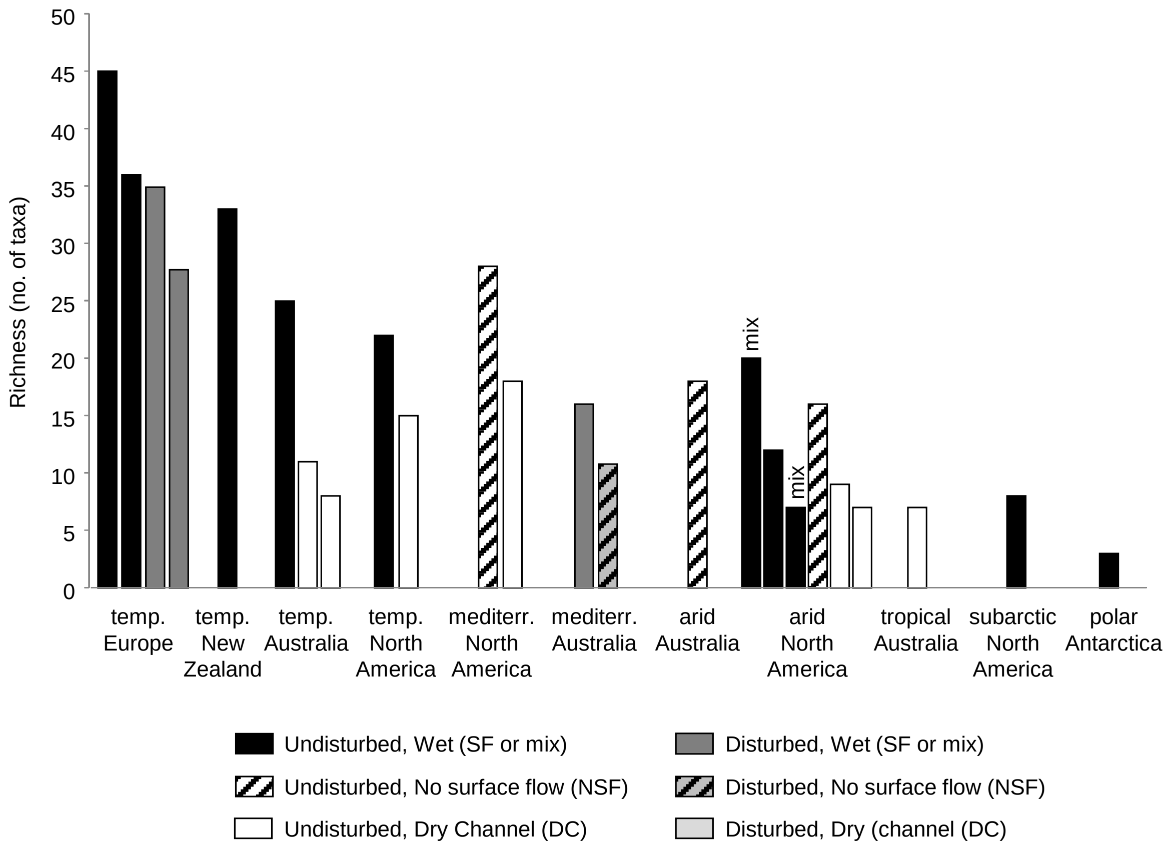
Richness (no. of taxa)
0
5
10
15
20
25
30
35
40
45
50
mix
mix
temp. Europe
temp. New Zealand
temp. Australia
temp. North America
mediterr. North America
mediterr. Australia
arid Australia
arid North America
tropical Australia
subarctic North America
polar Antarctica
Undisturbed, Wet (SF or mix)
Disturbed, Wet (SF or mix)
Undisturbed, No surface flow (NSF)
Disturbed, No surface flow (NSF)
Undisturbed, Dry Channel (DC)
Disturbed, Dry (channel (DC)

Figure 6

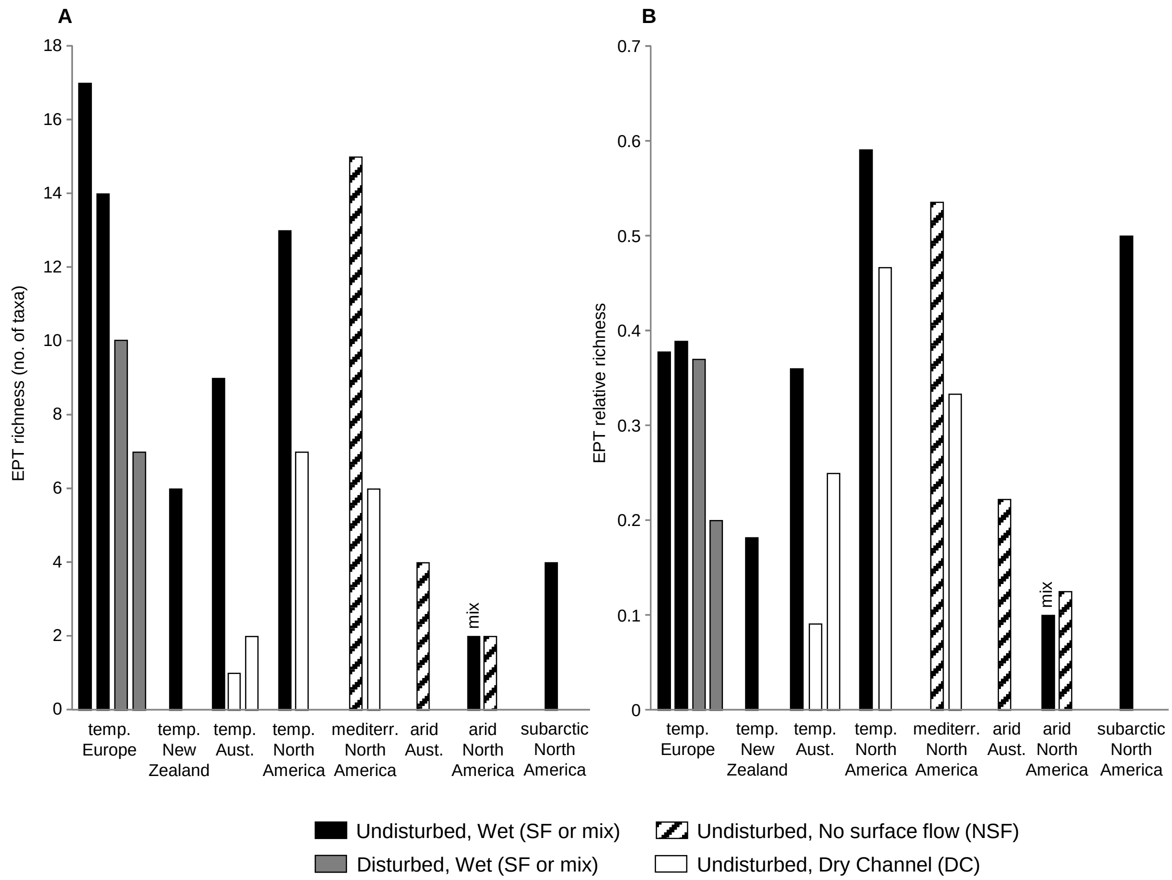
A
EPT richness (no. of taxa)
0
2
4
6
8
10
12
14
16
18
mix
temp. Europe
temp. New Zealand
temp. Aust.
temp. North America
mediterr. North America
arid Aust.
arid North America
subarctic North America
B
EPT relative richness
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
mix
temp. Europe
temp. New Zealand
temp. Aust.
temp. North America
mediterr. North America
arid Aust.
arid North America
subarctic North America
Undisturbed, Wet (SF or mix)
Disturbed, Wet (SF or mix)
Undisturbed, No surface flow (NSF)
Undisturbed, Dry Channel (DC)

Figure 7

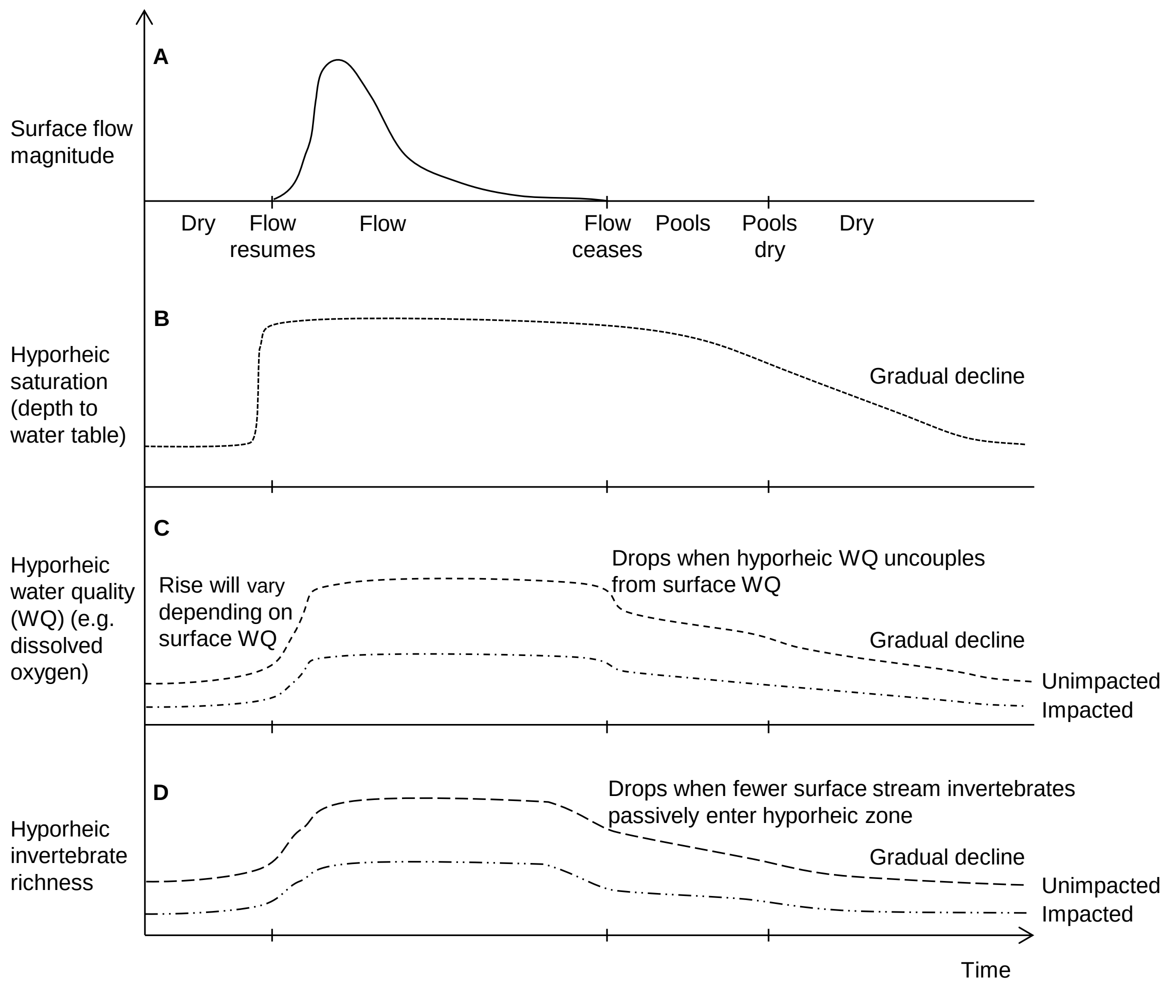
A
Surface flow magnitude
Dry
Flow resumes
Flow
Flow ceases
Pools
Pools dry
Dry
B
Hyporheic saturation (depth to water table)
Gradual decline
C
Hyporheic water quality (WQ) (e.g. dissolved oxygen)
Rise will vary depending on surface WQ
Drops when hyporheic WQ uncouples from surface WQ
Gradual decline
Unimpacted
Impacted
D
Hyporheic invertebrate richness
Drops when fewer surface stream invertebrates passively enter hyporheic zone
Gradual decline
Unimpacted
Impacted
Time

Figure 8