Looking beneath the surface: using hydrogeology and traits to explain flow variability effects on stream macroinvertebrates

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Abstract

Flow variability drives important instream ecohydrological processes. Nonetheless, generalisations about ecological responses to flow variability are elusive and complicated by interacting factors. Hydrogeological controls on groundwater inputs into streams is one often overlooked factor that may interact with flow variability and influence instream ecology. Flow effects on ecology are also complicated by flora and fauna trait diversity, which makes some organisms more sensitive to flow variability than others. To improve understanding regarding the effects of flow variability on instream communities we utilised a long-term 17 year data set of macroinvertebrate communities from 8 sites on the Upper Murrumbidgee River catchment, south eastern Australia. Hydrogeological mapping provided a proxy of groundwater influence on instream ecology. Generalised linear mixed models were used to test hydrogeology (i.e. groundwater influence) and flow variability effects on selected taxa and trait groups. Trait groups tested were those with drought resistant life stages, no drought resistant life stages and those with poor dispersal traits. Non-drought resistant and poor dispersing taxa responded to hydrogeology and stream flow variables, while taxa with drought resistant traits did not. Poor dispersing taxa displayed the strongest positive response to interactions between high mean flow and hydrogeological conditions that facilitate groundwater inputs. While the importance of flow variability is widely recognised, the combined role of hydrogeology and trait groups on macroinvertebrate responses has not been widely considered thus far. This study demonstrates that the consideration of hydrogeology and faunal traits can help to understand macroinvertebrate population and community responses to flow regime variability.

Introduction

Variation in stream discharge spatially and temporally, or flow variability, is a key driver of ecological change, with particular regime characteristics critical for the persistence of some communities, sediment transport, biogeochemical cycles and many other physico-chemical and ecological processes (Poff *et al.*, 1997; Larned *et al.*, 2011; Stubbington *et al.*, 2011). In recent decades, with increasing water abstraction, flow regulation and climate change, the importance of understanding flow regimes for conservation management has also become increasingly recognised (Belmar *et al.*, 2013; Acreman *et al.*, 2014). Nonetheless, while models for understanding flow-ecology relationships are constantly improving, it is still often difficult to generalise and quantify flow regime characteristics required for the conservation of freshwater species, communities and habitats (Acreman *et al.*, 2014).

Generalising flow-ecology relationships is difficult in areas subject to high flow variability and especially in those areas experiencing frequent low flow periods that are triggered by meteorological drought (reduced precipitation). The effects of low flows on freshwater species can be both obvious and dramatic (e.g. Lake, 2003; Stubbington *et al.,* 2009a; Stubbington *et al.,* 2009b) or subtle and difficult to discern, as well as varying amongst different stream types (e.g. Wood and Petts, 1999; Suren and Jowett, 2006; Bae *et al.,* 2014). For example, while some studies have demonstrated adverse low flow effects on macroinvertebrate communities (e.g. Thomson *et al.,* 2012), others report minimal changes to abundance (e.g. Suren and Jowett 2006) or even increases in density and diversity (Wood and Armitage 2004).

In some cases, the diversity of macroinvertebrate responses to flow variability may be attributed to interactions with other factors (Worrall *et al.,* 2014). Recently, Booker *et al.,* (2015) have argued that the importance of flow regimes may be more nuanced than previously thought; demonstrating that the importance of flow can be misinterpreted if relationships between the hydrological regime and other predictors such as upstream geology, upstream land cover, climate, and geomorphology are not considered. In addition, hydrogeology could also obscure ecological relationships with stream flow variability and also explain additional variation in macroinvertebrate community patterns.

Hydrogeology influences the volume of groundwater inputs, which in turn can influence surface water temperatures, dissolved oxygen concentrations and water chemistry and may influence the macroinvertebrate community present (Stubbington *et al.,* 2011). In the chalk streams of the UK, hydrogeological conditions that facilitate groundwater discharge buffered the impacts of meteorological drought on macroinvertebrate communities (Wood and Petts, 1999). In contrast, within streams where groundwater abstraction has depleted aquifers, or where hydrogeological controls mean that groundwater inputs are limited, streams are unlikely to be buffered against meteorological drought and instead may become intermittent, triggering significant changes in the macroinvertebrate communities present (Belmar *et al.,* 2013). Streams or reaches influenced by groundwater are therefore likely to have greater and more consistent inputs of water and potentially also differ in water quality (Stubbington *et al.,* 2011; Wood and Petts, 1999). Despite the potential importance of hydrogeological differences in determining ecological responses to flow variability, assessing and quantifying its importance is often limited by a lack of information over a range of low and high flow conditions (Monk *et al.*, 2008).

In addition to hydrogeology, traits (here defined as biological characteristics which may determine groups of macroinvertebrate responses to environmental changes) that influence susceptibility to flow variability could also help explain the variable macroinvertebrate responses recorded in previous research (Chessman, 2015; Tupinambás *et al.,* 2015). In some cases faunal traits may be more responsive to changes in flow than other metrics (e.g. richness), and thus be more appropriate for understanding the effects of flow variability on in-stream fauna (Tupinambás *et al.,* 2014). Taxa with drought resistant life stages or behaviours, such as refuge use or diapause/dormancy may be relatively insensitive to flow variability (Statzner and Bêche 2010; Bonada *et al.*, 2007a; Bonada *et al.*, 2007b). Along with taxon drought resistance, dispersal ability could also determine vulnerability to flow variability (Bonada *et al.*, 2007a; Bonada *et al.*, 2007b; de Szoeke *et al.,* 2015). Poor dispersers lack the mobility to track favourable hydrological conditions, and thus in the long term may be restricted to hydrologically stable stream reaches (e.g. where hydrogeology allows groundwater inputs that buffer against precipitation driven stream flow variability). Developing and refining conceptual and empirical understanding of traits, as well as hydrogeological differences that influence groundwater inputs, could greatly increase our ability to predict the effects of flow regime variability on macroinvertebrates. Addressing this knowledge gap could also help explain some of the diverse macroinvertebrate responses to flow variability highlighted in previous studies (Dewson *et al.*, 2007; Poff and Zimmerman, 2010).

To improve understanding regarding the effect of flow regime variability on in-stream biota, we investigated the response of lotic macroinvertebrates to flow regime variability and hydrogeology for different trait groups using a long-term (17 year) data set across four rivers from the Upper Murrumbidgee River catchment of south eastern Australia. Long-term data sets spanning greater than five years with repeat surveys across multiple rivers are relatively rare, but crucial for answering questions about flow variability effects on stream communities (Monk *et al.,* 2008; Booker *et al.,* 2015). The Upper Murrumbidgee also has stable (depth to water table ca. 5m) unpolluted and fresh groundwater (CSIRO, 2008). As a consequence, hydrogeological variations in the area provide a natural gradient of groundwater influences. The study area and dataset therefore provided an opportunity to investigate the role of hydrogeological groundwater influence and trait differences for potentially explaining the diverse responses of macroinvertebrates to flow regime variability.

In this study we sought to test two hypotheses: (i) hydrogeological differences that influence groundwater inputs, will explain variation in macroinvertebrate occurrence; and (ii) faunal traits will influence the response to flow regime variability; specifically in the context of this study taxa lacking drought resistant traits and with weak dispersal mechanisms will be more sensitive to flow variability and hydrogeological differences than taxa possessing drought resistant traits and life stages and with strong dispersal mechanisms.

Methods

Study area

The Upper Murrumbidgee catchment covers 13,140 km^2 in south eastern Australia (Figure 1). Mean annual rainfall in the area is 632.6mm (at Canberra). Mean minimum and maximum temperatures are 7 and 20 °C respectively (BoM, 2016). Land use and vegetation cover across the area varies with upland areas remaining largely forested and undisturbed, while lowland areas have been cleared and utilised for agricultural and urban development. The streams surveyed in this study were all located in the upland zones in relatively natural areas that have experienced little disturbance or locations designated for conservation (Figure 1). The streams surveyed were of stream order 3, 4 and 5 (Strahler 1952). Mean discharge also varied across rivers during the survey period (Goodradigbee (216 ML day^{-1}), Paddys (36 ML day^{-1}), Cotter (42 ML day^{-1}) and Queanbeyan (70 ML day^{-1})).

The hydrogeology of the area is diverse with local and intermediate groundwater flow systems of fractured rock aquifers, aeolian sands, colluvial fans, fractured basalts and upland alluvium (see Appendix A). Groundwater levels are stable, shallow, fresh and connected to rivers throughout the catchment, with limited groundwater abstraction that is well below recharge capacity (1 GL yr^{-1}) (CSIRO, 2008). As a consequence, any hydrogeological variations in the area provide a gradient of surface-groundwater connectivity and thus groundwater influence on stream segments. There was no significant salinisation upstream of the sites sampled.

Macroinvertebrate surveys

Data was utilised from macroinvertebrate surveys undertaken from 1994 to 2011 in stream riffle habitats of the Upper Murrumbidgee. Riffles were defined as habitat with flowing broken water over gravels, pebbles, cobbles or boulders and deeper than 10cm (Nichols *et al.*, 2000). Riffle habitats were surveyed with hand nets (250 µm mesh) using standardised ACT Australian River Assessment System (AUSRIVAS) methods (Nichols *et al.*, 2000). Briefly, this involved the operator sampling macroinvertebrates facing downstream with the net in front of their feet on the substratum while disturbing and dislodging the substratum by kicking and twisting the feet to a depth of approximately 10cm (Nichols *et al*., 2000). Macroinvertebrates collected were preserved using 70% ethanol and then in the laboratory samples were rinsed and placed in a sub-sampling box comprising 100 cells (Marchant, 1989) and agitated until evenly distributed. From each sample a subsample of 200 individual macroinvertebrates was randomly selected and identified to family, except for aquatic worms (Oligochaeta) and mites (Acarina), which were identified to class (Nichols *et al.*, 2000). We were restricted the use of family level data, which is routinely used in biomonitoring programmes, as species level data was not available due to taxonomic constraints (e.g., lack of species level keys for some groups in the region and the presence of cryptic species which could not be identified based on morphology alone).

In total 189 samples from 8 riffle habitat sites were collected from the Upper Murrumbidgee catchment. Each site had a minimum of 10 samples collected across multiple dry and wet years to ensure a spread of surveys across both low and high flow periods (Appendix B and Appendix C). Over the survey period many months and years were below and above long-term mean rainfall (1960-1990 climatological mean), with anomalies of around -50 to + 150 mm (monthly) and -100 to + 450 mm (yearly) being recorded (Figure 2, Appendix B).

Quantifying hydrogeological and groundwater influence

The influence of hydrogeology was assessed at each site using data layers of groundwater flow systems (ABARES, 2000) underlying the upstream river segments of each site. The hydrogeological influence index (HG index) was calculated as in Eq. 1 (Figure 3 represents the method graphically). For each site the HG index is based on hydrogeological characteristics and was calculated using a spatial approach similar to those used to measure landscape connectivity (Wiens, 2002).

$$HG\ index = log\ (\sum sl_i / log\ (d_i)) \qquad (Eq.\ 1)$$

Where *sl* is the length of the hydrogeological segment likely to facilitate groundwater movement (i.e. alluvial and colluvial segments, after Coram's et al. 2000 hydrogeological classifications) and *d* is the distance downstream from that segment to the site (Figure 3). The HG index thus reflects the porosity of a hydrogeological substrate and in turn the likely groundwater influence at a site. In areas where the hydrogeological substrate is highly permeable groundwater moves more easily into the stream (Hiscock and Bense, 2014). The HG index also gives a proxy measure of groundwater influence that can be compared between sites by incorporating the distance upstream from each study site to the location of the hydrogeological unit facilitating groundwater movement and the size of that hydrogeological segment (i.e. the closer to the site and the larger the hydrogeological segment that allows groundwater flows the greater the expected influence of groundwater at that site). Further details on the HG index are given in Appendix A.

Upstream of each site the HG index was calculated at distances of 0.5, 1, 1.5, 2, 2.5 and 5 km. River segments flowing into each site were also assessed at 100m either side of the river channel, to account for lateral groundwater flows from the parafluvial zone (Boulton and Hancock 2006). The HG index varied across the sites surveyed; 2 sites had high groundwater influence (HG index of 3.24 to 3.33 at 2 km upstream); 3 sites had moderate groundwater influence (HG index of 2.11 to 2.63 2 km upstream) and 3 sites had low groundwater influence (HG index of 0 to 1.9 at 2 km upstream). Correlations of the HG index with longitudinal effects (i.e. the distance (km) between the stream source and the site (after Nichols *et al.*, 2000)) that could obscure the HG index were low ($r \leq 0.3$).

Trait groups

We derived trait groups on the basis of dispersal ability and the presence/absence of life-history stages resistant to drying. The trait group categories applied were taxa with (1) drought resistant life-stages (hereafter drought resistant) (2) no drought resistant life stages (here after non-drought-resistant) and (3) poor dispersal traits (here after poor dispersing taxa). Taxa were assigned to each of these trait groups based on the literature as listed in Appendix D. Drought resistant taxa include those that have eggs resistant to desiccation, larvae or adults resistant to some desiccation, the ability to use refuges in moist sediments, under leaves or other organic debris, or can utilise temporary aquatic habitats. Non-drought resistant taxa were those with no drought / desiccation resistant traits. Poor dispersing taxa include weak or poor flyers, or those that do not fly far from where they breed. A range of life cycle lengths (i.e. number of generations per year classed as less univoltine, univoltine to bivoltine and more than bivoltine) were present in each trait group. The frequency of different life cycle length classes did not vary significantly within trait groups ($\chi^2 < 3.7$; $P > 0.16$; df =2) (Appendix E).

Data analysis

Generalised linear models (GLMMs) are models that extend linear mixed models (which include random effects) to non-normal data types such as counts or binary data, which widely occurs in ecological studies (Bolker *et al.*, 2009). GLMMs were used to test the relative importance of hydrogeological interactions with stream flow, and how these varied amongst taxa and trait groups. All macroinvertebrate taxa which occurred in > 10 % of surveys across all sites were modelled using GLMMs. A summary of the taxa modelled, as well as taxa within each trait group, are given in Appendix D and F. A separate model for each taxon and trait group was fitted using a logit link. For each model there were 189 samples. Within each of the 189 samples each taxon occurred a certain number of times out of the total 200 individuals collected. From this we modelled the probability that each taxon or trait group was present in a sample using a binomial distribution.

To allow for overdispersion a random effect with a unique value for each sample (from 1 to 189) was included (Table I). This allowed each sample to deviate from the modelled binomial distribution (Del Fava *et al.*, 2014). To allow for spatial and temporal clustering in the data random effects for site and year were also included (Table I). Fixed effects were season of sampling (spring, summer, autumn or winter), flow variability metrics were represented by log transformed mean flows in the preceding 6 months (flow 6 months), the co-efficient of variation of the previous months flows (CV month) and the co-efficient of variation of flows for the previous 6 months (CV 6 months) (Table I). CV 3 months and CV 1 year were not included in the final model as they were strongly correlated (spearman $r \geq 0.66$) with CV 6 months (Appendix G). The hydrogeological influence index (HG index) was included as a fixed effect at 2km upstream because this distance displayed the strongest relationship in preliminary analysis and because this measure was strongly correlated ($r \geq 0.74$) with HG index measures at each of the different distances measured. Interactions between the hydrogeological index and flow metrics were also included as fixed effects. To minimise the likelihood of finding relationships by chance we took a conservative approach to fitting fixed effects and only included those important for testing flow variability and hydrogeological relationships with macroinvertebrate responses. To this end we also calculated 95% confidence intervals for parameter estimates in each model using bootstrapping with 1000 replicates.

Prior to analysis, predictor variables were centred (x-mean(x) / 2.sd(x)), to allow comparison of effect sizes (Gelman and Hill, 2006). Centring also allows for regression results to be more easily interpreted when interactions are in a model, with main effects being the predictive difference with the other inputs at their average value (Gelman and Hill, 2006). A conditional and marginal R^2 for each model was also computed (after Nakagawa and Schielzith, 2013) using the MuMIn package (Bartoń, 2013) in R. Model checking included homogeneity of residual variance and normality and checking for overdispersion. All GLMMs were fit using the lme4 package (Bates *et al.,* 2012) and languageR package (Baayen, 2011) in R (R Development Core Team 2014).

Results

Taxon and trait group responses to groundwater influence and stream flow

The occurrence of several taxa were explained well by GLMMs, with a conditional $R^2 \geq 0.4$ (Table II). There was a diverse range of macroinvertebrate responses to the hydrogeological index proxy for groundwater influence (HG index) and flow variables tested (Table II) (Figure 4 and 5). Chironomidae and Hydrobiosidae were the only taxon positively associated with the HG index, albeit the explained variance for the Chironomidae model was low (marginal $R^2 = 0.02$) (Table II). In contrast, the occurrence of Coloburiscidae and Gripopterygidae was negatively associated with the HG index (Table II). The occurrence of Baetidae, Coloburiscidae, Glossosomatidae, Gomphidae, Gripopterygidae, Hydrobiosidae and Tipulidae was positively related to flow in the previous 6 months; of these macroinvertebrates, Glossosomatidae, Coloburiscidae and Baetidae had the strongest positive association with flow (Table II) (Figure 4). In contrast, an increased discharge had a negative association with Acarina, Ecnomidae and Oligochaeta (Table II) (Figure 4).

Ecnomidae, Empididae and Simuliidae had a positive association with CV 6 months (Figure 5). Ancylidae, Coloburiscidae, Leptophlebiidae, Elmidae, Glossosomatidae, Gripopterygidae and Gomphidae all responded negatively to CV 6 months (Table II). Elmidae was the only taxon with a relationship with CV 1 month (Table II). Baetidae, Hydrobiosidae and Hydroptilidae all responded negatively to interactions between the HG index and flow in the previous 6 months, while Coloburiscidae and Gripopterygidae responded positively (Table II). Baetidae and Simuliidae responded positively to interactions between the HG index and CV 6 months (Table II). No taxa responded to interactions between the HG index and CV 1 month.

Non-drought resistant taxa had a positive relationship with the HG index variable, but no relationship with any of the flow variables (Table II). Drought resistant taxa had no relationship with either the HG index or any of the flow variables considered (Table II).

Overall, poor dispersing taxa showed a positive response to interactions between the HG index and flow 6 months (Table II; Figure 6). More specifically, at mean flows or higher, as the HG index increased, the probability of occurrence of poor dispersing taxa also increased (Figure 4). In contrast, at low flows, as the HG index increased, the probability of occurrence of poor dispersing taxa decreased (Figure 4). Poor dispersing taxa also showed a negative relationship with the main effects of the HG index and CV 6 months. The negative relationship between poor dispersing taxa and the HG index and CV 6 months reflect the effects of these factors on poor dispersing taxa when other predictors in the model are at their average value.

Discussion

Ecological responses to flow regime variability are often diverse, with some biota showing significant changes in some instances, but little response in others (Stubbington *et al.*, 2009a; Stubbington *et al.*, 2009b; Wood and Petts, 1999; Suren and Jowett, 2006; Bae *et al.*, 2014). Understanding the reasons behind the diversity of ecological responses to flow variability is central to developing generalities that can guide research and management. To this end, we investigated whether hydrogeology and traits explain variation in macroinvertebrate responses to flow and thus whether these factors may help explain the diversity of ecological responses to flow variability documented in other studies.

Hydrogeological influences and macroinvertebrate responses to flow variability

This study suggests that stream macroinvertebrate responses to flow variability could be better understood by some measure of hydrogeology related to groundwater influence. The hydrogeological diversity of the Upper Murrumbidgee Catchment is not unique and similarly complex hydrogeological structures, and thus fine scale diversity in surface-groundwater connectivity are a common feature of rivers globally (BGR Hannover / UNESCO, 2012). The

HG index in this study reflects the porosity and permeability of a hydrogeological substrate. In areas where the hydrogeological substrate is highly permeable groundwater moves more easily into the stream (Hiscock and Bense, 2014). In turn, stream segments with highly permeable aquifers (e.g. alluvial segments) that allow greater groundwater influence may interact more strongly with flow variability to influence patterns in macroinvertebrate occurrence (e.g. Monk *et al.,* 2008).

We hypothesised that hydrogeological differences (reflecting groundwater influence) would explain variation in macroinvertebrate occurrences. The results were in agreement with this hypothesis for 7 out of the 24 taxa modelled. The seven taxa that the hypothesis was accepted for had a significant relationship with the influence of groundwater (HG index), or interactions between the HG index and flow variables. This suggests that not only do macroinvertebrate families within a community show a diverse range of responses to flow variability, but also that hydrogeological patterns that influence groundwater affect the occurrence of many macroinvertebrate families. This result is broadly consistent with others studies that highlight diverse responses between different taxa to flow variability and the importance of environmental factors additional to stream flow (Poff and Zimmerman, 2010; Booker *et al.,* 2015).

More specifically, the results for individual macroinvertebrate families showing significant responses to hydrogeological differences are also consistent with other studies (Corbin and Goonan, 2010; Bovill *et al.,* 2013). For example, Baetidae, Hydroptilidae and Hydrobiosidae responded negatively to interactions between the HG index and flow, reflecting a preference for minimal groundwater influence and lower flows and thus potentially for drier conditions. We know of no previous studies investigating groundwater influence on Baetidae, Hydroptilidae and Hydrobiosidae occurrence, but a preference for drier conditions is consistent with observations for several species within these families (Wells, 1985; Corbin and Goonan, 2010; Bovill *et al.,* 2013). A preference for drier conditions also fits well with some, but not all, known traits of Baetidae, which has some drought resistant life stages and desiccation-resistant eggs (Paltridge *et al.,* 1997). Hydroptilidae are also widespread, tolerant and commonly found in slow-flowing waters (Wells, 1985).

In contrast to the above taxa, Coloburiscidae and Gripopterygidae responded positively to interactions between the HG index and river flow (i.e. as the HG index increased, the influence of river flows became more positive). This could reflect a preference for hydrogeological conditions that facilitate greater groundwater influence, and thus relatively more consistent inputs of water (Wood and Petts, 1999; Stubbington et al., 2011; Wood and Petts, 1999). Coloburiscidae typically inhabit fast flowing waters (Gooderham and Tsyrlin, 2002), whereas Gripopterygidae are typically poor dispersers (Keast, 1981; Walker, 1981; Lancaster and Downes, 2013). A preference for fast flows and poor dispersal abilities may make both Coloburiscidae and Gripopterygidae sensitive to local surface flow fluctuations and hydrogeological differences. Consequently, additional to factors such as surface flows, fine scale (≤ 2km) spatial variations in hydrogeology, which influence groundwater inputs, may be important factors for several of the macroinvertebrate taxa investigated.

The models including the HG index's relationship, while significant for some taxa, had little explanatory power for others. In these weaker models significant relationships with the HG index are unlikely to be biologically relevant (e.g. Chironomidae). Furthermore the relationships observed in this study need to be considered alongside the limited taxonomic resolution used (Monk *et al.*, 2012). A limited taxonomic resolution may obscure variation between species within families (Chessman, 2015). Chironomidae and Baetidae, which responded to the HG index and HG index interactions with flow are globally widespread and occur in a diversity of habitats (Ferrington, 2008; Gattolliat and Nieto, 2009). Consequently, species-specific differences in these and many of the groups investigated need to be carefully considered when interpreting the results at the broad family level presented here. An important avenue for future research will be testing how species-specific differences within families may alter identified relationships with hydrogeology and flow variability.

Using traits to understand macroinvertebrate responses to flow variability

As hypothesised, non-drought resistant and poor dispersing taxa were significantly influenced by the HG index and flow variables, whereas taxa with drought resistant traits were not. Of the trait groups examined, poor dispersing taxa showed the strongest response, with a significant positive association with interactions between the HG index and flow. Poor dispersing taxa did show a negative relationship with the HG index, but this relationship is not the main effect of the HG index by itself, since its influence is conditional on other factors at their average value (Gelman and Hill, 2006). The highest predicted probability of occurrence for poor dispersing taxa was in conditions with a relatively greater HG index (i.e. greater relative groundwater influence) and high flow. This result suggests that over the long-term poor dispersing taxa may prefer areas with greater groundwater influence and higher flows, possibly because this increases hydrological stability and thus minimises the need for dispersal.

The importance of flow variability, or its inverse hydrological stability, coupled with taxon dispersal capability, is known to be a key determinant driving the occurrence of macroinvertebrates (e.g. Bonada *et al.*, 2007b; Stubbington *et al.*, 2011; Belmar *et al.*, 2013; de Szoeke *et al.*, 2015). However, while the importance of flow variability is well recognised, it has less frequently been linked to trait groups, such as macroinvertebrate families with poor dispersal abilities (but see Bonada *et al.*, 2007b; Tupinambás *et al.*, 2014). Although, Bonada *et al.* (2007b) have shown significant differences between taxa with different dispersal traits to varying levels of flow intermittency and these results are broadly consistent with the findings of the current study. Belmar *et al.* (2013) also argue that dispersal ability is a key determinant of macroinvertebrates in hydrologically variable habitats. The findings of this study also support these assertions and highlight that macroinvertebrates with poor dispersal abilities are more likely to occur in hydrologically stable conditions (here represented by high flow and hydrogeological conditions that reflect high groundwater influence).

While the current study's findings do have some similarities with previous research, comparisons between studies on macroinvertebrate dispersal and flow variability need to be made cautiously. In the case of Bonada *et al.* (2007b) and Belmar *et al.* (2013) macroinvertebrate responses were to seasonal drought, while in the current study macroinvertebrates responded to supra-seasonal droughts. There were also ephemeral habitats in the study of Bonada *et al.* (2007b), but not in the current study. Furthermore, there are differences in the taxa present and how trait groups were classified. Additionally, fine-scale differences in hydrogeology and interactions with flow were not assessed in Bonada *et al.* (2007b) or Belmar *et al.* (2013).

Future directions and implications

While, the HG index in this study was a useful predictor for several macroinvertebrate taxa and poor dispersing taxa, we stress that our HG index is not directly linked to groundwater inflows, but instead is a proxy for them. Numerous studies have highlighted fine scale and resource intensive methods for assessing hydrogeology and surface-groundwater connectivity (e.g. Baskaran *et al.*, 2009; Lamontagne *et al.*, 2014). For example, tracer, isotope or geochemical techniques have been frequently used to measure groundwater connectivity to streams (Atkinson et al. 2015). Ground testing of hydrogeological proxies using fine scale surface-groundwater hydrogeological techniques will be an important avenue for future research and could foster important collaboration between hydrogeologists and ecohydrologists.

Though an important future research direction, detailed surface-groundwater interaction information and studies may not be available for long-term studies or for historical ecological data sets at broader spatial scales (e.g. entire rivers or across multiple rivers within or between catchments). In this instance, proxies for groundwater influence on stream segments, such as the HG index, offer an alternative to resource intensive investigations and could be an essential first step for ecohydrological research where different resolutions and scales of ecological and hydrogeological data need to be linked.

In addition to utilising a novel index of hydrogeology reflecting groundwater influence, this study also demonstrated the use of different trait groups for understanding flow variability effects on macroinvertebrates. The use of trait groups offers important insights into the mechanisms behind macroinvertebrate responses to flow variability. In this study, the positive response to the interaction between the HG index and high flow on poor dispersing taxa suggests these taxa display an affinity for hydrologically stable areas. This finding, not only helps to explain why in some instances there may be diverse macroinvertebrate responses to flow variability (Dewson *et al.*, 2007), but also highlights important avenues of future research for developing and refining our conceptual and empirical understanding of ecohydrological responses to flow variability.

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Tables and Figures

Table I Summary of fixed and random effects in GLMM models

Table II Parameter estimates and model performance for taxa and trait groups in riffle habitats. Marginal R^2 ($R^2_{GLMM(m)}$) gives the variance explained by fixed factors. Conditional R^2 ($R^2_{GLMM(c)}$) is the variation explained by the entire model (after Nakagawa and Schielzith 2013). *b* [95% CI] = parameter estimate and bootstrapped 95% confidence interval. Only taxa with significant relationships are shown. Interactions between the Groundwater index and CV 1 month were not significant for any taxa and are not shown.

Figure 1 The Upper Murrumbidgee study area in south eastern Australia, showing river riffle (black circle) macroinvertebrate survey locations. The major city (Canberra) and location of long-term rainfall gauge (Tharwa) are shown by black squares.

Figure 2 Monthly rainfall anomalies over the survey period from 1994 to 2011 at Tharwa.

Figure 3 Graphical representation of method used to calculate the Groundwater influence index. The size of hydrogeological segments '*likely to be of groundwater influence*' (e.g. alluvial segments) (after Coram et al. 2000) = ***sl*** and the distance of that segment from the site = ***d*.** Segment length (sl) and distance (d) were all measured in ArcMap 9.3 using the measure tools.

Figure 4. Macroinvertbrate family responses to log Flow 6 month (ML day^{-1}) (mean in previous 6 months). Grey shaded areas are 95% confidence intervals. Ticks on x-axis show spread of data. Note different ranges on y-axis.

Figure 5. Macroinvertebrate family responses to CV 6 month (CV 6) (mean in previous 6 months). Grey shaded areas are 95% confidence intervals. Ticks on x-axis show spread of data. Note different ranges on y-axis.

Figure 6 Predicted probability of occurrence of Poor dispersing taxa in response to interactions between the hydrogeological influence index and log flow (mean in the previous 6 months).

Appendices

Appendix A Hydrogeological subunits in the study area and further detail and references and groundwater influence index method.

Appendix B (a) Monthly and (b) yearly rainfall anomalies over the survey period from 1994 to 2011.

Appendix C Sample time (black square) for all riffle sites in relation to flow percentile (grey line) for the corresponding river.

Appendix D Taxa list for each trait group. Families within each trait group have life stages that are characterised by the traits heading their respective column.

Appendix E Number of generations per year (in different classes), shown as a proportion, for each trait group examined.

Appendix F Taxa occurring in >10% of samples and trait groups modelled in GLMMs.

Appendix G Predictor fixed and random effects correlations (Spearman r) for GLMM models for frequently occurring taxa and trait groups

Table I Summary of fixed and random effects in GLMM models

Variable	Description	Data source
Random effects		
Site location	To account for spatial clustering.	Field data
Sample	Included to account for over-dispersion.	Field data
Year	To account for temporal clustering.	Field data
Fixed effects		
Season	Season of macroinvertebrate sampling, to account of seasonal differences.	Field data
log Flow 6 month (ML day^{-1}) (mean in previous 6 months)	Mean flow six months before the sampling date. (i.e. antecedent flow conditions).	Australian Capital Territory Electricity and Water Authority (ACTEW) and the Office of Water from the NSW Department of Primary Industries (2013)
CV month (CV) (mean in previous month)	Coefficient of variation (representing flow variability) for daily flow data a month before the sampling date	Australian Capital Territory Electricity and Water Authority (ACTEW) and the Office of Water from the NSW Department of Primary Industries (2013)
CV 6 month (CV 6) (mean in previous 6 months)	Coefficient of variation (representing flow variability) for daily flow data 6 months before the sampling date.	Australian Capital Territory Electricity and Water Authority (ACTEW) and the Office of Water from the NSW Department of Primary Industries (2013)
Hydrogeology influence (HG index)	Index reflecting amount of groundwater influence at site. See Figure 3 and Appendix A for further details.	Department of Agriculture: Australian Bureau of Agricultural and Resource Economics and Sciences Manager (ABARES) (2000) Australian groundwater flow systems – National land and water resources audit. http://data.daff.gov.au/anrdl/metadata_files/pa_agfs_r9abl_00111a00.xml

Table II Parameter estimates and model performance for selected taxa and trait groups in riffle habitats. Marginal R^2 ($R^2_{GLMM(m)}$) gives the variance explained by fixed factors. Conditional R^2 ($R^2_{GLMM(c)}$) is the variation explained by the entire model (after Nakagawa and Schielzith 2013). *b* [95% CI] = parameter estimate and bootstrapped 95% confidence interval. Only taxa with significant relationships are shown. Interactions between the Groundwater index and CV 1 month were not significant for any taxa and are not shown.

Taxon	**HG index** *b* **[95% CI]**	**Flow** *b* **[95% CI]**	**CV** $_{\textbf{1 month}}$ *b* **[95% CI]**	**CV** $_{\textbf{6 month}}$ *b* **[95% CI]**	**HG x Flow** *b* **[95% CI]**	**HG x CV** $_{\textbf{6 month}}$ *b* **[95% CI]**	$\mathbf{R^2_{GLMM(m)}}$	$\mathbf{R^2_{GLMM(c)}}$
Acarina	n.s.	-0.34 [-0.6, -0.11]	n.s.	n.s.	n.s.	n.s.	0.05	0.24
Ancylidae	n.s.	n.s.	n.s.	-1.81 [-3.38, -0.82]	n.s.	n.s.	0.12	0.46
Baetidae	n.s.	0.77 [0.41, 1.16]	n.s.	n.s.	-0.45 [-0.69, -0.22]	0.34 [0.1, 0.59]	0.16	0.46
Chironomidae	0.33 [0.14, 0.54]	n.s.	n.s.	n.s.	n.s.	n.s.	0.02	0.15
Coloburiscidae	-0.90 [-1.68, -0.19]	0.84 [0.57, 1.24]	n.s.	-0.96 [-2.19, -0.59]	0.26 [0.04, 0.49]	n.s.	0.45	0.59
Conoesucidae	n.s.	0.68 [0.05, 1.35]	n.s.	n.s.	n.s.	n.s.	0.12	0.57
Ecnomidae	n.s.	-0.57 [-0.96, -0.17]	n.s.	0.64 [0.12, 1.06]	n.s.	n.s.	0.16	0.51
Elmidae	n.s.	n.s.	0.69 [0.05, 1.23]	-0.54 [-1.31, -0.17]	n.s.	n.s.	0.12	0.40
Empididae	n.s.	n.s.	n.s.	0.39 [0.05, 0.64]	n.s.	n.s.	0.04	0.18
Glossosomatidae	n.s.	0.9 [0.48, 1.41]	n.s.	-0.76 [-1.95, -0.29]	n.s.	n.s.	0.36	0.61
Gomphidae	n.s.	0.5 [0.03, 1.1]	n.s.	-1.22 [-3.13, -0.56]	n.s.	n.s.	0.28	0.58
Gripopterygidae	-0.53 [-0.96, -0.09]	0.42 [0.15, 0.75]	n.s.	-1.55 [-2.54, -0.95]	0.24 [0.06, 0.41]	n.s.	0.43	0.69
Hydrobiosidae	0.52 [0.02, 1.28]	0.56 [0.21, 0.99]	n.s.	n.s.	-0.31 [-0.54, -0.1]	0.18 [0, 0.41]	0.26	0.52
Hydroptilidae	n.s.	n.s.	n.s.	n.s.	-0.24 [-0.44, -0.05]	n.s.	0.13	0.47
Leptophlebiidae	n.s.	n.s.	n.s.	-0.36 [-0.85, -0.01]	n.s.	n.s.	0.10	0.51
Oligochaeta	n.s.	-0.29 [-0.55, -0.07]	n.s.	n.s.	n.s.	n.s.	0.16	0.36
Simuliidae	n.s.	n.s.	n.s.	0.51 [0.17, 0.91]	n.s.	0.25 [0.03, 0.46]	0.11	0.45
Tipulidae	n.s.	0.43 [0.18, 0.75]	n.s.	n.s.	n.s.	n.s.	0.10	0.21
Trait group								
Drought resistant	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.02	0.14
Non-drought resistant	0.2 [0.03, 0.37]	n.s.	n.s.	n.s.	n.s.	n.s.	0.02	0.15
Poor dispersing	-0.87 [-1.27, -0.44]	n.s.	n.s.	-0.96 [-1.65, -0.51]	0.39 [0.22, 0.56]	n.s.	0.31	0.61

n.s. = bootstrapped 95% confidence intervals overlapping zero. Residual degrees of freedom = 175

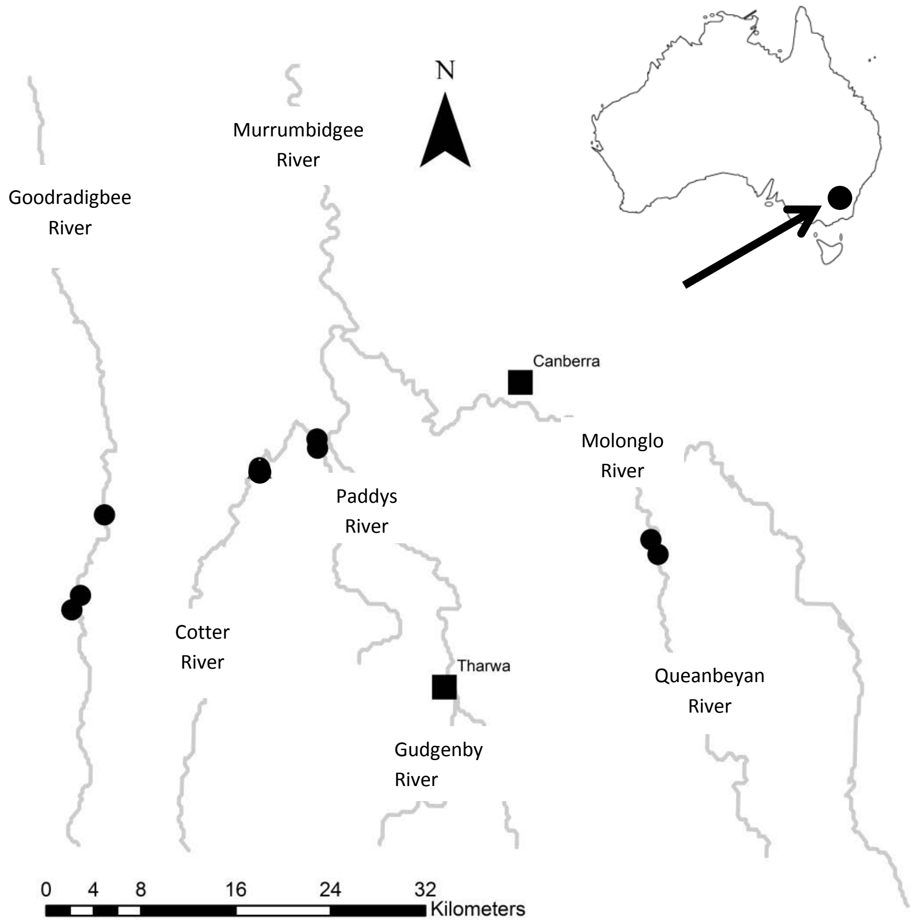


Figure 1 The Upper Murrumbidgee study area in south eastern Australia, showing river riffle (black circle) macroinvertebrate survey locations. The major city (Canberra) and location of long-term rainfall gauge (Tharwa) are shown by black squares.

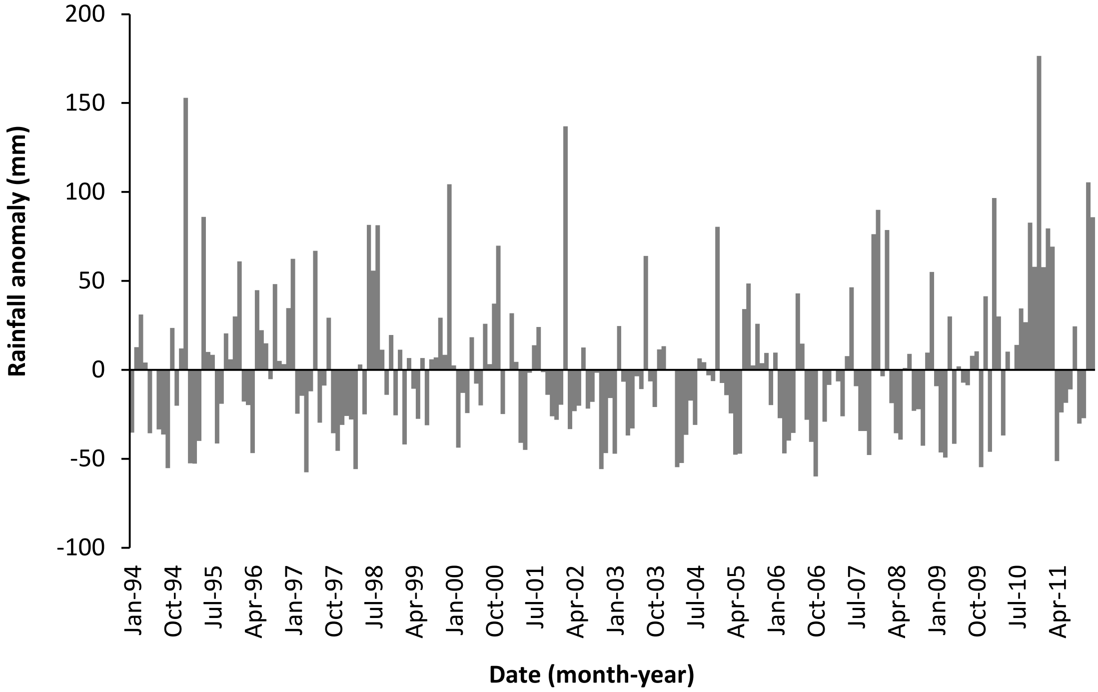


Figure 2 Monthly rainfall anomalies over the survey period from 1994 to 2011 at Tharwa.

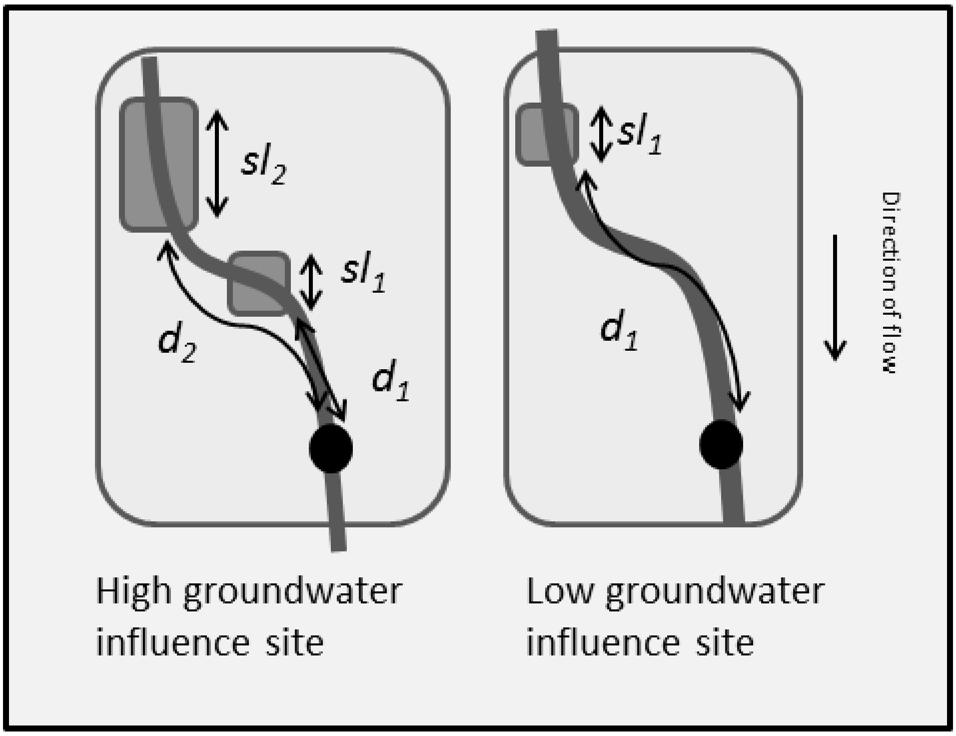


Figure 3 Graphical representation of method used to calculate the Groundwater influence index. The size of hydrogeological segments '*likely to be of groundwater influence*' (e.g. alluvial and colluvial segments) (after Coram et al. 2000) = ***sl*** and the distance of that segment from the site = ***d*.** Segment length (sl) and distance (d) were all measured in ArcMap 9.3 using the measure tools.

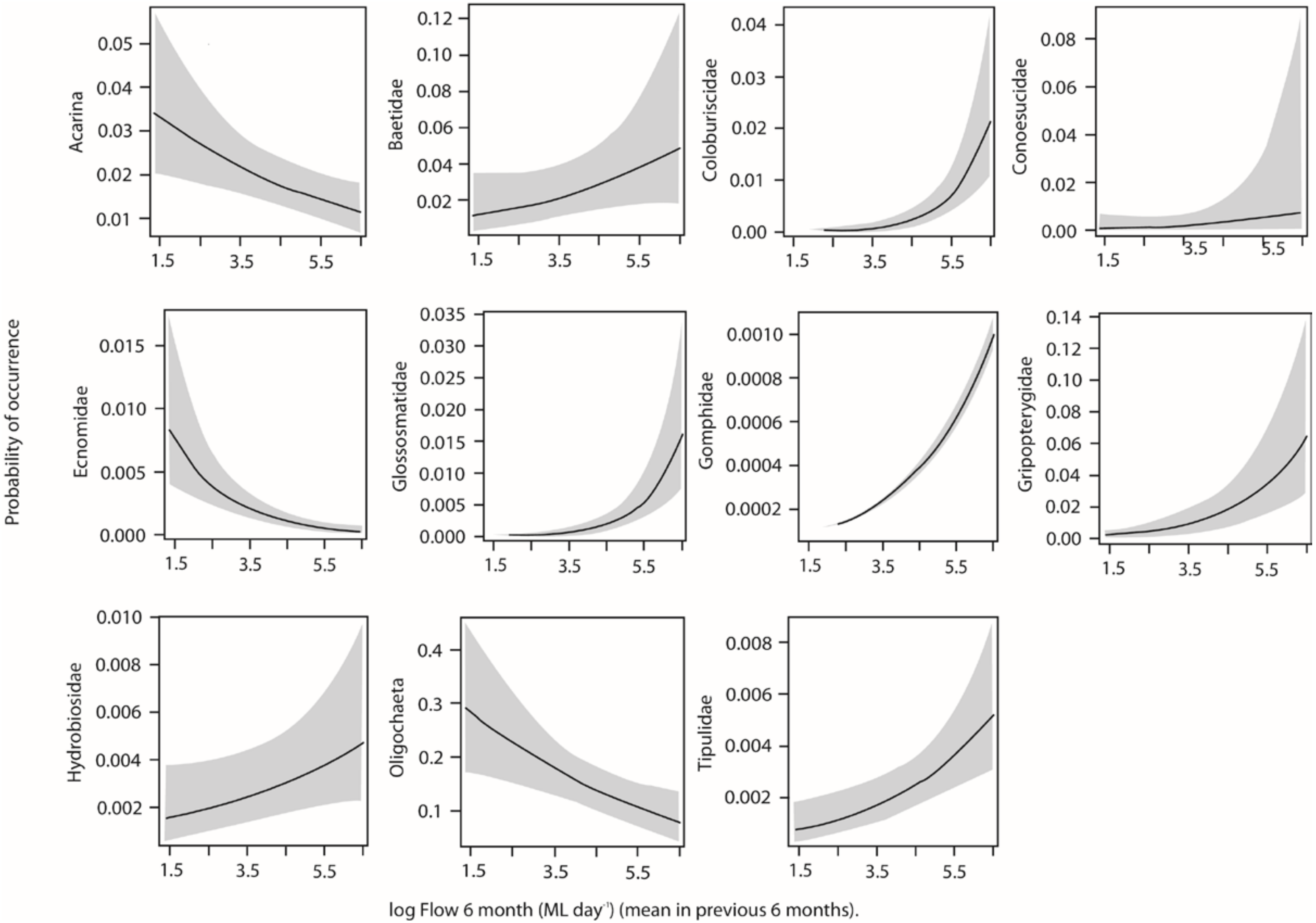


Figure 4. Macroinvertbrate family responses to log Flow 6 month (ML day^{-1}) (mean in previous 6 months). Grey shaded areas are 95% confidence intervals. Note different ranges on y-axis.

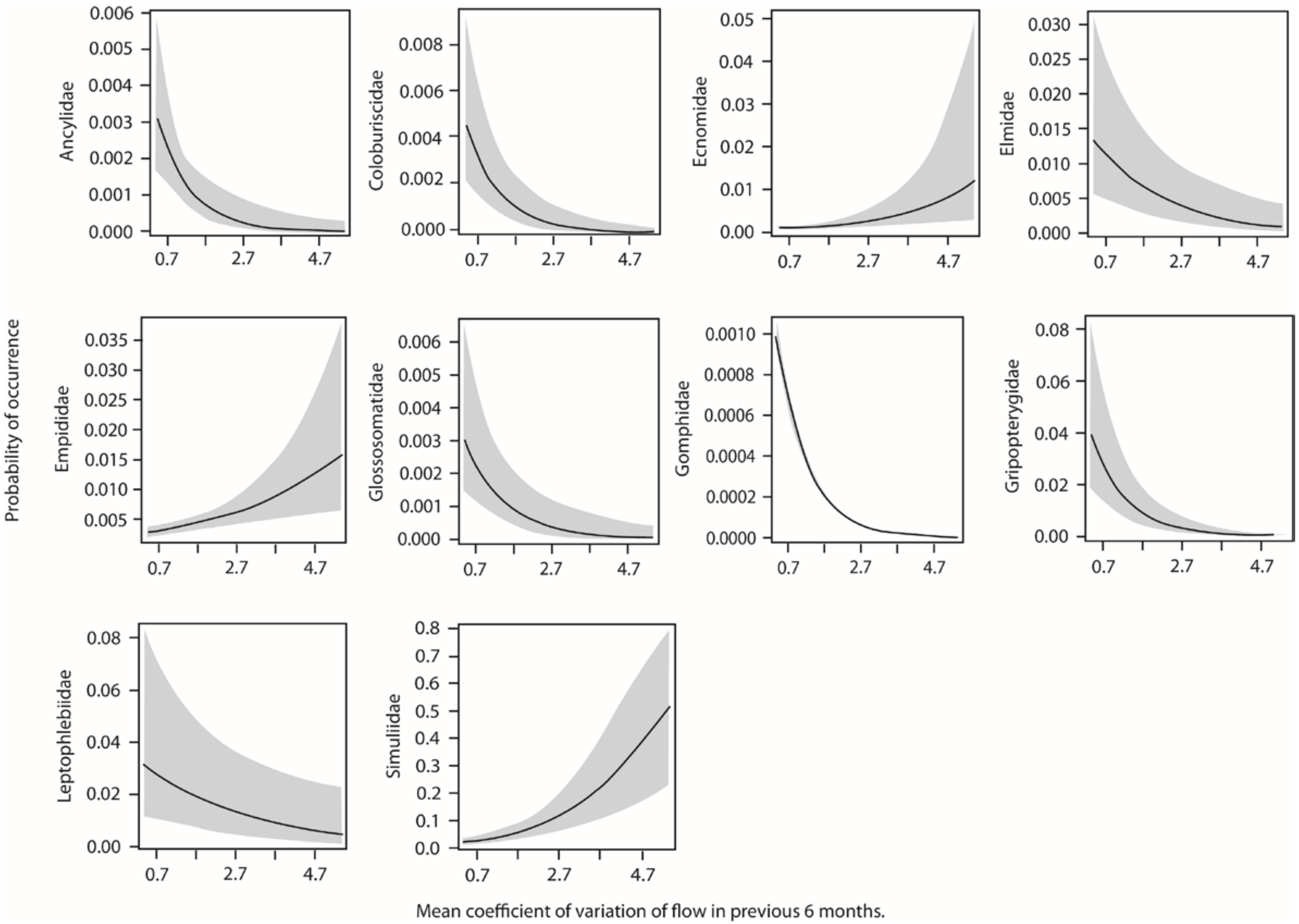


Figure 5. Macroinvertbrate family responses to mean coefficient of variation of flow in previous 6 months. Grey shaded areas are 95% confidence intervals. Note different ranges on y-axis

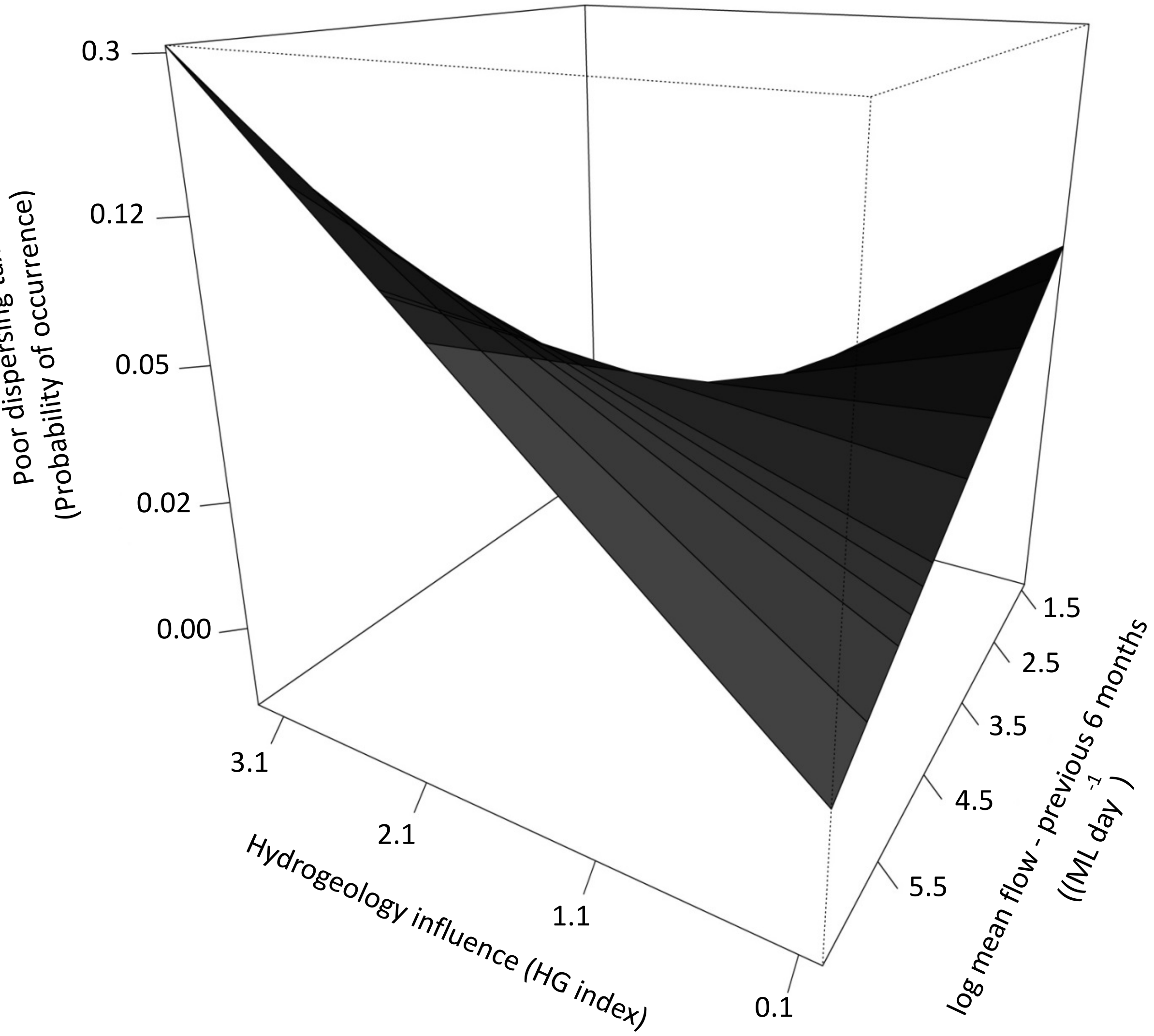
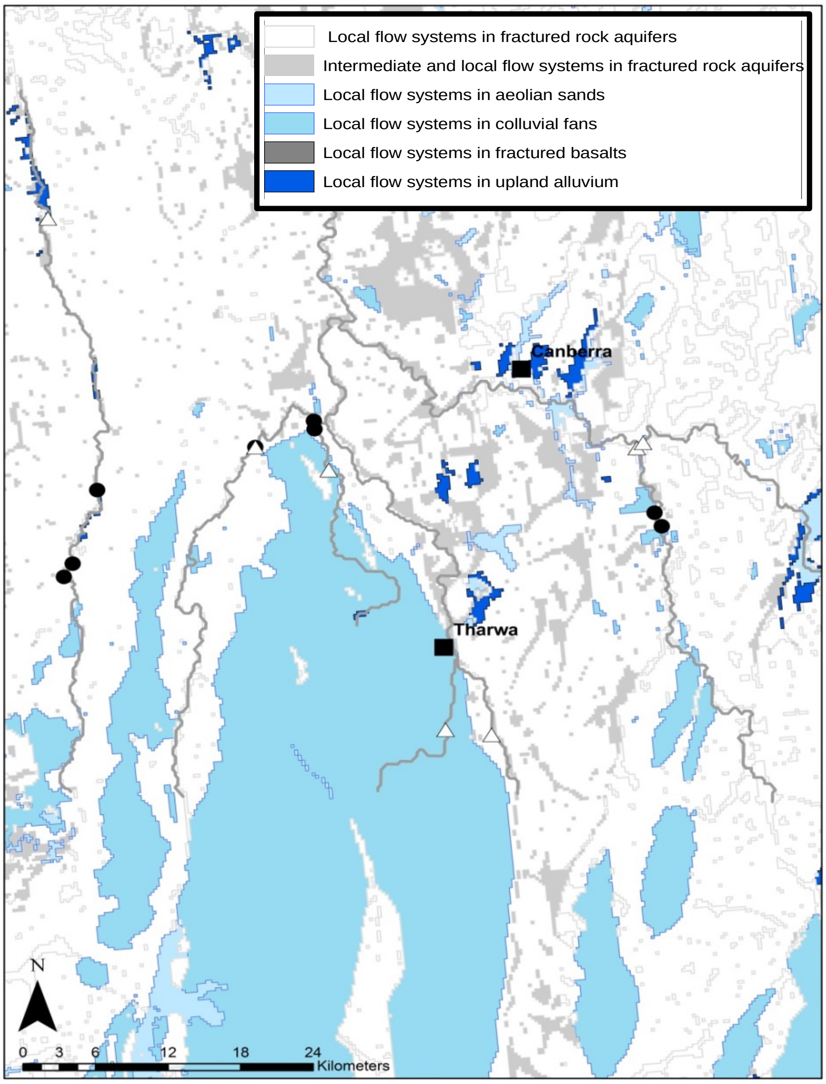


Figure 6 Predicted probability of occurrence of Poor dispersing taxa in response to interactions between the hydrogeological influence index and log flow (mean in the previous 6 months).

Appendices

Appendix A: Hydrogeological subunits in the study area and further detail and references and groundwater influence index method

Hydrogeological subunits in the study area are shown in the figure below. Riffle (black circle) macroinvertebrate survey locations are also shown. The major city (Canberra) and location of long-term rainfall gauge (Tharwa) are shown by black squares. The groundwater connectivity of segments was classified based on aquifer transmissivity (i.e. the ability to transmit groundwater through the aquifer) as either facilitating groundwater movement or not based on the classification of Coram et al. (2001). Alluvial and Colluvial groundwater flow segments were classified as facilitating high groundwater movement. Fractured rock segments were classified as having lower hydraulic conductivity and facilitating groundwater movement less readily. This approach was designed to capture broad surface-groundwater connectivity differences where information is limited. An assessment of temporal dynamics in groundwater connectivity was also not attempted because of the stable groundwater conditions in the study area (CSIRO 2008).



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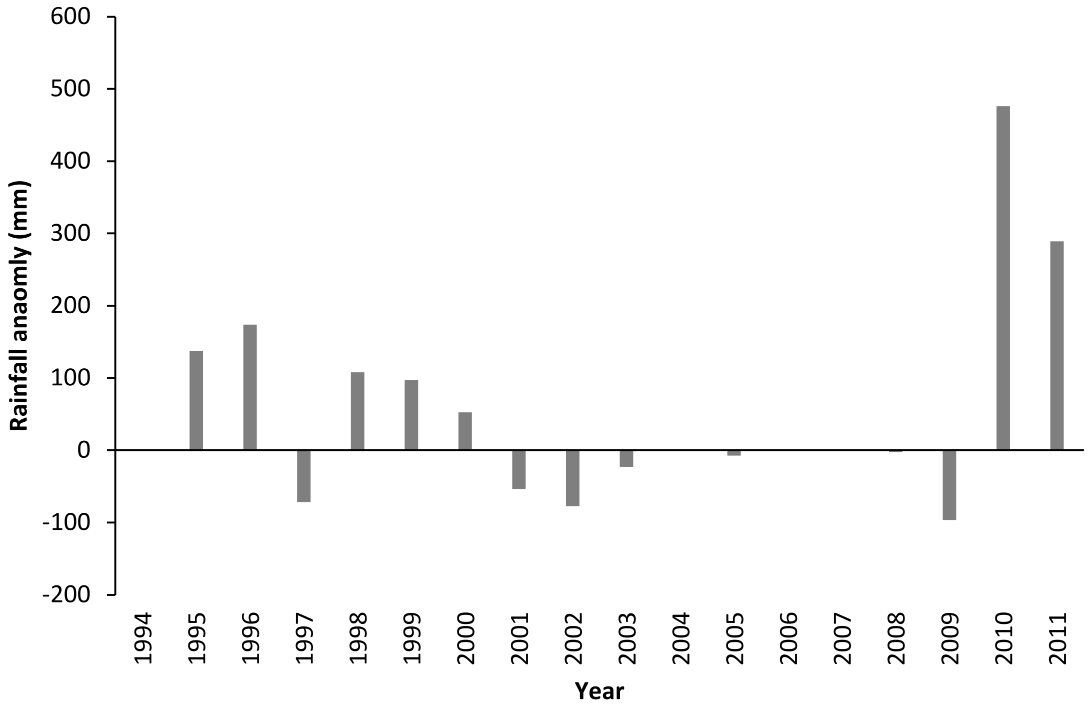
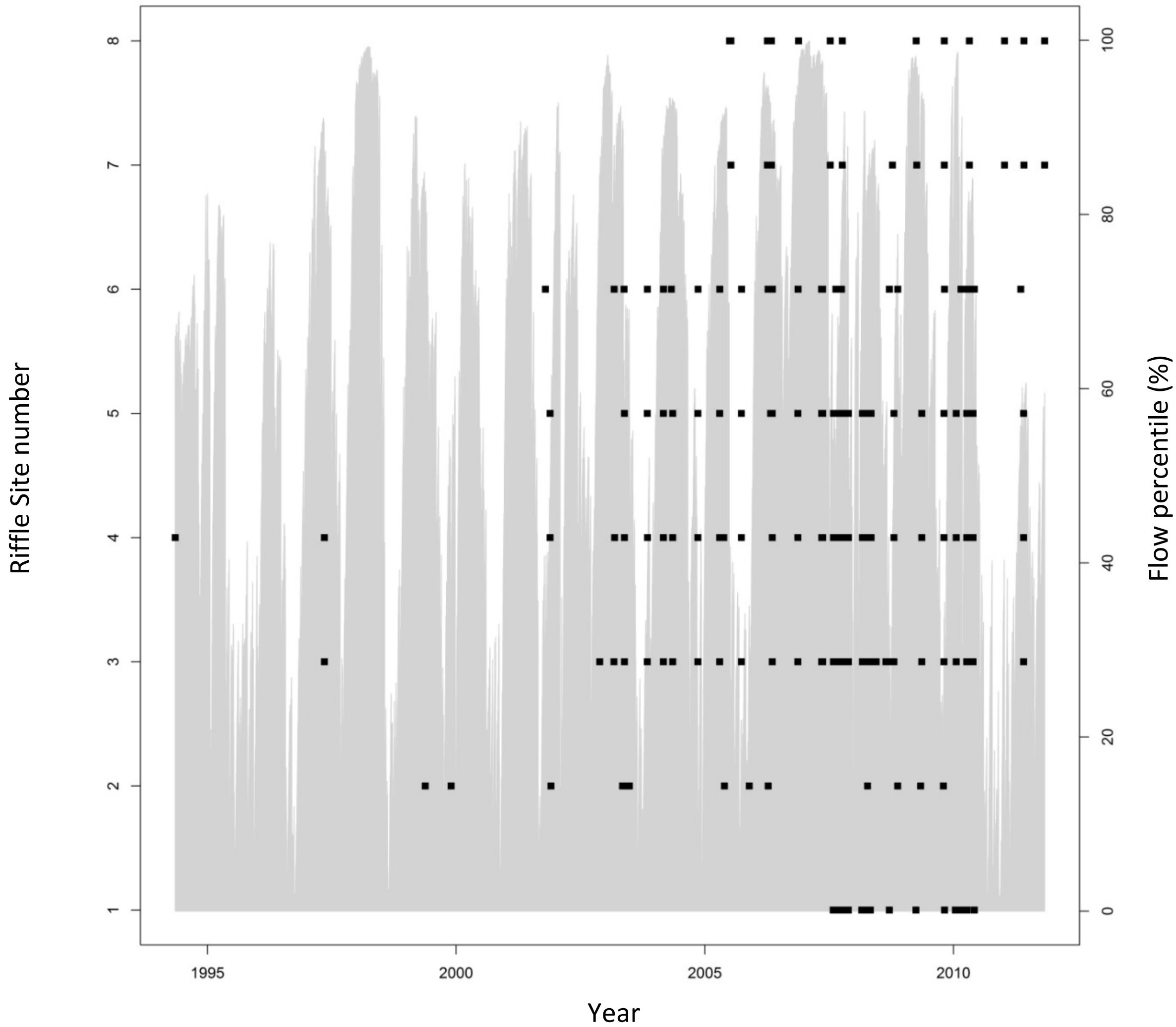
CSIRO (2008). Water availability in the Murrumbidgee. A report to the Australian Government from the CSIRO Murray-Darling Basin Sustainable Yields Project. CSIRO, Australia. 155pp

Appendix B: Annual rainfall anomalies over the survey period from 1994 to 2011 at Tharwa.



Appendix C: Sample time (black square) for all riffle sites in relation to flow percentiles (grey line) on the Cotter River, which is generally representative of flow conditions in other rivers in the catchment.



Appendix D: Taxa list for each trait group. Families within the drought resistant group have a life stage or stages that are characterised by being resistant of drought, while the non-drought and poor dispersal groups all life-stages are characterised by the traits heading their respective column. Number in parenthesis correspond to references and page number listed below (e.g. 6:1209 = page 1209 of reference 6).

Non drought resistant	Drought resistant	Poor dispersers
Corixidae (6:1209)	Aeshnidae (6:1152)	Austroperlidae (15:191; 6:1171)
Gerridae (6:1209)	Baetidae (9)	Corbiculidae (6:1243)
Hebridae (6:1209)	Ceratopogonidae (9)	Eustheniidae (15:191; 6:1171)
Mesoveliidae (6:1209)	Corbiculidae (15:83)	Gripopterygidae (15:191; 6:1171)
Naucoridae (6:1209)	Culicidae (3:732)	Notonectidae (15:191; 6:1171)
Nepidae (6:1209)	Dytiscidae (14:4)	Sphaeriidae (6:1243)
Ameletopsidae (5:63)	Gelastocoridae (6:1209)	
Austroperlidae (2)	Glacidorbidae (15:88)	
Caenidae (5:63)	Gripopterygidae (13:78)	
Chironomidae (7)	Hydrobiidae (15:88)	
Coloburiscidae (5:63)	Hydrometridae (1:31)	
Eustheniidae (2)	Leptoceridae (11; 12)	
Palaemonidae (15:166)	Leptophlebiidae (9)	
Pleidae (6:1209)	Lestidae (6:1152)	
Veliidae (6:1209)	Libellulidae (4)	
	Lymnaeidae (15:88)	
	Nematoda (15:55)	
	Notonectidae (15:224)	
	Notonemouridae (6:1180)	
	Oligochaeta (9)	
	Parastacidae (8:122; 15:168; 6:1122)	
	Phreatoicidae (15:155)	
	Physidae (15:88)	
	Planorbidae (15:88)	
	Psephenidae (10)	
	Simuliidae (15:238)	
	Sphaeriidae (15:83)	
	Synthemistidae (6:1152; 11)	
	Telephlebiidae (14:11)	
	Tipulidae (9)	

References for trait groups in Appendix D. Reference numbers correspond to those in Appendix D

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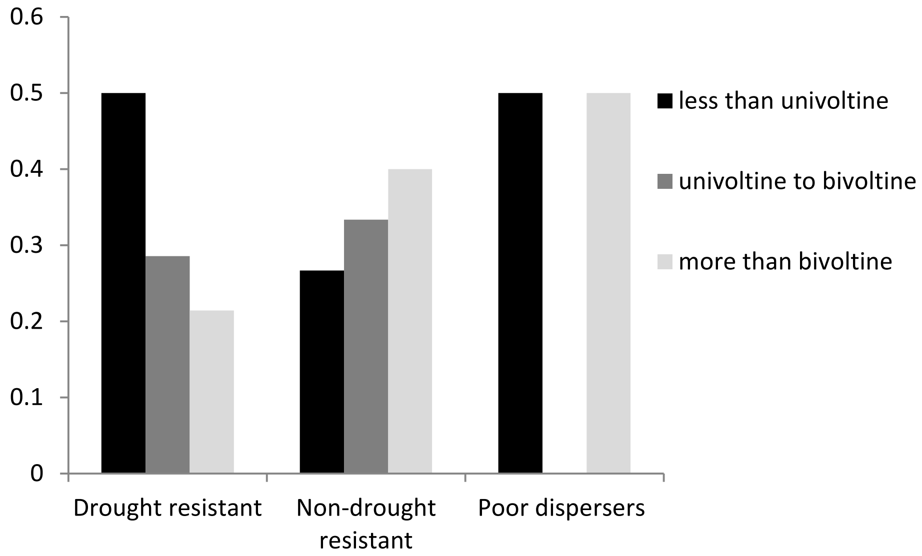
15. Watts, C.H.S. (1978): A revision of the Australian Dytiscidae. Aust. J. Zool. Suppl. Ser. 57: 1-166

Appendix E: Number of generations per year (in different classes), shown as a proportion, for each trait group examined.



Appendix F: Taxa occurring in >10% of samples and trait groups modelled in GLMMs.

Taxa
Chironomidae
Oligochaeta
Simuliidae
Acarina
Caenidae
Leptophlebiidae
Baetidae
Elmidae
Hydropsychidae
Gripopterygidae
Conoesucidae
Hydroptilidae
Psephenidae
Glossosomatidae
Coloburiscidae
Empididae
Leptoceridae
Philopotamidae
Tipulidae
Ecnomidae
Ancylidae
Hydrobiosidae
Scirtidae
Gomphidae

Appendix G: Predictor fixed and random effects correlations (Spearman r) for GLMM models for frequently occurring taxa and trait groups. Note that not all variables listed here were included in final models (see methods for details).

	CV (1month)	CV (6 months)	Flow (6 months)	Flow (3 months)	Flow (1 month)	Flow (1 year)	CV (3 months)	CV (year)	GW index	Sample	Year
CV (1 month)	1.00	0.33	-0.30	-0.27	-0.22	-0.33	0.53	0.20	-0.14	-0.10	0.20
CV (6 months)	0.33	1.00	-0.03	-0.06	-0.13	-0.17	0.70	0.66	-0.14	0.12	0.23
Flow (6 months)	-0.30	-0.03	1.00	0.89	0.84	0.90	-0.39	0.00	0.28	-0.14	-0.02
Flow (3 months)	-0.27	-0.06	0.89	1.00	0.96	0.75	-0.25	-0.10	0.30	-0.12	-0.02
Flow (1 month)	-0.22	-0.13	0.84	0.96	1.00	0.72	-0.29	-0.21	0.30	-0.16	-0.02
Flow (1 year)	-0.33	-0.17	0.90	0.75	0.72	1.00	-0.49	-0.03	0.25	-0.18	-0.10
CV (3 months)	0.53	0.70	-0.39	-0.25	-0.29	-0.49	1.00	0.43	-0.18	0.10	0.22
CV (year)	0.20	0.66	0.00	-0.10	-0.21	-0.03	0.43	1.00	-0.12	0.19	0.16
GW index	-0.14	-0.14	0.28	0.30	0.30	0.25	-0.18	-0.12	1.00	-0.11	0.09
Sample	-0.10	0.12	-0.14	-0.12	-0.16	-0.18	0.10	0.19	-0.11	1.00	0.06
Year	0.20	0.23	-0.02	-0.02	-0.02	-0.10	0.22	0.16	0.09	0.06	1.00