

Seasonal flow variation allows ‘time-sharing’ by disparate aquatic insect communities in montane desert streams

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SUMMARY

1. Flow variation can drive major abiotic changes in stream environments between seasons. Theoretically, disparate biotic communities could be maintained during different seasons at a single site if suitable refuges and colonist sources were available. Using isolated montane desert streams in south-east Arizona as a model system, we hypothesised that two disparate aquatic insect faunas (montane temperate and neotropical) could be maintained at the same sites through strong seasonal variation in abiotic conditions.
2. We collected aquatic insects representing 59 families from seven streams during high-flow (March–April) and low-flow (June) sampling periods across two years. We assessed changes in aquatic insect community and functional feeding group composition by habitat (riffle, pool) and season (high flow, low flow).
3. Within sites, wetted stream area decreased by an average of 97% between high-flow (predominately riffles) and low-flow (predominately pools) seasons. Community composition likewise showed strong seasonal patterns; the montane temperate fauna was strongly associated with the high-flow season while neotropical hemipterans and coleopterans were associated with the low-flow season. Increased water temperature was significantly associated with this shift from temperate to neotropical assemblages.
4. Functional feeding group composition shifted dramatically by season. The proportion of predators increased from 24.5% (high flow) to 75.2% (low flow) while collector–filterers and shredders declined from 38.4% (high flow) to 1.7% (low flow).
5. We suggest that habitat ‘time-sharing’ by disparate communities is facilitated via strong seasonal variation in temperature and flow and the presence of high elevation refuges or diapause stages for temperate montane taxa to survive the dry season.

Keywords: community composition, functional feeding groups, macroinvertebrates, multivariate analyses, seasonal variation

Introduction

Identifying the mechanisms that structure ecological communities and maintain species diversity is a major goal in ecology (Huston, 1979; Rosenzweig, 1995; Chesson, 2000). Similar species often can coexist in

discrete habitat patches despite theoretical predictions that limited resources and interspecific competition should prevent coexistence (Connell, 1978). Additionally, species with different environmental tolerances and resource requirements will often occupy the same sites (Morin, 1999). These seemingly paradoxical situations may be explained, in part, by strong seasonal variations in environmental conditions (Hutchinson, 1961; Tilman & Pacala, 1993). Seasonal environmental changes can act as a temporal analogue

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to landscape or habitat heterogeneity by preventing competitive exclusion and favouring certain species over others in different seasons (Chesson, 2000).

Seasonal variation in the occurrence and abundance of aquatic macroinvertebrate taxa depend mainly on biological traits, such as reproductive timing, longevity, and feeding habits (Wolda, 1988; Bêche, McElravy & Resh, 2006). In lotic ecosystems, the feeding habits, or functional feeding group, of a taxon is a very informative trait to examine in terms of seasonal variation. The abundance of a functional feeding group reflects a combination of seasonally varying factors including water velocity, discharge, and allochthonous food input (Vannote *et al.*, 1980). Generalist feeders (e.g. collector-gatherers) tend to be abundant year-round (Boulton & Lake, 1992b). In contrast, more specialised feeders (e.g. shredders), are dependent upon seasonal food resources (e.g. leaves of riparian trees) and thus may exhibit strong seasonality in abundance (Cummins *et al.*, 1989; Hawkins & Sedell, 1981). Abundances of many filter-feeders can change dramatically with season (Hawkins & Sedell, 1981; Boulton & Lake, 1992b), as they require both appropriate food resources and adequate flow to transport these resources to them, both of which can vary drastically by season.

Seasonal changes in functional feeding group composition imply seasonal changes in aquatic macroinvertebrate community composition as well. Indeed, strong seasonality in community composition has been demonstrated in many lotic systems (McElravy, Lamberti & Resh, 1989; Matthews, Matthews & Hachmoller, 1991; Thompson & Townsend, 1999; Cowell, Remley & Lynch, 2004). This community seasonality has even been noted in temperate streams with minor seasonal variation (Scarsbrook & Townsend, 1993). Streams in arid environments, however, are subject to extreme seasonal variation in flow, temperature, water chemistry and productivity (Gray, 1980; Poff & Ward, 1989; Boulton & Lake, 1992a; Stanley *et al.*, 1994; Lytle & Poff, 2004).

Responses of arid land lotic invertebrate communities to disturbances such as severe floods (Gray & Fisher, 1981; Grimm & Fisher, 1989; Lytle, 2000) and droughts (Stanley *et al.*, 1994; Clinton, 1996) have been well studied, but few studies have specifically examined community-level response to overall seasonal variability in these streams (but see Boulton *et al.*, 1992). While extreme seasonal drought may

seem to represent a type of disturbance, Resh *et al.* (1988) argue these droughts occur within a predictable temporal range to which organisms can adapt, and thus do not act as 'true' disturbances. Rather than a successional 'recovery' following seasonal droughts, seasonal shifts in community composition of arid land lotic communities may represent 'seasonal periodicity' (Boulton & Lake, 1992b), where differential adaptations to various flow conditions better explain community structure in different seasons.

In aquatic systems where seasonal variability has been well-studied, the main influence of seasonal variation is often expressed in terms of changed species abundances rather than complete species replacement (Thompson & Townsend, 1999; Brooks, 2000). In many lotic systems, certain taxa may be highly seasonal while the community as a whole may be less affected by seasonal variation (Thompson & Townsend, 1999; Gibbins *et al.*, 2001). Even in some arid-land streams with high seasonal abiotic variability and large numbers of seasonal taxa, there are taxa which are common in all seasons (Boulton & Lake, 1992b). Seasonal changes in macroinvertebrate community composition are often not as dramatic as changes along spatial gradients (e.g. longitudinal gradients: Hawkins & Sedell, 1981).

For taxa to be present in some seasons but absent in others, refuges must be available during unfavourable seasons. The hyporheic zone serves as an important refuge for some taxa to escape dry seasons, either as active individuals or as diapausing eggs or larvae (Boulton, 1989; Delucchi, 1989; Jacobi & Cary, 1996; Anderson, 1997; Hose, Jones & Lim, 2005). Neighbouring streams may serve as sources for seasonal populations in a given stream, though many taxa do not stray far from the stream corridor (e.g. Plecoptera and Trichoptera: Petersen *et al.*, 1999) and would not easily cross arid uplands. Upstream headwater reaches may also serve as a source for seasonal populations (via drift: Gray & Fisher, 1981). Significant longitudinal distances within a stream are often required, however, to achieve complete species turnover (Vannote *et al.*, 1980; Brussock & Brown, 1991), thus allowing the headwaters to act as a source for novel taxa in lower reaches. Streams with significant elevation changes over short distances may allow headwater reaches to serve as a source for seasonal species in lower reaches.

Here, we describe seasonal and habitat differences in taxonomic and functional feeding group composition of lotic macroinvertebrate communities in the Madrean Sky Islands (MSI). MSI streams have steep gradients and significant elevational relief within short distances and are situated between two mountain ranges (the Sierra Madre Occidental and the Rocky Mountains), which offer a large, diverse regional species pool affiliated with either warm water (Sierra Madre) or cold water (Rocky Mountain) streams. We hypothesised that seasonal variation in abiotic conditions such as flow and temperature drives dramatic changes in macroinvertebrate trophic structure and allows disparate faunas to coexist in the same site, but during different seasons.

Study area

The MSI consist of a series of parallel NW-SE trending mountain ranges in south-east Arizona, south-west New Mexico, and north-west Mexico (Fig. 1). The MSI are located in between the southern Rocky Mountain and the Sierra Madre Occidental cordilleras, and share floral and faunal associations with both regions. Each MSI range is isolated from other ranges by large areas of lowland desert and grassland. Permanent streams in the MSI are generally found between 1200 and

2200 m in the Madrean Evergreen Woodland vegetation zone, in arid oak and pine woodland. Streams in this elevation band are high-gradient and contain extensive sections of permanent bedrock pools interspersed with riffles and runs that usually dry up seasonally. Lower mountain ranges (<2700 m) lack perennial headwaters while higher mountain ranges (>2700 m) contain permanent headwater springs and relict Rocky Mountain conifer forests. Below 1200 m, stream channels are generally dry except during flash floods. The seven study streams are distributed across the northern MSI, with four streams in lower elevation ranges, and three streams in a higher elevation mountain range (Chiricahua Mountains). All seven streams occur in the Coronado National Forest.

Rainfall and stream flow in MSI streams are highly seasonal. In summer, convective monsoon storms bring torrential rains lasting from several minutes to a few hours and cause severe flash flood events. These events, however, do not significantly increase baseflow (Fogel, 1981; Lytle, 2003). Conversely, winter frontal storms tend to be prolonged, with rain falling over several days. Total precipitation is split fairly evenly between the two seasons. The consistency and duration of winter storms allow for a sustained increase in baseflow (high-flow season), lasting from several weeks to months. During the rest of the year

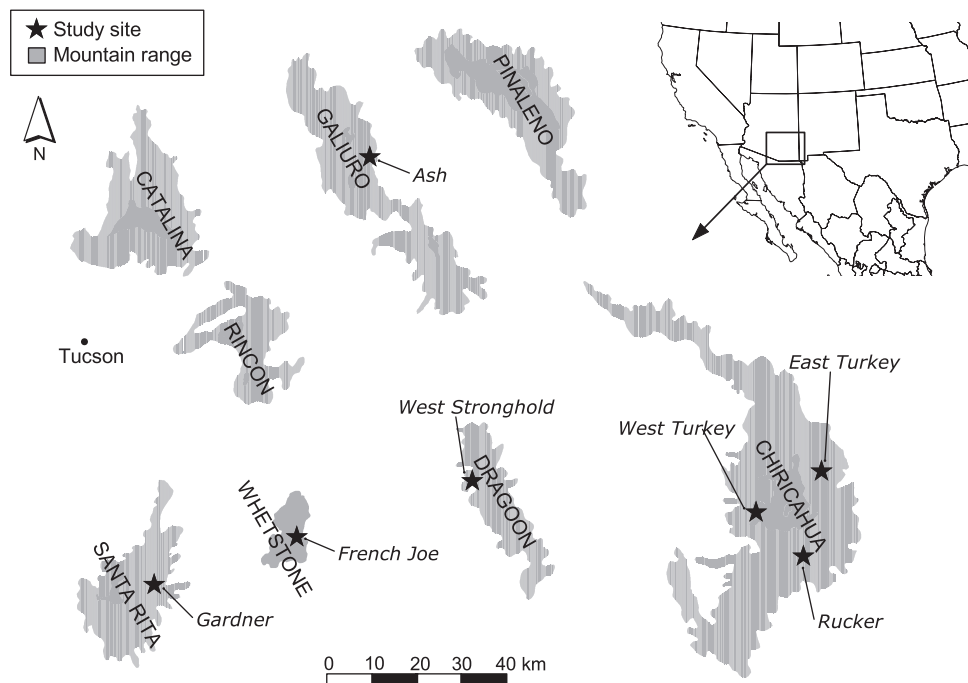


Fig. 1 Location of the seven study streams within Coronado National Forest, Arizona.

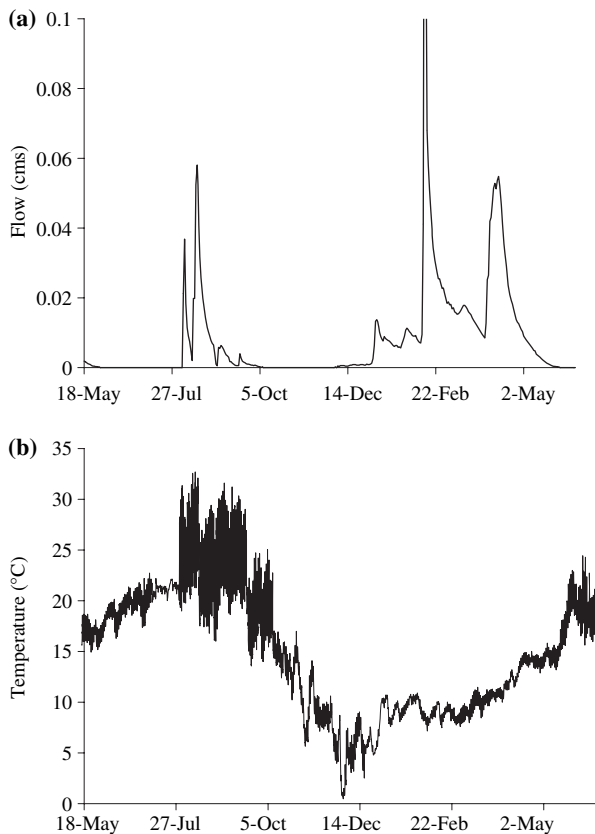


Fig. 2 (a) Daily mean discharge ($\text{m}^3 \text{s}^{-1}$) at Garden Canyon, Huachuca Mountains [USGS Gage 09470800] averaged over the study period (18 May 2003 to 12 June 2005). Most Madrean Sky Islands (MSI) streams are ungaged, but this flow regime exemplifies the seasonality of MSI streams (Lytle, 2003). (b) Stream temperature at 10 cm depth from Florida Canyon, Santa Rita Mountains, recorded with a HOBO Water Temp Pro© from 18 May 2004 to 12 June 2005. This site is 3 km from the study site at Gardner Canyon, and is representative of a typical MSI stream temperature regime.

(low-flow season), flow in most MSI streams is $<0.005 \text{ m}^3 \text{ s}^{-1}$ and is often zero (Fig. 2a). Stream temperature is also highly seasonal and variable. During the summer, diurnal fluctuations can be as great as $12 \text{ }^\circ\text{C}$, and during the winter temperatures can drop to near $0 \text{ }^\circ\text{C}$ and are subject to much lower diurnal flux (Fig. 2b).

Methods

Sampling

Sampling was conducted during March–April (high flow) and June (low flow) in both 2004 and 2005. Because aquatic communities often have a steep

compositional gradient in relation to elevation, a stratified random sampling scheme was devised. We sampled three pools (the dominant habitat type in MSI streams) and three riffles (when present) within each 300 m elevational band where surface water occurred. Entire pools were sampled by vigorously sweeping a D-net (1 mm mesh) above all pool substrata (usually bedrock) and on the surface of the water for 10 s m^{-2} of pool. This pool sampling effort was determined based on preliminary sampling of pools at three MSI streams in 2003; an effort of 10 s m^{-2} of pool captured over 95% of the species that were detected with more than twice that effort. Additionally, over 97% of species found in six pools within each 300 m elevational band were found within the first three pools at each of the three streams (M.T. Bogan, unpublished data). Riffles were sampled by taking a ‘kick-sample’, where 0.25 m^2 of riffle substratum was disturbed to a depth of 5 cm and insects were captured downstream with a D-net (1 mm mesh). For each season (low flow and high flow) anywhere from three to 12 samples are used to describe the insect community, depending on type of habitat present and elevation range occupied by each stream (Table 1).

Identification to family was all that was possible for early instars of several taxa (e.g. Capniidae, Chironimidae), so this conservative level of taxonomic resolution was used in the analyses, although many individuals were identified to genus or species. Since area sampled in riffles was 0.25 m^2 and pool size ranged from 2 to 5 m^2 , all abundance counts were converted to catch-per-unit densities (individuals m^{-2}) to make sample unit values comparable across sites and habitat types (Merritt, Resh & Cummings, 1996). We used Merritt and Cummins (1996) to assign taxa to functional feeding groups.

Streams at high elevation typically have cold, spring-fed flowing water year-round and are dominated by riffles and spring-head pools. These streams may harbour taxa that are rare or absent in lower elevation streams during periods of low flow. To examine this, two additional sites, Rustler Park (2560 m) in the Chiricahua Mountains and Grant Creek (2680 m) in the Pinaleno Mountains, were sampled in June 2004. Our purpose with including these ‘outgroups’ in the dataset was to evaluate whether high elevation stream insect communities

Table 1 Elevation range of perennial stream reaches in the seven study sites and sampling elevations for the two high elevation outgroups with the number of individual samples taken each year during high- and low-flow seasons. Seasonal contraction describes the reduction in wetted surface area between the high- and low-flow seasons. Permanent headwaters are high elevation (2200–3000 m) springs or seeps that occur above the perennial study reaches.

Study site	Elevation range (m)	High-flow samples	Low-flow samples	Seasonal contraction (%)	Permanent headwaters?
Rucker Canyon	1735–1940	12	6	94	Yes
West Turkey Creek	1780–1875	6	3	96	Yes
East Turkey Creek	1830–1930	6	3	94	Yes
West Stronghold Canyon	1560–1590	6	3	99	No
Gardner Canyon	1690–1730	6	3	99	No
French Joe Canyon	1700–1715	3	3	95	No
Ash Canyon	1810–1840	6	3	99	No
High elevation outgroups					
Rustler Park	2580	–	3*	–	–
Grant Creek	2680	–	3*	–	–

*Sampled in 2004 only.

were similar to those found in lower elevation streams during the high-flow season.

At each sample unit location, water temperature, conductivity, and pH were measured at 10 cm depth. Stream surface area was assessed during the low-flow season by walking along the entire wetted stream and visually estimating pool and riffle coverage area. During the high-flow season, starting and ending GPS points for flow were recorded to calculate total flowing length using stream lines on 7.5' USGS topographic maps. These lengths were then multiplied by the average wetted stream width ($n \geq 10$ haphazardly selected measurements) to roughly estimate total stream surface area.

Data analysis

Aquatic insect assemblage data matrices were analysed using non-metric multidimensional scaling (NMS) in PC-ORD (McCune & Mefford, 1999). Sorensen distances were used to calculate community dissimilarity between samples and sites. We used untransformed sample densities (individuals m^{-2}) in all analyses. While square-root transformations and relativisations reduced the coefficient of variation among the species and/or sample unit values, these transformations had little effect on the ensuing ordination. No sample units with a mean Sorensen distance to all other sample units of >2.0 standard deviations from the grand mean were identified. After performing the NMS analyses, we examined correlation coefficients between each taxon and axis of the

ordination to determine which taxa were influential in the ordination and with which environmental variables those taxa were associated.

Samples were categorised into three *a priori* groups using flow and habitat types [high-flow riffle (HFR), high-flow pool (HFP) and low-flow pool (LFP)]; riffle habitat was dry during low-flow periods. These three groups were also further subdivided according to the presence or absence of permanent, high-elevation headwaters. We used Multi-Response Permutation Procedure (MRPP) with Sorensen distances to quantify and test within-group agreement and distinctness (see Mielke & Berry, 2001). This procedure yields two statistics: an *A*-statistic ($-1 \leq A \leq 1$), describing the effect-size of the grouping, and a *P*-value, which evaluates the likelihood that observed differences are due to chance (McCune & Mefford, 1999).

Indicator species analysis (ISA) was used to determine if particular taxa were indicative of the groups defined by flow, habitat, and headwater-type. The highest possible indicator value (IV) for a taxon is 100, meaning that the taxon is always present in a particular group (faithful) and does not appear in other groups (exclusive) (McCune & Grace, 2002). A species' IV is the product of two multipliers: 'faithfulness' (the proportional abundance of the species in a group relative to its abundance in all groups) and 'exclusivity' (the percentage of plots that the species occupies within a given group). Thus, both multipliers must be high for a species to gain a high IV. The statistical significance of each IV was tested using a Monte Carlo randomisation with 1000 runs.

Differences in aquatic insect densities (total and by functional feeding group) and taxon richness between season, habitat, site, year, and streams with and without permanent headwaters were analysed using Kruskal–Wallis tests, as both sample sizes and variances between sites and habitats were uneven. When testing for differences between season and habitat type, all sites in both years were combined. When testing for site differences, all habitat types' and both years' data were grouped for each site. Differences in environmental parameters (temperature, pH and conductivity) between season, year, and streams with and without permanent headwaters were tested using two-sample *t*-tests.

Results

Fifty-nine aquatic insect families were recorded across the streams, seasons and habitats. On average, the study streams were very small and did not have large wetted surface areas in either season (mean low-flow area = 343 m²; mean high-flow area = 9934 m²). Wetted stream area contracted by nearly 97% between high and low-flow seasons. The magnitude of seasonal change varied between streams with and without permanent headwaters (Table 1). During the high-flow season, stream surface area increased by 2.1 orders of magnitude in streams without permanent headwaters and by 1.3 orders of magnitude in streams with permanent headwaters. French Joe Canyon, a limestone spring-fed system, was atypical; habitat expansion during the high-flow season created only additional pools; riffle habitat was never present. Additionally, the stream dried completely after March 2005 and could not be sampled during the low-flow season of 2005.

Functional feeding groups and taxon richness

Relative abundances of functional feeding groups were significantly affected by season and habitat types (Fig. 3). Collector–filterer and predator relative abundances varied significantly by season-habitat type ($\chi^2 = 24.0$ and 22.9 respectively, $P < 0.0001$). Collector–filterers achieved greatest density in the HFRs (742 m⁻²), while predator density peaked in LFPs (386 m⁻²). Relative abundances of shredders also varied significantly by season-habitat type ($\chi^2 = 8.3$, $P = 0.004$). Shredders were most abundant in HFRs

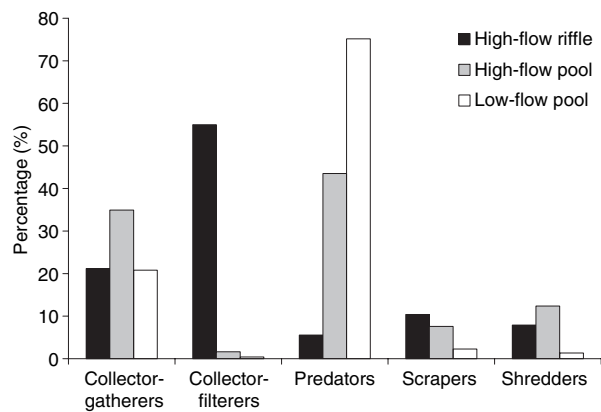


Fig. 3 Mean relative abundances of functional feeding groups by season and habitat type.

(131 m⁻²). These functional feeding group differences contributed to a highly significant effect of season and habitat type on overall aquatic insect density ($\chi^2 = 12.2$, $P = 0.0005$). Scrapers and shredders were more abundant in 2005 than in 2004 ($\chi^2 = 4.8$, $P = 0.03$ and $\chi^2 = 6.9$, $P = 0.009$, respectively), contributing to a significant effect of year on overall density of aquatic insects ($\chi^2 = 4.5$, $P = 0.03$). Significant differences between streams were only observed with scrapers and overall taxon richness ($P < 0.001$; Table 2). The source of these differences was elucidated by grouping streams by headwater type. Scraper and shredder density and overall taxon richness were significantly higher in streams with permanent headwaters (Table 2). Taxon richness did not vary significantly by season/habitat type or by year, but there were differences between streams ($P < 0.001$; Table 2). Streams with permanent high elevation headwaters supported more taxa than those without ($P < 0.001$; Table 2).

NMS ordination

Non-metric multidimensional scaling ordination with the reduced (singleton-deleted), untransformed species matrix converged on a stable, two-dimensional solution (stress = 13.830, final instability = 0.00001, $p = 0.0196$; see Fig. 4). The two axes accounted for nearly 73% of the variation in community composition between sample units (axis 1: $r^2 = 0.543$; axis 2: $r^2 = 0.184$). The two habitat types (pool and riffle) in the ordination clearly represent distinct communities (Fig. 4). HFPs and LFPs generally occupy distinct

Table 2 Average sample densities (no. m⁻²) of functional feeding groups and average taxon richness across streams and by headwater type. Chi-squared statistics from Kruskal–Wallis tests examining variation of densities and taxon richness between streams and headwater types.

	Stream							Headwater		χ^2	
	Ash	Etu	Frj	Gnr	Ruc	Wst	Wtu	Permanent	None	Stream	Headwater
Sample density											
All taxa	531	684	244	624	526	506	941	717	508	2.3	0.3
Collectors-gatherers	34	299	106	74	155	115	120	191	81	7.8	2
Collectors-filterers	177	96	0	423	134	151	417	216	216	10.89	7.5**
Predators	265	70	128	120	110	187	307	162	177	2.9	0.6
Scrapers	0.4	84	1	2	112	10	71	89	4	22.0***	19.7***
Shredders	55	135	9	6	16	43	27	59	30	11.4	8.4**
Taxon Richness	8	23	18	15	22	12	21	22	13	24.9***	19.5***

Significance level, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

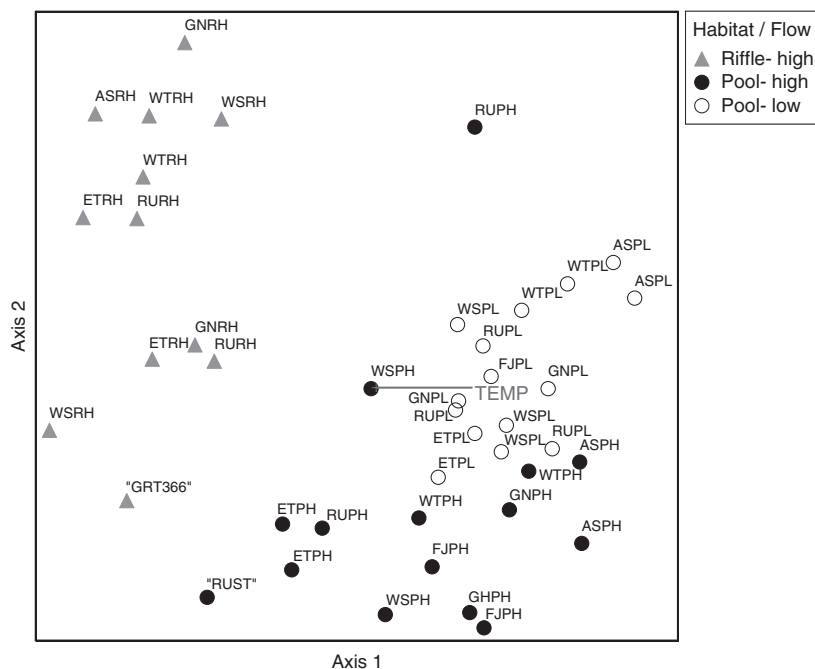


Fig. 4 Non-metric multidimensional scaling ordination results coded by first letters of name, habitat (R = riffle, P = pool), and season (H = high flow, L = low flow) type. The high elevation 'outlier' sites are GRT366 (Grant Creek) and RUST (Rustler Park). Of the environmental parameters examined, only temperature was strongly correlated ($r = 0.57$; axis 1) with an axis.

areas of species space, with some overlap due to variability in HFPs. The two 'outgroup' low flow, high elevation samples (GRT366- Grant Creek; RUST- Rustler Park) occupied the high-flow region of species space. Thus, during the low-flow season these high elevation headwater stream communities are compositionally similar to lower elevation stream communities during the high-flow season.

By examining which taxa are associated with each axis, broader generalisations can be made about the gradients in community composition that are expressed in the ordination. Axis 1 represents a gradient

from a community that requires cool and/or flowing water to a community dominated by lentic and warm water taxa (Table 3). Many of the taxa with negative relationships to axis one (i.e. Blephariceridae, Heptageniidae) are characteristic of cool, Rocky Mountain-type streams. Conversely, those with positive correlations to axis 1 (i.e. Dytiscidae, Notonectidae) increase in diversity and dominance in warm, neotropical streams. Axis 2 represents a weaker gradient in community composition, and may illustrate community response to an environmental variable not measured in this study.

Table 3 Correlations (r) between aquatic insect families and non-metric multidimensional scaling ordination axes

	Axis 1	Axis 2
Chironomidae	-0.62	0.36
Corydalidae	-0.58	0.62
Simuliidae	-0.54	0.69
Hydropsychidae	-0.49	0.30
Hydrobiosidae	-0.42	0.33
Blephariceridae	-0.37	0.26
Heptageniidae	-0.36	0.17
Hydrophilidae	0.35	-0.02
Gyrinidae	0.43	0.07
Gerridae	0.45	0.08
Notonectidae	0.46	0.06
Veliidae	0.49	0.14
Dytiscidae	0.56	0.21

Abiotic stream characteristics

Temperature was the only environmental variable to be strongly associated with an ordination axis (axis 1, $r = 0.57$), although pH and conductivity showed some correlation with axis 1 ($r = 0.39$ and 0.25 , respectively). Stream size, per cent canopy cover, and geographical location were not substantially correlated with the NMS ordination. Thus, temperature, pH and conductivity were chosen for further examination with t -tests (Table 4). Season significantly affected temperature, pH and conductivity: all were significantly lower during the high-flow season. Additionally, streams without permanent headwaters had significantly higher temperature, pH and conductivity. Stream temperature and conductivity were lower in 2005, which may have resulted from greater precipitation amounts associated with El Niño conditions during the 2005 high-flow season.

MRPP and indicator species analysis

The three *a priori* groups (HFR, HFP and LFP) were clearly distinct in community composition ($A = 0.18$,

$P < 0.001$). Several taxa received very high indicator values for the LFP and HFR groups, but no taxon scored a statistically significant indicator value for the HFP group. Simuliidae ($IV = 85$, $P = 0.001$), Corydalidae ($IV = 69.7$, $P = 0.004$) and Heptageniidae ($IV = 66.7$, $P = 0.016$) were all good indicators of HFRs. Notonectidae ($IV = 88.9$, $P = 0.001$), Dytiscidae ($IV = 86.9$, $P = 0.001$) and Hydrophilidae ($IV = 77.7$, $P = 0.001$) were among the best indicators of LFPs. Only Siphonuridae and Polycentropodidae ($IV = 22.7$ and 17.9 , respectively) were identified as indicators of HFPs, and these values were not significant ($P > 0.4$).

The three season and habitat groups were further subdivided by headwater type (permanent or not). The resulting six groups were also distinct in community composition ($A = 0.21$, $P < 0.001$). ISA of these six groups illustrates a clear split between communities in streams with and without permanent headwaters (Table 5). HFR samples from streams with headwaters were characterised by taxa typical of cold, fast-flowing water (e.g. Blephariceridae and Hydropsychidae), while HFR samples from streams lacking headwater refuges were characterised by taxa with diapause stages (e.g. Capniidae) or hyporheos-dwelling potential (e.g. Corydalidae). Again, indicator species of HFP samples were not statistically significant, although the marginal significance of Nemouridae and Limnephilidae for HFP with permanent headwaters may be biologically meaningful. All 59 families collected in this study and their affinities (or lack thereof) with season are listed in Table 6.

Discussion

Biogeographical considerations

Madrean Sky Island streams exhibit strong community responses to seasonal flow variation and habitat type. MRPP tests clearly distinguished between the

Table 4 Abiotic factors averaged by season, year and headwater type with t -test results for differences among types

	Season		Year		Headwater		t		
	Low flow	High flow	2004	2005	Permanent	None	Season	Headwater	Year
Temperature	20.0	10.2	15.2	12.4	12.8	14.9	16.2***	2.0*	2.8**
pH	7.7	6.9	7.1	7.3	7.1	7.3	10.8***	2.1*	-1.9
Conductivity	244.3	143.3	220.6	139.5	119.7	239.7	3.6***	4.5***	2.9**

Significance level, * $P = 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 5 Indicator values (IV) and significance (*P*-value) from indicator species analysis of aquatic insect taxa when grouped by season, habitat and headwater type

Group	Taxa	IV	<i>P</i> -value
Permanent headwaters			
High-flow riffle	Heptageniidae	90	0.001
	Blephariceridae	85	0.001
	Hydropsychidae	65	0.002
High-flow pool	Nemouridae	33	0.087
Low-flow pool	Corixidae	62	0.001
	Naucoridae	53	0.003
	Belostomatidae	39	0.015
Non-permanent headwaters			
High-flow riffle	Capniidae	78	0.001
	Corydalidae	61	0.001
	Simuliidae	61	0.001
High-flow pool	Libellulidae	30	0.338
Low-flow pool	Hydrophilidae	65	0.003
	Notonectidae	65	0.001
	Lestidae	58	0.008

three sample types (HFR, HFP and LFP), indicating that they occupied distinct areas of taxonomic space. NMS ordination showed a strong gradient from communities requiring cold, lotic conditions to those tolerant of warm, lentic conditions. Although temperature was most strongly associated with this gradient, pH and conductivity were also potentially relevant environmental factors. Most aquatic insect taxa are quite sensitive to temperature (Ward &

Stanford, 1982; Wallace & Anderson, 1996; Hawkins *et al.*, 1997). Additionally, both pH and conductivity can be significant drivers of aquatic insect community composition (Lancaster & Scudder, 1987; Clenaghan *et al.*, 1998; Woodward, Jones & Hildrew, 2002; Sanderson, Eyre & Rushton, 2005).

The community gradient elucidated by the ordination describes a compositional shift from a temperate Rocky Mountain stream to a neotropical Sierra Madre stream. This transition occurs not geographically, however, but seasonally within the same stream. The environmental requirements of Rocky Mountain and Sierra Madre affiliated fauna are seemingly incompatible, but the extreme seasonal variation of flow and water characteristics (Fig. 2a,b; Tables 1 and 2) allows temporal coexistence. In this sense MSI streams offer 'time-share' habitat, where during a brief part of the year high-flow conditions are ideal for taxa adapted to cold fast-flowing water, while the Sierra Madre fauna flourishes under the warm, lentic conditions of the low-flow season.

Indicator species analysis of the three sample types supported this concept. Simuliidae, Heptageniidae, Hydropsychidae, and Blephariceridae were all significant indicators of HFR. These taxa are abundant in Rocky Mountain streams and are believed to have temperate origins and centres of diversity (Edmunds, Jensen & Berner, 1976; Hogue, 1981; McCafferty,

Table 6 Affinity of the 59 families collected to low- and high-flow seasons. 'Reduced' indicates significant declines in abundances from 75% to 99% (usually approaching the latter) in the specified season. 'Less affected' signifies abundance declines of <75%, and generally was <40%. Rare taxa comprised, on average, <0.5% of the total individuals of each sample, and thus are not viewed as being good indicators for either season.

Absent during high flow	Absent during low flow	Reduced during high flow	Reduced during low flow	Less affected	Rare
Helophoridae	Ameletidae	Belostomatidae	Chironomidae	Baetidae	Aeshnidae
Uenoidae	Arctiidae	Corixidae	Corydalidae	Calamoceratidae	Caenidae
	Blephariceridae	Dytiscidae	Elmidae	Coenagrionidae	Ceratopogonidae
	Capniidae	Haliplidae	Heptageniidae	Culicidae	Dixidae
	Chloroperlidae	Hydrophilidae	Lepidostomatidae	Dryopidae	Hydraenidae
	Glossosomatidae	Lestidae	Leptophlebiidae	Gerridae	Hydrochidae
	Hydrobiosidae	Nepidae	Limnephilidae	Gyrinidae	Hydroptilidae
	Hydropsychidae	Notonectidae	Nemouridae	Helicopsychidae	Leptoceridae
	Odontoceridae		Tipulidae	Libellulidae	Naucoridae
	Psychodidae			Siphonuridae	Philopotamidae
	Simuliidae			Veliidae	Polycentropodidae
	Taeniopterygidae				Pylalidae
	Leptohiphidae				Saldidae
					Scirtidae
					Stratiomyidae
					Tabanidae

1981). Conversely, Dytiscidae, Belostomatidae and Notonectidae were significant indicators of LFP. While these families are present in temperate streams, they increase in diversity and dominance in neotropical streams (Usinger, 1956; Menke, 1969; Vinson & Hawkins, 2003) and can thus be considered characteristic of Sierra Madre streams. During the low-flow season, these families are not just occasionally found in marginal habitats, as in temperate streams, but instead numerically dominate the entire stream. Additionally, most species representing these families in our samples (e.g. Dytiscidae: *Laccophilus mexicanus*; Belostomatidae: *Lethocerus medius*) have their centres of distribution in the Sierra Madre Occidental. HFPs did not have any significant indicator species and were differentiated from HFR and LFP mainly by significantly reduced numbers of HFR taxa and a lack of many LFP taxa.

As many of the indicator taxa for HFR and LFP have incompatible environmental requirements, the seasonal variation that allows site coexistence also increases overall, year-round site diversity. These results are congruent with past studies which found that streams with considerable seasonal flow variation are more species-rich than neighbouring streams with relatively constant flow (Dieterich & Anderson, 2000). Without the brief high-flow season, many of the HFR taxa would never be present in the stream (e.g. Blephariceridae, Capniidae), greatly reducing year-round diversity. Filter-feeding HFR taxa, such as Simuliidae, can only obtain resources during the high-flow season, and are absent the rest of the year in streams with temporally discontinuous flow (Boulton & Lake, 1992b). Additionally, if the streams exhibited low-flow conditions year round, the diversity of LFP fauna would likely be reduced. With increasing flow stability, we expect that biotic interactions like competition and predation would increase in importance (Poff & Ward, 1989), potentially limiting the diversity of LFP taxa. Also, if pools were isolated year round without flushing flows, abiotic conditions would likely deteriorate (e.g. reduced oxygen concentrations). In Australian intermittent streams, these deteriorating pool conditions led to sharp declines in species richness, and yielded a small community composed mainly of air-breathing predators (Boulton & Lake, 1992b). Without hydrologic 'recharge' during the high-flow season, we expect that MSI pool communities would follow

the same trajectory, which would greatly reduce the high diversity we observed in LFPs.

For taxa to occur only seasonally in streams, off-season refuges must exist to serve as a source for colonisation. In this study, we found significant aquatic insect community differences between streams with and without permanent, high elevation headwaters. Additionally, communities with permanent headwaters were significantly more taxon rich than those with ephemeral headwaters. Ordination analyses showed that the two high-elevation, headwater 'outgroup' samples taken during the low-flow season were compositionally similar to low elevation streams during the high-flow season. Thus, the year-round inhabitants of these headwater springs and streams are likely the source of Rocky Mountain-type seasonal populations in lower elevation MSI streams. Colonisation of lower reaches by headwater taxa is most likely to occur through drift during the high-flow season (Gray & Fisher, 1981). Additionally, many adult aquatic insects are active fliers along the stream corridor (Petersen *et al.*, 1999; Sanderson *et al.*, 2005), so adults emerging from high elevation sources may be ovipositing in lower elevation reaches.

Many MSI streams do not have permanent, high elevation headwaters and yet still have distinct high-flow communities composed mostly of taxa which are completely absent during the low-flow season. Most MSI streams are quite isolated (>10 km) from other streams. For some taxa, colonisation from neighbouring sites is unlikely considering the short distances (often < 50 m) most aquatic insects travel laterally from stream corridors (Petersen *et al.*, 1999; Malmqvist, 2002; Petersen *et al.*, 2004). As aerial colonisation and drift are unlikely sources in these streams, the hyporheos may serve as the most important recolonisation source for seasonal inhabitants. Although in some stream types the hyporheos may not be a significant refuge (del Rosario & Resh, 2000), many studies have demonstrated the use of hyporheos as a temporal refuge from drying surface conditions (Anderson, 1997; Hose *et al.*, 2005; Clinton *et al.*, 1996).

Indicator species analysis identified three taxa as significant indicators of HFRs in streams without permanent headwaters: Capniidae, Simuliidae and Corydalidae. Capniid larvae have been found in hyporheic substrata in other Arizona streams (Clinton *et al.*, 1996) and may exhibit both egg (Gray, 1980) and larval diapause (Harper & Hynes, 1970; Jacobi & Cary,

1996). In the desert south-west, most capniid species are restricted to streams with temporary seasonal flow (Jacobi & Cary, 1996). Simuliid flies are also capable of egg diapause and can pass rapidly through the larval stage (≥ 4 days), a useful trait in seasonal habitats (Peterson, 1996). These diapause periods provide a form of temporal dispersal and are functionally equivalent to spatial dispersal in streams with head-water source populations (Bohonak & Jenkins, 2003). Corydalid larvae are semivoltine and thus need several years to complete the larval stage, but have been observed in the substratum of dry streambeds (Evans & Neunzig, 1996) and in riparian areas (M.T. Bogan, personal observation), and may survive the dry season as active larvae. Thus, high-flow taxa characteristic of streams lacking permanent headwaters have life history adaptations which allow them to take advantage of habitats that are only available for a few months out of the year.

Ecological considerations

The significant seasonal variation observed in community composition was not limited to shifts in taxonomic composition and biogeographical origin. Functional feeding group abundances also changed considerably between season and habitat in the seven study streams. Shifts in functional feeding group composition have been observed in many temperate streams (Hawkins & Sedell, 1981; Cummins *et al.*, 1989; Boulton & Lake, 1992b), although seasonal taxonomic changes are often of much greater magnitude than shifts in biological trait composition, including functional feeding groups (Bêche *et al.*, 2006). During the high-flow season, collectors-filterers, shredders and scrapers made up a substantial percentage of MSI aquatic insect communities (28%, 9% and 10% respectively: pool and riffle averaged). As habitat shrank in the low-flow seasons, however, these groups were nearly absent (4% cumulative; Fig. 3). Meanwhile, the proportion of predators (mainly adult Coleoptera and Hemiptera) increased from 24% to 75%. This pattern has been observed in other intermittent streams (Boulton & Lake, 1992b; Stanley *et al.*, 1994), but not to this extreme extent.

In a sense, LFPs are concentrated versions of HFPs but lack all of the filterers, shredders and scrapers that are sensitive to higher temperatures, reduced allochthonous input and lentic conditions. What remains

is a concentration of large predators which were observed to quickly devour any available aquatic or terrestrial prey (e.g. amphibians, terrestrial moths, flies and beetles). Some families of predators were present during the high-flow season, although with greatly reduced abundances and species diversity, while other predator taxa seemed to appear just as the low-flow season was beginning. As MSI streams contract and warm during the high-flow to low-flow transition, predator taxa present during the high-flow season likely respond to these environmental cues by moving into permanent pools via swimming or flying (Velasco & Millan, 1998). Many predator taxa absent during the high-flow season (e.g. Nepidae, many species of Dytiscidae), may migrate from lower elevation habitats, such as stock ponds, to permanent stream pools during the high-flow to low-flow transition period. The reproductive period of many of these taxa peaks in May and June (Gray, 1981), so it would be appropriate for these taxa to migrate at this time to contracting stream pools with abundant prey items for their larvae to consume. Thus, the dramatic increase in predator abundance between the high-flow and low-flow seasons is likely the result of both an increased concentration of resident predators and seasonal immigrants taking advantage of concentrated prey resources.

Collector-gatherers seem to be the only group immune to seasonal variation. Their abundances peak in the high-flow season (28%: pool and riffle averaged), but are reduced by just 25% during the low-flow season (Fig. 3). Collector-gatherers are the least specialised functional feeding group (Cummins & Merritt, 1996), which may explain their continued abundance despite the lack of flowing water and the presumably reduced allochthonous input that other groups (e.g. filterers and shredders) require. The abundance of LFP predators may be causing reduced abundances of collector-gatherers, however this interaction was not examined as part of our study.

Conclusion

Madrean Sky Island streams support two types of 'time-share' communities via seasonal flow variation (Fig. 5). In streams with high-elevation permanent headwaters, relictual Rocky Mountain fauna may colonise lower elevations during the high-flow season to take advantage of expanded suitable conditions. In

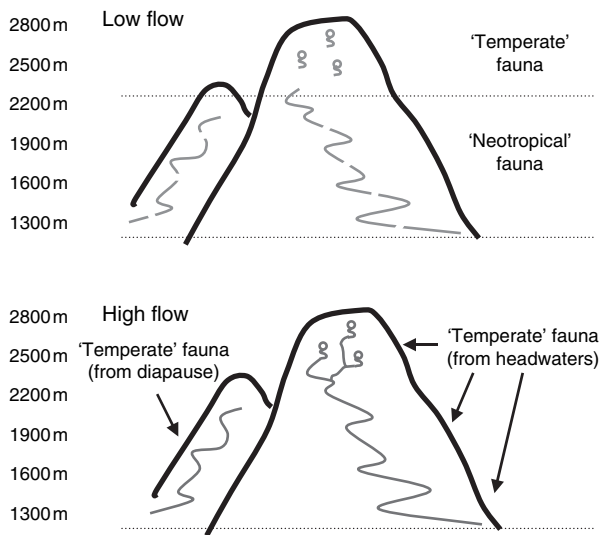


Fig. 5 Illustration of how multiple faunas persist in Madrean Sky Islands streams of high and low elevation mountain ranges. During low flow, interrupted perennial reaches between c. 1200 and 2200 m support neotropical taxa, while most temperate taxa are restricted to high elevation springs. During high flow, temperate taxa colonise the expanded, continuous stream habitat between 1200 and 2800 m. Colonisers emerging from a diapause stage are the likely source of temperate taxa found in lower elevation mountain streams during the high-flow season.

streams lacking permanent headwaters, the hyporheos and diapause stages likely serve as refuges until high-flow conditions return, allowing growth and development to continue during the brief, suitable season. Both high elevation and hyporheic/diapause refuges must be stable over long time periods, as MSI streams occasionally endure multi-year droughts without a significant high-flow season. During the low-flow season, streams of both headwater-types are dominated by a diverse 'Madrean' fauna of hemipterans and coleopterans which prefer warmer, lentic conditions. Dramatic seasonal fluctuations were also observed with functional feeding groups. Collectors, shredders and scrapers dominate during the high-flow season, but after streams are concentrated into remnant permanent pools in the low-flow season the vast majority of insects present are predators.

This sharp transition between high- and low-flow communities in our study represents a form of seasonal periodicity (Boulton & Lake, 1992b). Rather than a slow transition between seasons, we observed a sharp, stepped transition between high- and low-flow communities. In general, MSI streams do not have large drainage areas or alluvial basins for hydrologic

recharge, thus when precipitation stops, flow ceases within a couple weeks and sometimes days (see Fig. 2a). The rapid shift in abiotic conditions associated with drying facilitates a stepped transition in community composition (Boulton, 2003), where numerous high-flow taxa disappear completely until the following year's high-flow season (Table 6). Many MSI taxa dependent on high flow or cooler temperatures have life history adaptations (e.g. egg or larval diapause), which ensure their persistence through seasonal droughts and unfavourable abiotic conditions. Such adaptations indicate that seasonal drought is not a disturbance from the organism's point of view, but rather a predictable occurrence with which the organism has evolved (Resh *et al.*, 1988).

Several recent studies have shown the sensitivity of aquatic insect communities to long-term changes in climatic patterns and stream chemistry. Cold-water taxa have been lost from streams experiencing continued warming trends (Daufresne *et al.*, 2003), and interactions between warming summer temperatures and increased pH have significantly altered communities in naturally acidic streams (Woodward *et al.*, 2002). We suggest that MSI streams and their seasonal 'time-share' communities might be sensitive to climatic changes as well. Slight changes in rainfall patterns or increased temperatures could eliminate the ability of streams to seasonally support remnant Rocky Mountain fauna, reducing overall stream diversity, or could cause formerly permanent streams to become intermittent. The complete drying of one of our study streams illustrates this point. Small, seasonally variable streams, like those of the MSI, are often surprisingly diverse. The factors supporting high aquatic insect diversity in these streams and their sensitivity to changing climatic conditions are deserving of further study.

Acknowledgments

This study was conducted under USDA Forest Service Special Use Permit #SUP0092. A portion of the work was conducted at the American Museum of Natural History's Southwestern Research Station. Effie Greathouse, Debra Finn, Laura McMullen, and two anonymous reviewers provided useful criticism on earlier drafts. Thanks to Frank Drake and Justin Miles for assistance with sorting and processing of samples at Oregon State University. Special thanks to Claire

Zugmeyer for essential logistical support during field sampling. This project was supported in part by Oregon State University and National Science Foundation grant DEB-0445366 to D.A.L.

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(Manuscript accepted 3 November 2006)