Article

A long-term study of the factors that influence compositional stability of stream invertebrates

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Abstract

Long-term studies have seldom considered the compositional stability (i.e., invariability of community composition) of stream invertebrate communities. Compositional stability could potentially be related to variations in species richness, habitat complexity, or hydrological and physicochemical conditions. Invertebrate species data were obtained for 21 sites that had been sampled over 16 to 20 years in Victoria, southern Australia. Stability of community composition at a site was measured with the mean Bray-Curtis coefficient, which was calculated for all comparisons between samples taken over the sampling period using only presence/absence data. Three datasets were compiled: one containing all species, one containing only insects, and one with family-level data. Multiple regressions demonstrated that stability at a site was related directly to species richness and habitat complexity and inversely to daily discharge; stability was not related to physicochemical conditions. The first 2 factors accounted for 45–49% of the variance while flow accounted for 9–16% but was not significant at the family level. The positive relation between stability and species richness may be due to higher variability in colonization at species-poor sites and thus lower compositional stability, while increased habitat complexity enhances stability by providing more refuges. Increased flow may result in more invertebrate drift and movement and thus lower stability, but the relationship was weak and provided little support to the idea that hydrology is an important ecological characteristic for invertebrates of southern Australian rivers.

Key words: community stability, freshwater invertebrates, predictor variables, southern Australian rivers

Introduction

Long-term studies of stream invertebrate communities are usually concerned with the degree of change in the composition of these communities through time. Such studies have related change in composition to yearly variations in climatic indices, development of drought, effects of catchment disturbance as measured by vegetation clearing or urbanisation, or interannual changes in flow or water quality (Bradley and Ormerod 2001, Scarsbrook 2002, Chessman 2009, Thomson et al. 2012, Vaughan and Ormerod 2012). While knowing how stream communities vary in the long term is clearly informative, the stability of species composition is a neglected but equally important feature. Here we are not equating stability with resistance to or recovery from disturbance,

but merely to the invariability of community composition. Thus, although a series of sites may vary in composition through time, do all sites change to the same extent, or are some sites more stable and better able to maintain their species composition? Furthermore, are there any factors or predictors related to stability?

A practical way to measure stability is to calculate the mean similarity of community composition at a site over a series of samples; a site with high mean similarity would be considered to have a higher stability than one with a lower level of similarity. Such an index of stability, which can be termed compositional stability, requires that a coefficient of community similarity is determined for all possible comparisons through time among samples taken at a site. In several previous studies (e.g., Scarsbrook 2002), only comparisons between consecutive samples

were considered. These comparisons are better termed indices of persistence because they are mostly concerned with examining trends from year to year, but they do not necessarily give a reliable measure of temporal stability at a site because short-term changes are emphasised and longer-term changes are ignored.

Recently, Mykra et al. (2011) measured similarity of stream invertebrate communities at 32 sites in Finland over 4 years. Mean similarity or compositional stability was calculated from comparisons taken over every pair of years, thus accounting for both long- and short-term variation. The aim of their study was to determine the extent to which compositional stability was related to species richness, habitat complexity, stream hydrology, and various physical and chemical features. It was the first study to examine these relationships for stream invertebrates.

High species richness has long been thought to promote community stability, as shown by Elton (1958) and other pioneering ecologists; however, most studies have been concerned with stability in numbers, biomass, or productivity (review by McCann 2000) rather than stability in species composition, and none has dealt with stream communities. McCann concluded that high species richness can lead to stability but suggested that richness or diversity is not the underlying agent. Instead, stability within a community relies on the presence of species with differential ecological responses. High species richness in aquatic invertebrate communities also discourages invasive species (Shurin 2000) and promotes more complex and robust food webs (Thompson et al. 2012), both of which would increase stability. In addition, stream invertebrate communities have been shown to be more stable in spatially heterogeneous habitats (Brown 2003).

Increasing habitat complexity is thought to promote stability in streams by providing refuges against the effects of floods, a common form of physical disturbance (Hildrew and Giller 1994). In dry regions, drought may be an equally important disturbance (Lake 2000); hence, hydrological variability may also influence stability. Natural spatial variability in water quality has long been known to influence species composition of stream invertebrates (e.g., community composition varies markedly with conductivity in Victorian streams; Marchant et al. 1999), and this influence may extend to community stability if variability becomes extreme.

Stability of invertebrate communities in rivers in southeastern Australia has been ignored, yet lotic habitats in this region are generally considered to be subject to much ecological variability, driven largely by the high variability of flows (Puckridge et al. 1998, Boulton and Brock 1999, Kennard et al. 2010). Broad-scale analyses of spatial changes in composition of invertebrate communities in Victoria and New South Wales (NSW) have demonstrated that geographic and downstream gradients are the most obvious (Marchant et al. 1999, Turak et al. 2011), while factors such as mean discharge and coefficient of variation in discharge seem to have less influence.

Temporal changes in stream invertebrate communities based on long-term data from this region have also been examined (Metzeling et al. 2002, Chessman 2009, Thomson et al. 2012). Some of these studies have shown that low flows due to drought can influence community composition. In addition, the consequences of long-term climate change for southeastern Australian rivers have been considered (Turak et al. 2011), but projected changes in rainfall and discharge were so uncertain that few firm conclusions could be reached about potential effects on invertebrate communities.

Our aim was to analyse invertebrate compositional stability of a series of sites across the state of Victoria, approximately 800 km east to west, based on samples taken over 16 to 20 years and identified to the species level. At the least, from 16 to 40 generations of aquatic insects (which make up >90% of the invertebrate species at sites in Victoria; Marchant et al. 2006) will have taken place over this period because many of the insect species in this region have univoltine or bivoltine, if not multivoltine, life cycles (Marchant 1986, Dean and Cartwright 1987). If compositional stability calculated over this number of generations does not show patterns, then it would seem unlikely that meaningful patterns exist. The Finnish study encompassed many fewer generations, probably as few as 4 if the majority of species were univoltine (as claimed by Mykra et al. 2011), and thus spanned a more limited temporal scale.

We expected that compositional stability of invertebrate communities in Victorian rivers would be related to several factors. Hydrological variables were obvious candidates because variations in discharge have long been held as an important ecological characteristic of Australian rivers (Boulton and Brock 1999, Warfe et al. 2013). Variable discharge is thought to lead to large changes in species composition and thus a low level of compositional stability. In addition, species richness and habitat complexity were likely predictors of compositional stability, as suggested by Mykra et al. (2011), because increases in both are thought to increase stability in other ecosystems.

Finally, stability of physicochemical conditions may promote compositional stability of an aquatic fauna. These factors typically vary widely over a landscape and are potentially likely to be influential when the invertebrate data are collected over a similarly large region, such as Victoria. Species-level data were used in most analyses, but family-level data were also employed. Family composition will vary to a lesser extent than species composition, resulting in higher ambient values for mean similarity. If the same trends are evident at different levels

of community similarity, the predictor variables can be considered consistent.

Methods

Long-term biological data

Invertebrate species records were obtained from the Environment Protection Authority of Victoria (EPA Vic) for 21 sites that were sampled across Victoria from the early 1990s to 2011 (EPA Vic long-term dataset). The majority of sites (17 of 21) were sampled over 16 to 20 years, and the remaining sites over 14 (or in one case 13) years. Not all sites were sampled in each year of this period; however, at all sites samples were taken either in spring, or autumn, or in both seasons in each year that sampling occurred; no site was sampled solely in a single season throughout the study period. To determine whether season had an effect on conclusions, analyses were repeated with data subdivided into spring and autumn samples (see Results). The number of samples (or visits) per site ranged from 11 to 32 (mean 21.4). On each visit, sampling consisted of a collection over a distance of 10 m in the main channel (usually a riffle) with a kick net (250 μm mesh), followed by at least 30 minutes picking of live specimens and preservation in 70% ethanol (for further sampling details see EPA Vic 2001).

The sites were spread across 12 of the 29 Victorian river basins and were up to 100 km apart in an attempt to represent much of the known variation in stream invertebrate communities. Few sites could be considered as beyond the reach of human disturbance. Although no sites were directly downstream of point sources of pollution or dams, all sites were exposed to catchments with a variety of land uses and subject to different degrees of clearing of native vegetation. Despite the influence these factors might have on species composition, no site was excluded because we wished to retain as wide a range of values of species richness as possible. Changes in species composition across Victorian rivers correlate most strongly with geographic and downstream gradients (Marchant et al. 1999); there is no *a priori* reason why either of these gradients should be related to compositional stability.

Samples were identified to the species level; however, immature or small specimens could usually only be identified to the family or genus level. These taxa were removed so that only species records remained in the dataset. Species composition was dominated by aquatic insects (93% of species). Analyses were carried out on the full dataset and on a subset consisting solely of the insects. It was worthwhile to determine whether the trends seen with all species were repeated with this subset because

Table 1. Mean and range of environmental variables, habitat complexity, and total species and family richness.

	mean	max	min
altitude (m)	533	1620	20
conductivity (μS cm^{-1})	646	4850	7
turbidity (NTU)	7.9	30.3	1.2
particle size (phi)	−1.2	6.3	−7.1
flow (ML d^{-1})	194	291	112
CV of daily flow	4.1	8.7	2.0
habitat complexity	102	130	70
species richness (all species)	134	198	57
species richness (insect species)	124	189	45
family richness	44	60	27

aquatic insects were the most reliably identified taxa over the sampling period. A quality control system ensured the accuracy and consistency of species identifications (EPA Vic 2001). Species richness at a site (Table 1) was considered as the total number of invertebrate species or insect species recorded over the sampling period.

Stability of community composition was measured with the Bray-Curtis (BC) coefficient (a widely used measure of community similarity; Clarke and Warwick 2001), which was calculated for all comparisons between samples taken at a site over the sampling period. Only presence/absence data were used for these calculations. The mean of these BC scores was considered to be the best measure of overall stability, with higher mean values indicating a more stable community. A site with 21 samples (the mean number) provided 210 comparisons. These large sample sizes resulted in standard errors 1–4% of the mean BC value at 19 of the 21 sites; 2 sites had standard errors of 5%. At all sites, probability plots showed that BC values were normally distributed, and there was no correlation between mean BC values and their standard errors.

Family-level data were also extracted from the EPA Vic long-term dataset. As before, only presence/absence data were compiled, and the mean BC coefficient was calculated over all comparisons at a site using the complete list of family taxa.

Environmental data

Physicochemical variables were measured at each site by EPA Vic, but not on all sampling occasions. Thus, these measurements spanned somewhat shorter periods than the macroinvertebrate samples (e.g., 12–15 years rather than 16–20 years). Three variables were extracted from the data accumulated by EPA Vic: conductivity (μS cm^{-1}),

turbidity (NTU), and mean particle size of the substratum (mean phi; Table 1). These variables reflect much of the environmental variation among streams in Victoria (Marchant et al. 1999). Conductivity and turbidity were transformed to logs so that the data more closely approximated a normal distribution. The 3 variables were then standardised (i.e., subtract mean, divide by standard deviation) before Euclidean distances were calculated for all comparisons between samples at a single site and a mean distance calculated. This mean was thus a composite measure of the degree to which these variables changed through time at a site; the higher the mean value the greater the degree of change.

Mean daily discharge and coefficient of variation (CV) of daily discharge (Table 1) were derived for each site for the period 1990–2009 from statistical models developed by Bond et al. (2011) for Victorian rivers. Some uncertainty surrounds hydrological indices determined for individual sites from such hydrological models, but these values have proved to be useful predictors in other analyses of long-term invertebrate data from Victoria (Thomson et al. 2012) and were used in a similar spirit in this analysis.

A mean habitat score was also available for each site. This score was based on 10 or 11 physical characteristics of the river channel and the riparian zone, which were visually assessed at each site (EPA Vic 2001). Mean values were calculated from assessments made on many, but not all, visits to a site. Mean habitat score was positively correlated (r = 0.63, p = 0.025) with altitude of a site and negatively correlated with mean values over the sampling period for log conductivity, log turbidity, and mean particle size (Table 1; r = −0.67 to −0.71, p < 0.007). Thus, the habitat score does not represent environmental change through time at a site as does the Euclidean distance considered above, but rather is an overall measure of the integrity and complexity of the physical habitat at a site, with higher values indicating greater complexity and less disturbance. Hereafter, this mean score is termed habitat complexity.

Statistical analysis

Before embarking on detailed analyses, the effect of varying sampling effort (i.e., the different number of sampling occasions at different sites) was assessed. There was a linear correlation between species richness at a site and number of samples (r² = 0.70–0.72, p < 0.001) for the full dataset and the aquatic insect subset (Fig. 1), and between mean BC score and number of samples (r² = 0.22–0.28, p < 0.03; Fig. 1). As a result, adjusted species richness or adjusted mean BC scores (hereafter adjusted BC scores) were calculated by adding residuals from the linear regressions of mean BC or species richness against number of samples to the overall means of these 2 variables. The adjusted scores thus had means equal to the mean species richness or mean BC score across all sites rather than means of zero, which would have occurred if residuals alone had been used.

Linear regression was used to determine which potential predictor variables were related to community stability as measured by adjusted BC scores. Adjusted species richness, habitat complexity, mean daily flow, mean CV of daily flow, and mean Euclidean distance for the physicochemical factors at each site were included in multiple regressions against adjusted BC. Potential predictor variables were weakly correlated with each other (r < 0.3–0.4, none significant), except for mean daily flow and CV of daily flow, which were strongly inversely correlated (r = −0.75, p <0.001) and were thus not used together in an individual regression. Tolerance values in multiple regressions always confirmed an absence of collinearity among predictor variables. Hierarchical partitioning (Quinn and Keough 2002) was used to separate the independent and joint contributions to explained variance from each variable in the multiple regressions.

The multiple regressions were repeated using family-level invertebrate data (Table 1) to determine whether the predictor variables at the species level remained evident at a lower level of taxonomic discrimination, and thus higher mean BC values. In the same manner as for the species data, the BC scores and family richness values were adjusted for differences in sampling effort between the sites.
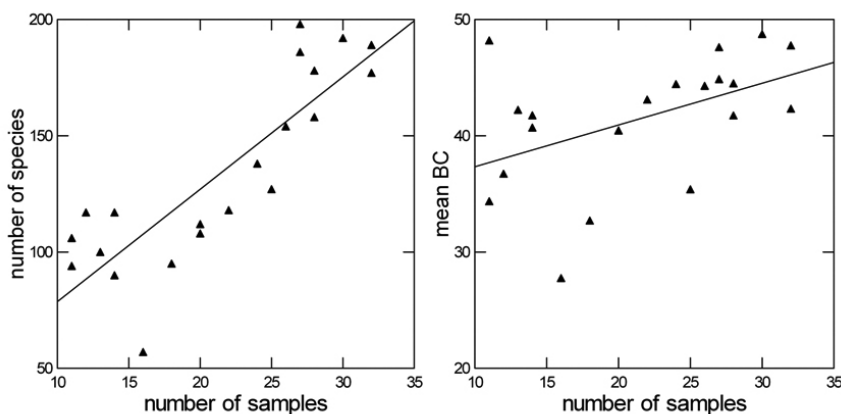

Fig. 1. Total number of species and mean BC score plotted against number of samples at each site for the full species dataset. Lines indicate significant trends.

Results

Initially, multiple regressions were run with 4 independent variables: adjusted species richness, habitat complexity, mean daily flow or CV of daily flow, and Euclidean distance. Euclidean distance was not related to adjusted BC for any of the 3 datasets (all species, insects, or family; $p = 0.4–1.0$). The CV of daily flows was weakly related or unrelated to adjusted BC ($p = 0.06–0.5$). Therefore, Euclidian distance and CV of daily flows were both excluded from further consideration. Single interaction terms were also tested (e.g., flow × habitat complexity, flow × adjusted species richness, and habitat complexity × adjusted species richness), but none of these was significant and therefore were also excluded. Thus multiple regressions were re-run with adjusted species richness, habitat complexity, and mean daily flow as predictors.

The regression model for all species was significant ($F_{3,17} = 9.1$, $p = 0.001$) and all predictors were significant (Table 2). Partial regression plots (Fig. 2) for each of the predictors indicated that adjusted BC increased with species richness and habitat complexity but decreased with flow. Adjusted species richness made the greatest contribution (28%) to the explained variance, while habitat complexity and flow each contributed about half as much (Table 2).

These 3 predictors were also significant for the insect subset ($F_{3,17} = 7.7$, $p = 0.002$) with much the same trends as before (Table 2). Adjusted species richness was dominant (37% of explained variance) and was positively related to adjusted BC, while habitat complexity (positively related) and flow (negatively related) accounted for much less of the explained variance. In both regressions, joint contributions to explained variance by the predictors were negligible. The predictors were thus acting essentially independently.

When family-level data were used in the multiple regressions, adjusted BCs were positively related to habitat complexity and family richness but were not related to flow ($F_{3,17} = 4.8$, $p = 0.01$; Table 2). At this lower level of taxonomic discrimination, family richness and habitat complexity each accounted for just >20% of explained variance and each acted independently.

Analyses were repeated with the all-species dataset subdivided into spring and autumn to test the possibility that seasonal differences influenced which predictors were significant. In spring, stability was related to species richness and habitat complexity but not flow; in autumn, stability was related to species richness and flow but not to habitat complexity. Despite these differences, the regression coefficients for each variable in both seasons were similar to those from the nonseasonal regression. In

autumn, 2 sites had so few samples (<3) that these sites could not be used in the analysis. In addition, nearly all sites had <15 samples in each season, and thus many fewer possible comparisons were available than with the nonseasonal dataset. For these reasons, analysis of single season data was not pursued.
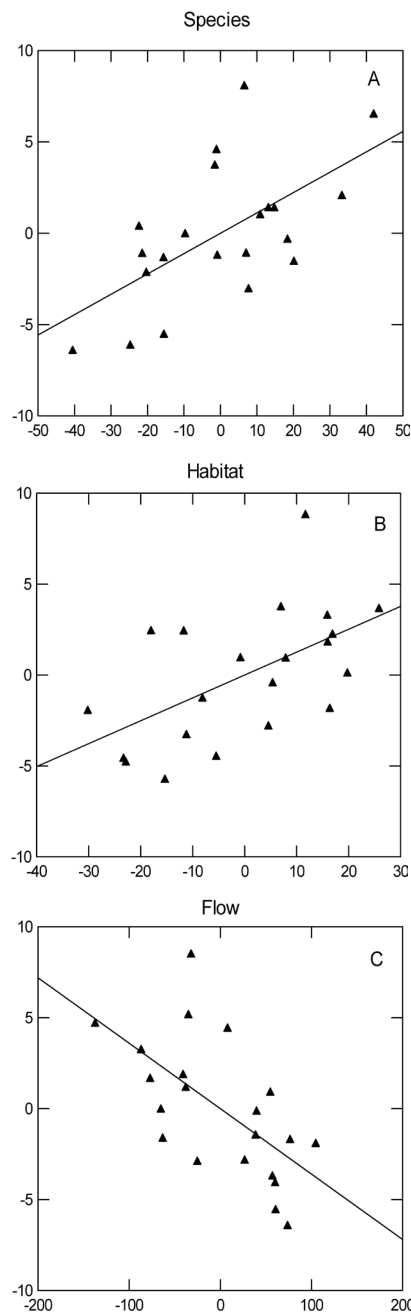

Fig. 2. Partial regression plots from the linear model (for all species) relating adjusted BC score to (a) adjusted species richness, (b) habitat complexity, (c) and daily flow. These plots show residuals, which represent the relationships between adjusted BC (the y-axis) and each of the 3 predictors when the other 2 predictors are held constant. Lines indicate significant trends.

Table 2. The regression coefficients for the 3 predictor variables and their significance (p) in the multiple regressions for: all species, insect species, and families. The independent contributions (as r^2) of each predictor were determined by hierarchical partitioning.

	taxon richness	**habitat complexity**	**daily flow**	**total r^2**
all species				
coefficient	0.111	0.126	−0.036	
p	0.006	0.01	0.005	
r^2	0.28	0.17	0.16	0.61
insect species				
coefficient	0.150	0.107	−0.033	
p	0.002	0.07	0.03	
r^2	0.37	0.12	0.09	0.58
families				
coefficient	0.654	0.192	0.002	
p	0.004	0.03	0.93	
r^2	0.21	0.24	0.02	0.47

Discussion

Temporal variation in compositional stability was directly related to species richness and to habitat complexity and inversely related to flow for both species level datasets. At the family level, family richness and habitat complexity remained positively related to stability, but flow ceased to have any influence. Taxon richness and habitat complexity displayed similar positive trends at different mean levels of community similarity (41.4 species vs. 64.5 family), indicating that these 2 variables were consistent predictors of compositional stability. The credibility of these results is enhanced by the fact that tens of generations of aquatic insects will have grown and emerged during the 16–20 years of this study, giving ample scope for BC scores to vary.

Taxon richness and habitat complexity accounted for about 45–49% of the variance in stability in all datasets, but it was only with the species-level data that species richness was dominant. This may reflect the comparative lack of ecological and environmental sensitivity of family-level data. The total amount of variance explained in all datasets (50–60%) shows that together the 3 variables were strong predictors of stability. This contrasted markedly with the obvious lack of significance for temporal variation in physicochemical factors (as measured by Euclidean distance). The conductivity component of this measure of temporal variation typically increased from spring to autumn in Victoria, while turbidity varied with discharge and more rapidly than conductivity. Mean particle size generally varied little through time but could change for varying periods after flooding. It is possible that the water quality samples missed episodes of maximum turbidity, during which community composition may have altered; however, the mean BC score at a site is unlikely to respond to such short-term changes in community composition.

Several pioneer ecologists (e.g., Elton 1958) proposed that species-rich communities should be more stable than species-poor ones, but this idea had not been examined for stream invertebrate communities until the study by Mykra et al. (2011) in Finland. They were able to demonstrate that stability was related to species richness and habitat complexity, as measured by the extent of macrophyte cover. Once variations in abundance among the sites had been eliminated using a resampling technique that calculated species richness for a fixed number of individuals, however, species richness was no longer influential, but habitat complexity remained a significant predictor ($r^2 = 0.37$). They concluded that the effect of species richness was a sampling artefact. Their BC scores were calculated from untransformed species abundances and would have been dominated by variation in those species with high abundances (Clarke and Warwick 2001). Unsurprisingly, they concluded that compositional stability at their sites was related to the presence of a few dominant species. In contrast, our BC scores were based solely on presence/absence data and gave prominence to a much greater fraction of species at a site. The measures of stability in the 2 studies were thus based on different underlying data. Our analysis, by giving prominence to a larger proportion of species, may have provided a greater scope for demonstrating relationships with the various predictor variables than did the Finnish study. Whether this is true or not, our study emphasised variation in species occurrence with time, whereas the Mykra et al.

(2011) study emphasised differences in species abundances. Both these approaches seem legitimate ways of measuring compositional stability.

Shurin (2007) investigated the relationship between species richness and stability with simple models of the temporal dynamics of species. He found that temporal variability in species composition was related to feedback between colonization and species richness. Experimental studies on the recolonization of stream benthos after disturbance (Marchant et al. 1991) have demonstrated that colonization rates of stream invertebrates (expressed as numbers of species or individuals returning per unit area per day relative to ambient densities of species or individuals) were most variable at sites with low species richness. Higher variability in relative colonization rates at species poor sites would lead to lower compositional stability and thus a positive correlation between stability and species richness. The patch dynamics model of community structure in running waters (Allan 1995) lends credibility to this mechanism by emphasising the continual recolonization of disturbed patches of habitat. In addition, if increases in habitat complexity provide more refuges for species (Hildrew and Giller 1994, Brown 2003), then it is possible to understand how both variables may promote stability of stream invertebrate communities.

Stream invertebrates continually move over the river bed at about the same spatial scale as sampling takes place (e.g., 1–10 m d^{-1}; Elliott 2002, Humphries and Ruxton 2003). Thus, small-scale changes in distribution of species between sampling events are probably common. By sampling over many years and calculating stability as a mean BC score of all possible comparisons over those years, however, both long- and short-term variations in community structure, including these small-scale changes, are accounted for. Also the number of possible comparisons at a site was large (average 210 for our sites) resulting in low inherent variability (or standard error) for each mean BC score; therefore, there is little scope for the effects of different seasonal sampling frequencies among sites to influence the results. The regressions based on single season data had trends similar to those shown by the overall regression, emphasising the advantage of obtaining long-term datasets before analysing the influence of various potential predictors on compositional stability. Mykra et al. (2011) sampled over 4 years, which provided 6 comparisons at each site from which to calculate the mean BC score. Thus, standard errors as a percentage of their mean BC scores were probably higher than ours, and consequently assessment of predictors was somewhat more uncertain.

Mykra et al. (2011) recorded a mean of 33 invertebrate species per site (range 22–48 species), whereas the Victoria sites had a mean of 134 species per site (Table 1). This 4-fold increase in number of species suggests that predictors of compositional stability may also vary according to the prevailing diversity of a region. In particular, it suggests that a greater number of species, such as in Victoria, allows a more sensitive analysis of the factors that can potentially influence compositional stability. When species were amalgamated into families, diversity and habitat complexity were still evident as predictors, even though the mean number of families (44; Table 1) was only slightly greater than the mean number of species encountered by Mykra et al. (2011). Differences between the 2 studies about which predictors were influential may reflect that families contributed more equally to the calculation of our mean BC scores than did species in the Mykra et al. study.

The weak correlation or lack of correlation of CV of daily flow with stability provided no evidence for the idea that variable discharge results in large changes to invertebrate species composition. Although high hydrological variability may be an important ecological characteristic of rivers in southeastern Australia (Boulton and Brock 1999) and in tropical northern Australia (Warfe et al. 2013), it does not seem to affect stability of species composition. Stability at the species level did decrease as flow increased, however, suggesting that sites with high mean flows had difficulty retaining a stable community, perhaps because drift and movement of invertebrates in general was higher; yet, the relationship accounted for only a relatively small percent of explained variance (Table 2). In addition, its lack of influence at the family level, while taxon richness and habitat complexity were still clearly influential, suggests it has a more minor role as a predictor of stability. Note that the values for flow used in the regressions were estimates from hydrological models, and that actual measurements of discharge for each site might have yielded a somewhat different result.

Many of the data used in this analysis were gathered during a 13-year drought in Victoria (Thomson et al. 2012), and it is plausible that different or additional predictors of compositional stability may emerge from analysis of samples collected during wetter periods. Chessman (2009) and Thomson et al. (2012) demonstrated for NSW and Victoria, respectively, that this long drought, which was evident in both states, resulted in noticeable changes to the stream invertebrate fauna with an increase in the occurrence of families tolerant of high temperatures, low flow, and poor water quality. These findings reflect average conditions across many sites but are not incompatible with the idea that certain sites may have had a more stable composition than others during the drought, as this study has shown.

Acknowledgements

References

Allan JD. 1995. Stream ecology: structure and function of running waters. London (UK): Chapman and Hall.

Bond N, Thomson JR, Reich P, Stein J. 2011. Using species distribution models to infer climate change-induced range shifts of freshwater fish in southeastern Australia. Mar Freshw Res. 62:1043–1061.

Boulton AJ, Brock MA. 1999. Australian freshwater ecology: processes and management. Glen Osmond (South Australia): Gleneagles Publishing.

Bradley DC, Ormerod SJ. 2001. Community persistence among stream invertebrates tracks the North Atlantic Oscillation. J Anim Ecol. 70:987–996.

Brown BL. 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. Ecol Lett. 6:316–325.

Chessman BC. 2009. Climatic changes and the 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. Glob Change Biol. 15:2791–2802.

Clarke KR, Warwick RM. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth (UK): PRIMER-E Ltd.

Dean JC, Cartwright DI. 1987. Trichoptera of a Victorian forest stream: species composition and life histories. Aust J Mar Freshw Res. 38:845–860.

Elliott JM. 2002. Time spent in the drift by downstream-dispersing invertebrates in a Lake District stream. Freshw Biol. 47:97–106.

Elton CS. 1958. The ecology of invasions by animals and plants. London (UK): Chapman and Hall.

[EPA Vic] Environment Protection Authority, Victoria. 2001. The Australia-wide assessment of river health: final report on the National River Health Program from Victoria. Melbourne (Victoria): Environment Protection Authority.

Hildrew AG, Giller PS. 1994. Patchiness, species interactions and disturbance in the stream benthos. In: Giller PS, Hildrew AG, Raffaelli DG, editors. Aquatic ecology: scale, pattern and process. Oxford (UK): Blackwell Scientific Publications. p. 21–62.

Humphries S, Ruxton GD. 2003. Estimation of intergenerational drift dispersal distances and mortality risk for aquatic macroinvertebrates. Limnol Oceanogr. 48:2117–2124.

Kennard MJ, Pusey BJ, Olden JD, MacKay SJ, Stein JL, Marsh N. 2010. Classification of natural flow regimes in Australia to support environmental flow management. Freshwater Biol. 55:171–193.

Lake PS. 2000. Disturbance, patchiness, and diversity in streams. J N Am Benthol Soc. 19:573–592.

Marchant R. 1986. Some quantitative aspects of the life history of aquatic insects in temperate Australian rivers. In: De Deckker P, Williams WD, editors. Limnology in Australia. Melbourne: CSIRO Publishing. p. 151–158.

Marchant R, Hirst A, Norris R, Metzeling L. 1999. Classification of macroinvertebrate communities across drainage basins in Victoria, Australia: consequences of sampling on a broad spatial scale for predictive modelling. Freshwater Biol. 41:253–268.

Marchant R, Lake PS, Doeg TJ. 1991. Longitudinal variation in recolonization rates of macroinvertebrates along an upland river in south-eastern Australia. Freshwater Biol. 25:349–356.

Marchant R, Ryan D, Metzeling L. 2006. Regional and local species diversity patterns for lotic invertebrates across multiple drainage basins in Victoria. Mar Freshw Res. 57:675–684.

McCann KS. 2000. The diversity-stability debate. Nature (Lond). 405:228–233.

Metzeling L, Robinson D, Perriss S, Marchant R. 2002. Temporal persistence of benthic invertebrate communities in south-eastern Australian streams: taxonomic resolution and implications for the use of predictive models. Mar Freshw Res. 53:1223–1234.

Mykra H, Heino J, Oksanen J, Muotka T. 2011. The stability-diversity relationship in stream macroinvertebrates: influences of sampling effects and habitat complexity. Freshwater Biol. 56:1122–1132.

Puckridge JT, Sheldon F, Walker KF, Boulton AJ. 1998. Flow variability and the ecology of large rivers. Mar Freshw Res. 49:55–72.

Quinn GP, Keough MJ. 2002. Experimental design and data analysis for biologists. Cambridge (UK): Cambridge University Press.

Scarsbrook MR. 2002. Persistence and stability of lotic invertebrate communities in New Zealand. Freshwater Biol. 47:417–431.

Shurin JB. 2000. Dispersal limitation, invasion resistance, and structure of pond zooplankton communities. Ecology. 81:3074–3086.

Shurin JB. 2007. How is diversity related to species turnover through time? Oikos. 116:957–965.

Thomson JR, Bond NR, Cunningham SC, Metzeling L, Reich P, Thompson RM, MacNally R. 2012. The influences of climatic variation and vegetation on stream biota: lessons from the Big Dry in southeastern Australia. Glob Change Biol. 18:1582–1596.

Thompson RM, Dunne JA, Woodward G. 2012. Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. Freshwater Biol. 57:1329–1341.

Turak E, Marchant R, Barmuta LA, Davis J, Choy S, Metzeling L. 2011. River conservation in a changing world: invertebrate diversity and spatial prioritisation in south-eastern coastal Australia. Mar Freshw Res. 62:300–311.

Vaughan IP, Ormerod SJ. 2012. Large-scale, long-term trends in British river macroinvertebrates. Glob Change Biol. 18:2184–2194.

Warfe DM, Pettit NE, Magierowski RH, Pusey BJ, Davies PM, Douglas MM, Bunn SE. 2013. Hydrological connectivity structures concordant plant and animal assemblages according to niche rather than dispersal processes. Freshwater Biol. 58:292–305.