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SPECIAL REVIEW

Filters and templates: stonefly (Plecoptera) richness in Ouachita Mountains streams, U.S.A.

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SUMMARY

1. We collected adult stoneflies periodically over a 1-year period at 38 sites in two headwater catchments in the Ouachita Mountains, Arkansas, U.S.A. The 43 species collected were a subset of the Ozark-Ouachita fauna and the much larger fauna of the eastern U.S.A. We estimated 78–91% species coverage in the two catchments using jackknife extrapolation of species richness from our survey.
2. Many streams, especially small ones, lacked surface water for months, but others, both small and large, flowed permanently.
3. Using published regional presence–absence and coarse ecological data in a discriminant function analysis (DFA), we identified stream size (negative) and regional frequency of occurrence (positive) as predictors of presence in these headwater catchments. For the combined catchments, the extrapolated richness (51 spp.) was similar to an estimate (48 spp.) based on predicted absences from DFA and the Ouachita provincial total of known stonefly species (57 spp.).
4. Local species richness (1–27 spp. per site) was correlated strongly with stream size (catchment area) but was independent of stream drying. Generic richness was correlated negatively with stream drying and positively, but less strongly, with stream size.
5. Regionally endemic stoneflies dominated in drying streams, and widely distributed species dominated in more permanent streams. The composition of stonefly assemblages was associated with regional factors (species pools, regional abundance, evolution of tolerant endemic species, regional climate) and local factors (drying, stream size).

Keywords: diversity, local effects, regional effects, stream drying, stream size

Introduction

The interplay and relative strengths of regional and local effects in determining the diversity and composition of ecological assemblages remain unclear (Rosenzweig, 1995). Two concepts are commonly invoked: a 'local-to-regional' control over diversity and a 'regional-to-local' control over diversity. Local conditions and biological interactions are often emphasised as determinants of diversity in small areas and ultimately, as strong influences on regional diversity (Huston, 1999), i.e. local-to-regional control. In contrast, the regional-to-local view proposes that evolutionary processes operating over large areas and long durations, the effects of historical contingency (Ricklefs, 1987, 2004; Ricklefs & Schluter, 1993), or climate and other factors expressed over large areas are the drivers of observed diversity gradients (Whittaker, Willis & Field, 2001; Currie *et al.*, 2004).

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The filter concept is closely related to the notion of regional control of local species richness and composition. Conceptually, processes occurring at successive scales from global to local sequentially 'winnow' community membership and diversity to produce the observed local faunal assemblage (Smith & Powell, 1971; Tonn *et al*., 1990; Poff, 1997; Lawton, 2000). Ultimately, however, the filtered assemblage must match local conditions although the fit need not be precise (Janzen, 1985). We use the term template (*sensu* templet of Southwood, 1977; Poff & Ward, 1990) for the set of characteristics (e.g. climate, water chemistry, physical structure) important at the scale at which diversity and composition are actually measured. Some would consider this template as no more than a final filter, but this logic predisposes one to a view that regional processes dominate, and minimises the recognition of significant local control or the possibility of local to regional influences.

Streams and their fauna are good subjects for investigation of diversity patterns. Stream communities on different continents share taxa and functional traits (Hynes, 1970). Many animal taxa, including our focal group Plecoptera, are virtually restricted to streams. Stream networks are hierarchically arranged, constrained by geomorphic principles, and replicated across landscapes and continents (Richards, 1982; Frissell *et al*., 1986). Recent reviews of stream insect diversity emphasise conservation issues, the many unknowns including regional-local linkages, and the potential for stream research to contribute to general concepts of biological diversity (Vinson & Hawkins, 1998; Jacobsen, 1999; Voelz & McArthur, 2000).

Stoneflies (Plecoptera) are one of the dominant insect orders in temperate streams and are an excellent probe into stream ecosystems. The seven families of stoneflies considered here occur across the Holarctic. Stonefly species occupy varied stream habitats and are functionally diverse, filling trophic roles from shredding/detrivory to carnivory (Stewart & Stark, 2002). Life cycles are typically fairly long (uni- or semivoltine) so they integrate the full annual cycle of stream conditions.

Our focal catchments contain experimental and reference sites for a large forest management project (USDA Forest Service, Ouachita Mountains Ecosystem Research Management Project). Our general goal was to develop quantitative descriptions of stonefly diversity (reported here) and composition to serve as baselines for evaluation of streams following experimental forest treatments. Our data are based on intensive collections of adult stoneflies identified to species at multiple sites within two catchments that differed in stream-flow permanence. We extended our comparisons spatially to the regional and sub-continental scales (North America north of Mexico) by synthesising existing information on plecopteran species richness from published sources. Specifically, we asked (i) how many species occurred at the local level relative to the numbers of species at the catchment and regional levels, (ii) how strongly species and generic richness was related to environmental factors and (iii) if there was evidence for convergence of species richness in physically similar environments. Finally, having observed that regionally endemic species played a strong role in species richness patterns, we conducted *a posteriori* analyses of richness and endemism.

Methods

Study sites

We collected stoneflies at 38 sites in two catchments within the Ouachita Mountains province of the Ozark-Ouachita region, Arkansas, U.S.A. (Fig. 1). The unglaciated multiple ridges of the Ouachita Mountains (U.S. Department of Agriculture, Forest Service, 1999) run east-west and consist of intensely folded rocks (Fenneman, 1938) covered by oak-pine forests. The Alum Fork catchment (Saline River drainage) included North Alum, South Alum and Bread creek subcatchments (hereafter North Alum, South Alum, Bread) and contained 22 sites, all of which lie within the Ouachita National Forest. Highest altitude in the Alum Fork catchment is 539 m, and our lowest site was at 244 m. Valley slopes are steep, stream flow is highly variable, and most stream channels are completely dry or with isolated pools by late summer (Taylor & Warren, 2001; Williams, Taylor & Warren, 2003b; Williams *et al*., 2003a). Alum Fork has average (minimum, maximum) recorded pH of 6.2 (5.2, 7.8) and conductivity of 21 μS cm^{-1} (13, 47) at 25 °C. Seasonal average (minimum, maximum) water temperatures are 8 °C (1, 12) in winter, 16 °C (7.6, 25.6) in spring, 25 °C (18, 30) in summer and 17 °C (10, 23) in autumn (calculated from U.S. Geological Survey, 2007). The Little Glazypeau Creek catchment (hereaf-

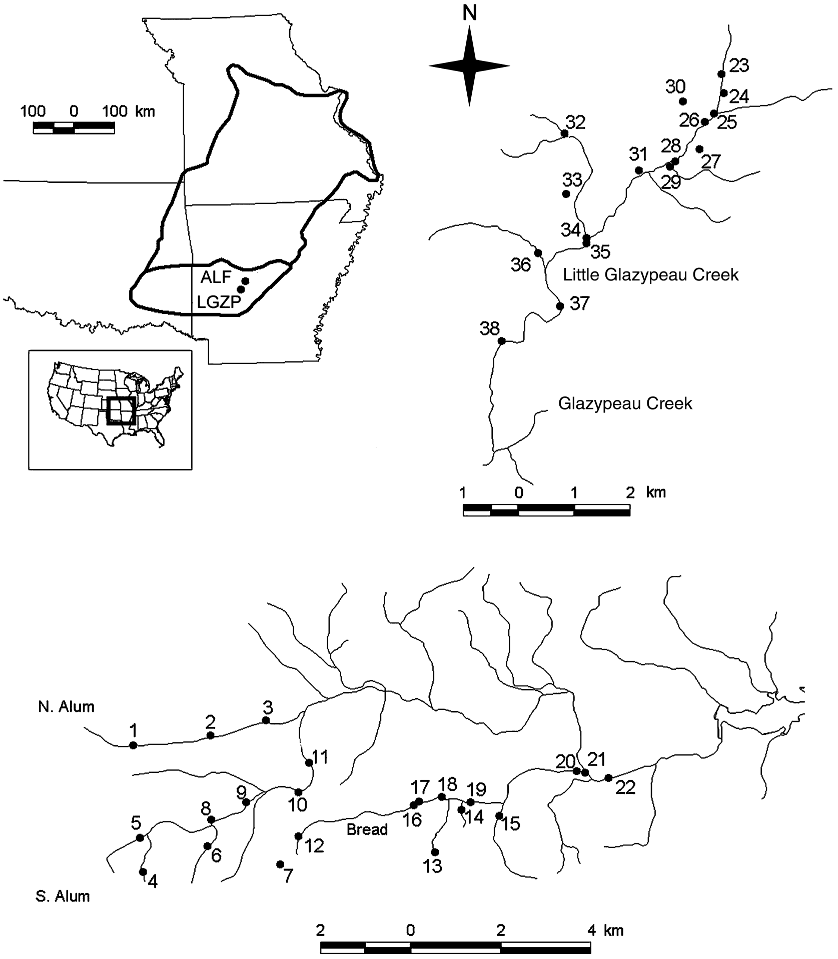

Fig. 1 Catchments and sample sites within the Ouachita province of the inclusive Ozark-Ouachita region, Arkansas, U.S.A. ALF, Alum Fork of the Saline River; LGZP, Little Glazypeau Creek (Ouachita River drainage).

ter Little Glazypeau) (16 sites) (Ouachita River drainage) drains commercial pine forest, is lower in altitude (maximum 382 m, lowest site 171 m), has less steep slopes, and is a more water retentive catchment. Some streams both large and small in Little Glazypeau are permanent. Little Glazypeau has average (minimum, maximum) recorded pH of 7.3 (6.5, 7.9), and conductivity of 59 μS cm^{-1} (0, 462) (H. Liechty, unpubl. data). Seasonal average (minimum, maximum) water temperatures are 8 °C (1, 16) in winter, 16 °C (5.4, 25) in spring, 23 °C (16, 29) in summer and 17 °C (6, 25) in autumn (J. Nettles, unpubl. data). Stream substrata in both catchments range from bedrock to gravel and sand and, except during peak flows, streams are clear. Although the two catchments are over 400 km distance by river network, they are <12 km apart by straight line distance. At *c.* 34 45′N, summers are hot and winters cool with incursions of cold continental air; snow cover seldom persists more than a few days or weeks. Annual precipitation is *c.* 115 cm but variable, and floods and droughts, both seasonal and long period, are common.

Study design

Within catchments, we chose sites using a stratified random design based on stream size (Shreve link magnitude, Gordon, McMahon & Finlayson, 1992), which allowed sampling of multiple reaches within a given stream size and allocated sites longitudinally in catchments and subcatchments (Fig. 1). We arbitrarily added site ALF-22 to extend sampling to a larger stream but, because it is unreplicated, we treated it separately in some analyses. We marked sites on 1 : 24 000 topographic maps, located them in the field, and then permanently marked 50-m stream sections at each site. We determined catchment area, altitude and stream gradient using GPS site coordinates and a GIS.

We used temporally extended sampling and several collection methods in an attempt to sample the stonefly fauna completely at every site. Identification of stonefly species in several families is impossible or difficult without adult specimens, and adult-based analyses of environmental disturbances can be more informative than those from taxonomically unresolved larvae (Tixier & Guerold, 2005). Adult stoneflies emerge in a seasonal succession throughout the year, so we collected at each site 17 times (31 July 2000–23 July 2001). We collected adults with a beating sheet, by search and aspiration from rocks and wood, and in March-October with UV light traps (BioQuip Products, Rancho Dominguez, CA, U.S.A.). Because adults of some families (i.e. Perlodidae and Perlidae) are secretive or disperse away from the stream, we supplemented adult collections by sampling larvae at every station with a kickscreen in March–April. Ernst & Stewart (1985) discuss the efficiency and selectivity of these methods. Specimens preserved in 70% ethanol were identified by ALS using keys and illustrations in Poulton & Stewart (1991). Nomenclature follows Poulton & Stewart (1991) except their *Acroneuria evoluta* Klapalek is *A. frisoni* Ross and Ricker (Stark & Brown, 1991).

Statistical analysis

We compiled a presence/absence species by site matrix and a presence/absence species by catchment and subcatchment matrix and tallied observed species and generic richness for each site, catchment and subcatchment. We used a jackknife extrapolation to estimate species richness in the two focal catchments, excluding site ALF-22, and over the entire study area (including ALF-22). Various approaches have been developed, tested and evaluated to extrapolate the total number of species from samples (e.g. Colwell & Coddington, 1994; O'Hara, 2005), but often too little is known about the true number of species present to judge the performance of estimators (O'Hara, 2005). Because the well-known regional stonefly fauna is of moderate size, sampling of the focal catchments was on an intensive spatiotemporal scale, and stoneflies inhabit systems (streams) with sharp boundaries, we could plausibly employ estimates of species richness to evaluate the completeness of our sampling. To estimate richness (and 95% confidence intervals), we used the first order jackknife and its variance (Heltshe & Forrester, 1983; Brose, Martinez & Williams, 2003), $\hat{S} = S_{\text{obs}} + (1 - 1/n)\ S_{1,}$ where $\hat{S}$ is the estimated number of species, S_{obs} the total number of species collected, n the number of collection units, and S_1 the number of singleton species, each collected in a single unit. The jackknife is a bias correction to the estimate S_{obs}; an intuitive explanation for increasing S_{obs} by S_1 is that each species rare enough to be collected just once probably had an uncollected counterpart.

We used collections as our sampling unit since all 38 sites received an equal number of visits. We captured some species several times at one site only, but these are not singletons when collections are the unit. If sites were the unit, S_1 and $\hat{S}$ would have increased slightly (data not shown).

We derived two environmental variables: catchment area and a stream drying metric. The variable AREA is $\log_{10}$ (catchment area) and serves as a surrogate for site-specific channel dimensions, discharge and longitudinal position (Leopold, Wolman & Miller, 1964; Richards, 1982; Gordon *et al.*, 1992). To describe stream drying, we measured the linear extent of visible surface water in the marked 50-m sections on each visit, converted the wetted extent to a proportion, and calculated a time-weighted annual average, $P(\text{wet})$, for each site. We assumed that stream drying was a stress to stoneflies and that longer dry periods were increasingly more stressful than shorter ones. The stream drying metric was calculated as $\text{DRY} = (1 - P(\text{wet}))^2$, which incorporates these assumptions. We note, for example, a value of 0.25 could indicate a stream with water for 50% of its length for the entire year or one totally dry for 6 months. In reality, all streams flowed continuously through winter and early spring and then dried gradually, so the stream drying metric is primarily an index of time without surface flow.

We used polynomial and linear regression to quantity the relationship between the independent variables AREA and DRY and the dependent variables site species richness or site generic richness. Because stream drying and area at sites <30 ha were strongly confounded, we eliminated from the linear regressions four sites below this threshold. For correlation, regression, and other statistical analyses, we followed Sokal & Rohlf (1981) & Zar (1984) and used SYSTAT 10.2 (SYSTAT, 2002).

We used an independent data set (Poulton & Stewart, 1991) in a backward elimination discriminant function analysis (DFA) to test for ecological differences between species present or absent in our collections. The filter concept implies selection, so that species with particular histories or ecological characteristics will be available to form local assemblages and others will enter different assemblages or become extinct. Poulton & Stewart (1991) tabulated the range of stream size (orders 1–6), scored flow permanence in streams occupied by Ozark-Ouachita stoneflies (four categories from 'dry stream bed for part of year' to 'permanent with significant spring source'), and reported occurrence of stonefly species in 126 catchment units across the region. We reconstructed range maps and counted the number of catchments occupied by each species within the Ouachita province. The resultant data set used in a DFA with cross validation contained 43 species present and 14 species absent, minimum and maximum stream order, minimum and maximum permanence and $\log_{10}$ (catchments occupied). Although the size and permanence data are coarse, we treated them as ordinal (SYSTAT, 2002).

Finally, we explored the role of endemism in characterising the observed fauna. We compared the proportion of endemic species in each catchment using chi-square analysis. We also compared the occurrence of endemic and non-endemic stoneflies between the two catchments using chi-square analysis. We defined occurrence as the sum of the number of species occurring at each site within a catchment summed across all sites.

Results

Filters and barriers

We collected 6373 adult stoneflies representing 43 species, 17 genera, and seven families (Appendix S1). The estimated stonefly fauna of North America north of Mexico (Fig. 2) is >600 species, the fauna being about evenly divided between eastern and western areas (Stewart & Stark, 2002) (Fig. 2). The Ozark-Ouachita regional fauna, sharing species and genera with the eastern area, is considerably smaller and lacks one family (Peltoperlidae); the Ouachita province has still fewer species and lacks Pteronarcyidae (Poulton & Stewart, 1991). Our collections in the two focal catchments, including the large-stream site ALF-22, yielded 75% of the entire Ouachita stonefly fauna.

The number of shared and non-shared stonefly species illustrates the species turnover among the two catchments and the single large stream site ALF-22. The Alum Fork subcatchments have similar faunas (Appendix S1) and nearly all the species, including a core set of 14, are shared with Little Glazypeau and ALF-22 (Fig. 3). Both the large stream ALF-22 and the Little Glazypeau catchment have more unshared species. Although not explicit in Appendix S1, most of the unique species in Little Glazypeau occurred at sites with permanent flow.

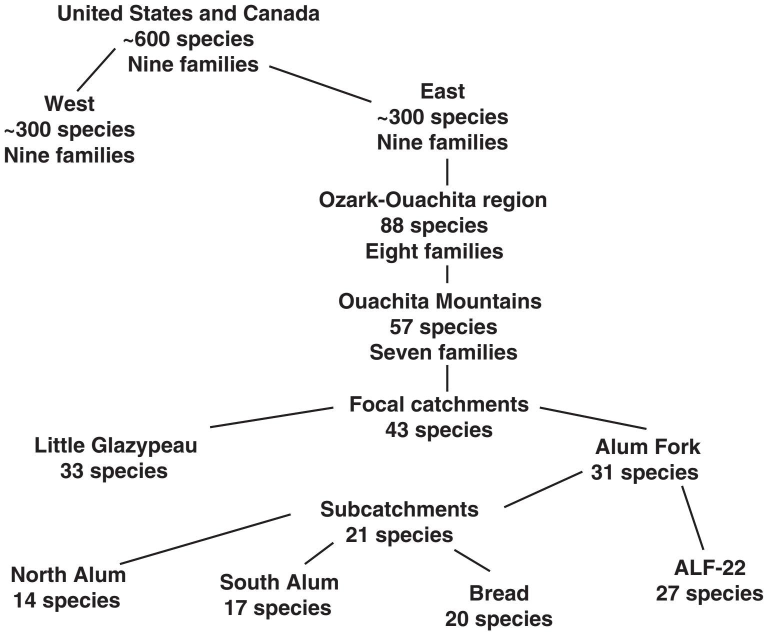

Fig. 2 Hierarchical reductions (filters) of stonefly species richness from continental to subcatchment scales.

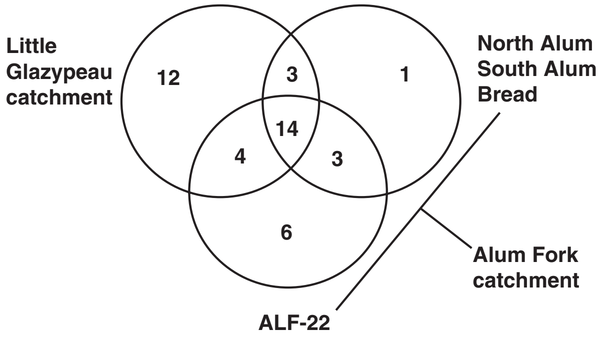

Fig. 3 Shared and unique species in two catchments (Little Glazypeau and Alum Fork), subcatchments of Alum Fork and a single large-stream site (ALF-22, also Alum Fork catchment) in the Ouachita Mountains, Arkansas, U.S.A.

Environmental factors

Flow permanence in the two catchments differed greatly, but catchment area and the stream drying index were negatively correlated ($r_s = -0.48$, $P < 0.005$) (Fig. 4). Small streams in both catchments dried severely. Although some sites in Little Glazypeau dried, all permanently flowing sites were in Little Glazypeau, and all Alum Fork sites dried. Confounding of catchment identity and drying means that no truly independent test of drying effects is possible (but see below).

Species richness

Species richness ranged from 1 to 27 species per site, which implies that additional filters or constraints limit local occupancy by members of the regional or catchment species pools. The Alum Fork headwaters (North Alum, South Alum, Bread creeks) had 21 observed species and an estimated richness (95% confidence limits) of 23 (21, 25.8) species yielding an estimated sample coverage ($S_{obs}/\hat{S}$) of 91%. In Little Glazypeau, 33 species were observed, representing 78% of an estimated species richness of 42 (36.1, 47.9). For all sites, the observed richness of 43 species was 84% of an estimated 51 (45.4, 56.6) species, which approaches but does not exceed known richness (57 species) in the Ouachita province.

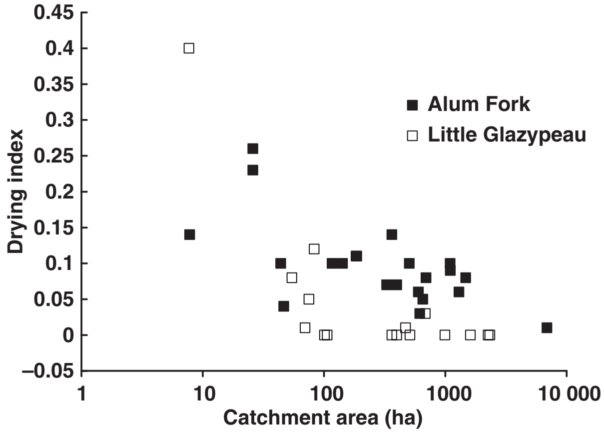

Fig. 4 Stream drying index relative to catchment area at individual sites in the Alum Fork and Little Glazypeau catchments in the Ouachita Mountains, Arkansas, U.S.A. The *x*-axis is offset for clarity.

Species richness, generic richness, stream size and stream drying

Species richness increased with stream size and distance downstream (Fig. 5) which suggests that

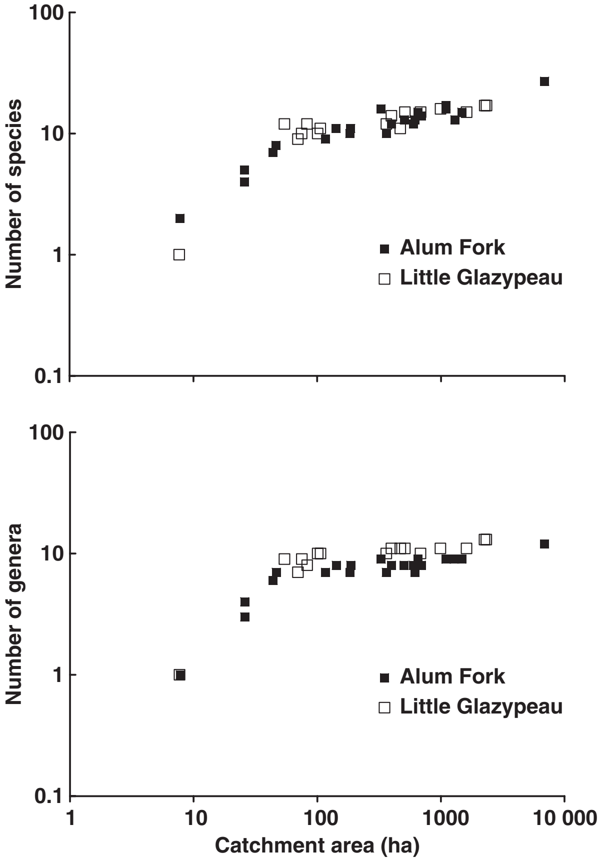

Fig. 5 Stonefly species richness (upper) and generic richness (lower) relative to catchment area at individual sites in the Alum Fork and Little Glazypeau catchments in the Ouachita Mountains, Arkansas, U.S.A. The *x*-axis is offset for clarity.

streams of the same size in the two catchments, even those with different drying regimes, have similar numbers of stonefly species. Similarly, generic richness increased with stream size, but the slope was less steep and Alum Fork sites tended toward fewer stonefly genera than similar-size sites in Little Glazypeau (Fig. 5).

Relationships between taxon richness, stream size and flow permanence were strong. Since some Little Glazypeau sites dried and Alum Fork sites differed in intensity of drying, we computed regressions as if the sites were independent. The regressions are valid descriptors of the focal streams, and we propose that the strong qualitative effects detected are true at the regional level. Variables in the polynomial regression (AREA, AREA^2 and DRY) were all significant, and the regression explained relatively high proportions of variability in both species and generic richness (Table 1). Stream size was related positively to taxon richness, and stream drying was related negatively to taxon richness. However, these strong relationships included the combined effects of stream size and severe drying of the four smallest streams (catchments <30 ha, Figs 4 & 5). Elimination of those sites from analysis linearised the relationship. Linear regressions of taxon richness against stream size and stream drying remain significant and explain much of the variance (Table 1). However, the standard partial regression coefficients reveal species richness was related strongly to stream size ($P < 0.001$) but was independent of stream drying ($P > 0.450$) (Fig. 6). Generic richness, in contrast, was related more strongly to drying than stream size although both effects were significant ($P < 0.001$).

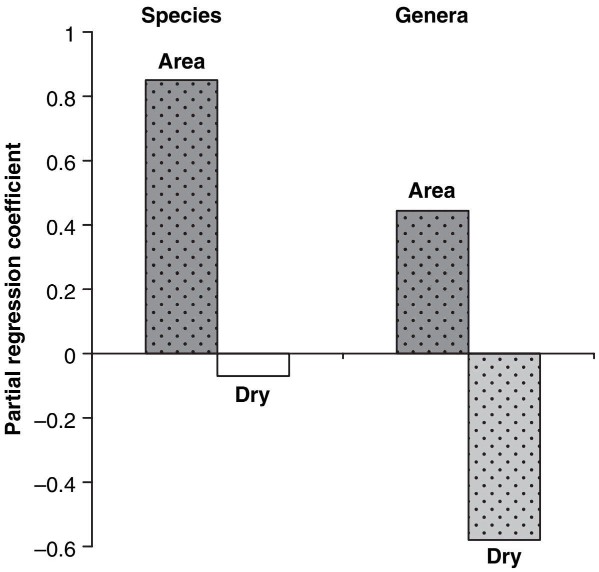

Fig. 6 Standard partial regression coefficients separating effects of catchment area (AREA) and stream drying (DRY) on species and generic richness of stoneflies in catchments in the Ouachita Mountains, Arkansas, U.S.A. Shaded bars are significant at $P < 0.001$.

Species occurrence and endemism

Stream size and the number of catchments occupied were significant discriminators of stonefly species presence. Backward stepwise DFA eliminated all variables except minimum stream order and catchments occupied. The correct classification rate was 70% with leave-one-out validation ($P < 0.004$). A local effect, stream order (standardised coefficient, −0.767), was a stronger predictor of presence than a regional variable, catchments occupied (coefficient, 0.577).

Table 1 Polynomial and linear regression results for stonefly taxon richness, log drainage area (AREA), and stream drying (DRY) among stream sites in the Ouachita Mountains, U.S.A. N was 38 and 34 stream sites for the polynomial and linear regressions, respectively

	Intercept	AREA	AREA^2	DRY	Adj R^2	Model (P<)
Log (no. species)	−0.076	0.785	−0.116	−0.860	0.89	0.001
(P<)	0.643	0.001	0.001	0.001		
Log (no. genera)	−0.170	0.844	−0.144	−1.093	0.86	0.001
(P<)	0.326	0.001	0.001	0.001		
Log (no. species)	0.654	0.178	–	−0.180	0.74	0.001
(P<)	0.001	0.001		0.451		
Log (no. species)	0.638	0.180	–	–	0.74	0.001
(P<)	0.001	0.001				
Log (no. genera)	0.803	0.068	–	−1.101	0.66	0.001
(P<)	0.001	0.001		0.001		

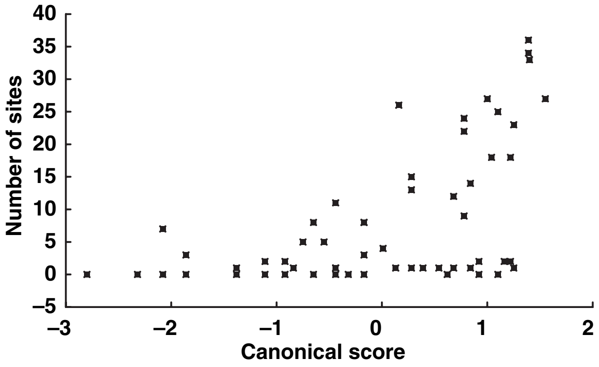

Fig. 7 Number of sites of occurrence of stonefly species in two study catchments relative to canonical scores (discriminant function analysis) for those species calculated from presence-absence data and an independent set of environmental variables from catchments in the Ouachita Mountains, U.S.A. The *x*-axis is offset for clarity.

Canonical scores from presence–absence and the ecological variables are correlated with frequency of occurrence of stonefly species observed at our sites ($r_s = 0.549$, $P < 0.001$) (Fig. 7). Species with high probabilities of presence (canonical scores) occurred at many sites, and species wrongly predicted to be absent occurred at only a few sites. However, some species had high scores but low frequencies, and we did not collect three species with high scores [in descending order, *Isoperla mohri* Frison, *Strophopteryx fasciata* (Burmeister)and *Perlinella drymo* (Newman)]. Some misclassifications are likely in any statistical procedure and, in this case, the data may be incomplete. Within the Ouachita province, these three species seem to inhabit larger streams (Stark & Stewart, 1973; B. Stark, unpubl. data) than described for the entire Ozark-Ouachita region by Poulton & Stewart (1991). The DFA also provided an estimate of species richness based on different logic than the jackknife extrapolations. The DFA correctly predicted the absence of nine species. Subtracting this estimate from the Ouachita province total (57 species) gives an estimated richness of 48 species, a value similar to the jackknife extrapolation of 51 species.

Of the 88 Ozark-Ouachita stonefly species, 25 are endemic to the region (Poulton & Stewart, 1991); 17 of these occurred in Alum Fork (12 species) and Little Glazypeau (13 species) (Appendix S1). The proportions of endemic species in the two catchments were not different ($\chi^2 = 0.21$, $P > 0.50$) but occurrences of endemic species were different ($\chi^2 = 26.88$, $P < 0.0001$, Table 2). Regionally endemic species dominated in Alum Fork, but 70% of occurrences in Little Glazypeau were of widely distributed species, a pattern consistent with differences in flow regime (Fig. 4).

Table 2 Occurrences of stonefly species for two catchments in the Ouachita Mountains, Arkansas, U.S.A. Occurrence is defined as the sum of the number of species at each site summed across all sites within a catchment

Catchment	Endemic	Non-endemic
Alum Fork	140	120
Little Glazypeau	59	140

Discussion

Partitioning diversity of stream fauna into regional and local components has produced varied results. Fishes often show strong regional and historical effects of drainage connectivity (Angermeier & Winston, 1998; Matthews & Robison, 1998; Williams *et al.*, 2003a,b), but local effects are also strong (Taylor & Warren, 2001; Taylor *et al.*, 2005). Aquatic macroinvertebrates, often with winged, dispersive adults, tend to reflect local factors (Williams *et al.*, 2003a,b; Bonada *et al.*, 2005; McCreadie, Adler & Hamada, 2005; Stendera & Johnson, 2005), but weak to dominant regional effects also are reported (Heino, Muotka & Paavola, 2003; Stendera & Johnson, 2005). Results are scale-dependent (Stendera & Johnson, 2005), and there is a fundamental conceptual problem (Huston, 1999) recognised by Heino *et al.* (2003). If, for example, severe diversity-reducing environments prevail across a region, both local and regional richness will be low but control can not be labelled regional or local.

We did not attempt a quantitative partition of our data into regional and local components but evaluated our results at different hierarchical levels from regional vs. local and filter vs. template perspectives. At large scales, the hierarchical filter concept is supported (Fig. 2). The stoneflies of the Ouachita province are <10% of the North American fauna, and biogeographic regionalisation is the dominant theme. Most stonefly species in the continental fauna are unavailable for participation in local assemblages. Although the pattern is easily described, identifying important factors and assigning directionality are more difficult. The Great Plains block colonisation by virtually all western taxa (Poulton & Stewart, 1991), and a dispersal filter of low relief and decreasing precipitation westward from the Appalachian Mountains could explain the reduced richness of Ozark-Ouachita stoneflies. Within the region, the wide Arkansas River Valley may limit dispersal between the northern Ozark uplands and the Ouachita uplands (Mayden, 1988; Poulton & Stewart, 1991). Alternatively, ecological constraints of limited area, modest topographic relief, and variable precipitation and stream discharge may limit regional diversity.

At lower hierarchical levels (Fig. 2) dispersal limitation of diversity is unlikely. Sites within Alum Fork and Little Glazypeau are connected along stream courses, and the catchments are separated by a short distance across an intervening catchment (Middle Fork Saline River). Stepping-stone routes between Little Glazypeau and Alum Fork require overland flights of only 2–3 km which are within the directly measured or inferred flight distances of some stoneflies (Briers *et al.*, 2004; Masters *et al.*, 2007). Most stoneflies are distributed widely across the region (Poulton & Stewart, 1991); 75% of the fauna occurred in the two focal catchments, and a single site (ALF-22) produced 47% of the Ouachita fauna. These high proportions of total regional richness might incorrectly suggest that local effects are minimal (see Loreau, 2000). Rather, longitudinal gradients from small to large streams have strong effects as reported for other streams and taxa (Sheldon, 1968; Malmqvist & Mäki, 1994; Malmqvist,1999; Reyjol *et al.*, 2003; Finn & Poff, 2005; Taylor *et al.*, 2005). Discriminant function analysis showed that absent (filtered) species inhabit larger streams than those we studied. At single sites species richness was both constrained (1–27 species) and highly correlated with stream size and longitudinal position (Fig. 5), giving evidence of local effects (the template) operating at scales smaller than the catchment.

We expected the absence of water to be a major stress for aquatic insects (Williams, 1996; Chaves *et al.*, 2008), which would be manifest in reduced species richness, but stream drying produced mixed responses. Drying had a strong influence on species composition at sites (A. Sheldon & M. Warren, unpubl. data) but had no effect on species richness (Fig. 6). At a higher taxonomic level, generic richness was correlated negatively with drying (Fig. 6). We interpret these mixed effects as follows. Species richness is constrained by factors correlated with stream size. Within this constraint, severity of drying determines which species occur, but the regional fauna is taxonomically and physiologically diverse enough to compensate for species excluded by drying. The negative response of generic richness suggests, however, that compensation is incomplete and assemblages of permanent and drying streams are not fully equivalent. If the evolutionary units recognised as genera are viewed as major adaptive themes and species within genera as variations on those themes, reduction of generic richness may imply loss of functional attributes. However, resistance to drying itself may be the key trait possessed by some genera, and no functional losses may be entailed. The linkages among phylogeny, trait diversity and functional diversity remain far from resolved (Heino *et al.*, 2007; Prinzing *et al.*, 2008).

In our study catchments, a major stressor (drying) produced very different effects on two commonly used diversity metrics in biomonitoring and community ecology. The differing responses of species and generic richness to an environmental stress raise methodological concerns. Biological monitoring frequently relies on generic or higher taxon identification to reduce cost and because larvae often can not be identified to species. Our results suggest that the sign and magnitude of response metrics, as well as sensitivity and precision, may vary with taxonomic resolution. Major ecological analyses may be affected (e.g. Vinson & Hawkins, 2003).

The regional stonefly distributional data of Poulton & Stewart (1991), although coarse, have real predictive power. Species absent from our collections were mostly from streams larger than those we studied. Stream permanence had no predictive value because our sites and species sampled a wide range of permanence (Fig. 4). Regional distribution (catchments occupied) had predictive value, as it did in similar analyses of plant and fish assemblages (Tofts & Silvertown, 2000; Taylor *et al.*, 2005). Interpretation of this result is problematic. At its simplest, this is equivalent to a gambler who wagers on an event with high prior probability (e.g. a team on a winning streak). Alternatively, high regional occurrence may provide additional information about the abundance of particular habitats and the match of species to them. And lastly, regional abundance may be a good predictor because some form of source-sink or metapopulation dynamic is operating (Pulliam, 1988;

Hanski & Gaggiotti, 2004). These alternatives are not easily separable.

The longitudinal gradient of increasing species richness with stream size is clear evidence for local control. The convergence of assemblages from permanent and drying streams to equal species richness, conditional on stream size, supports both local control and community saturation. The usual test for saturation requires data from multiple regions differing in regional species richness and testing for independence or asymptotic curvature in the regression of local species richness on regional species richness (Srivastava, 1999; Heino *et al*., 2003; McCreadie *et al*., 2005). This test, which has significant weaknesses (Srivastava, 1999), tests only one of three predictions of local control (Ricklefs, 2004). The other predictions are that (i) diversity should be correlated strongly with physical aspects of the environment and (ii) local diversity in comparable habitats should not vary between regions. Substituting regimes (permanent and seasonally dry) for regions, both predictions are met in our study catchments. A conclusion that assemblages are saturated is preliminary, being limited by the number of catchments, but is strengthened by proximity of the catchments within a region of similar climate and geology. Permanent and drying sites shared some species so contrasts of richness are not fully independent. However, the dominance of endemic species in the drying sites (Table 2) suggests evolutionary convergence of species richness.

Endemics, important at local sites in drying streams, probably evolved in response to frequent and widespread drying across the Ozark-Ouachita region (Brown & Matthews, 1995). The seasonally dry streams of Alum Fork are typical of the Ozark-Ouachita region (Brown & Matthews, 1995; Williams *et al*., 2003a,b) with its distinctive hydrology (Poff, 1996; Lins, 1997). Species which evolved in the region or have been long associated with it are expected to adapt to seasonal drying and exploit commonly available although ostensibly stressful habitats (Terborgh, 1973). Endemics constituted 40% of the collected species and six of seven families contained endemics suggesting that opportunities for speciation and any selective pressures were regionally widespread. Thus a regional and historical process contributed to diversity patterns at the scale of single sites. The dominance of endemics at seasonally dry sites reflects evolved tolerance and possibly the absence of intolerant competitors.

We introduced this paper as dichotomous contrasts of the concepts of regional and local factors and of filters and templates. A hierarchical view recognising multiple spatial scales (Poff, 1997; Heino *et al*., 2003; Lowe, Likens & Power, 2006) is more realistic than any simple dichotomy. Variance partitioning analyses (Heino *et al*., 2003, 2007; Mykrä, Heino & Muotka, 2007; Galbraith, Vaughn & Meier, 2008) typically demonstrate increasing influence of local environmental variables at smaller spatial extent and conversely. We suggest that the regional vs. local issue is analogous to top-down vs. bottom-up control in trophic and ecosystem dynamics (Nyström, McIntosh & Winterbourn, 2003). Both regional and local effects may interact, especially at intermediate scale. Like Huston (1999), we see ample opportunities for local effects to propagate upwards in spatial scale perhaps to interact in complex or context-dependent fashion at intermediate scale (Mykrä *et al*., 2007), as do trophic effects (Nyström *et al*., 2003).

Significant practical problems remain and caution against rigid categorisation into *regional: high-level filter: top-down* or *local: template: bottom-up* explanations. Defining variables as uniquely regional or local is not easy (Huston, 1999; Mykrä *et al*., 2007). As a simple example, we used catchment area as a proxy variable for site-specific stream discharge, channel dimensions, and the other correlates (e.g. temperature regime) of longitudinal position; this decision is supported by well-known quantitative relationships (Leopold *et al*., 1964). In contrast, Galbraith *et al*. (2008) included area and discharge in their set of regional variables, and discharge (but not its likely correlate, area) contributed to the regional component of variation of caddisfly (Trichoptera) assemblages in Ouachita rivers. Applying our logic would have weighted local factors more heavily than concluded by Galbraith *et al*. (2008), although regional- or landscape-scale variables such as road density and cultivated area certainly would have remained important. Similar decisions probably affect other analyses.

Streams, replicated across landscapes, regions and continents, are excellent subjects for comparative studies (e.g. Mulholland *et al*., 2002; Bonada *et al*., 2008). Our own conclusions would be much strengthened by sampling across the Ouachita province with a design including the full range of stream size and permanence and independence of sites by ensuring that no site was downstream from any other. Spatially extensive studies usually lack temporal replication (Wiley, Kohler & Seelbach, 1997), and communities of drying streams vary among years (Feminella, 1996) so multi-year sampling also is desirable. Although the proportional contribution of stonefly families to regional and local assemblages varies geographically (Sheldon, 2008), Plecoptera, or other well studied groups, set against the template of stream structure provide opportunities for explicitly comparative ecology within and among regions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Families and species of stoneflies (Plecoptera) observed in subcatchments (North Alum, South Alum, Bread) and a single site (ALF-22) within Alum Fork catchment and the entire Little Glazypeau catchment, Ouachita Mountains, Arkansas, U.S.A.

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