MACROINVERTEBRATE STRUCTURE AND DRIFT IN THE BLANCO RIVER: A KARST TEXAS STREAM SUBJECT TO HYDROLOGIC VARIABILITY

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ABSTRACT

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Patterns in benthic macroinvertebrate communities were assessed within the Blanco River drainage of central Texas to determine structuring mechanisms related to abiotic and biotic influences of the watershed. The Blanco River is a flashy karst system and naturally fragmented because of water loss to the Trinity and Balcones Fault Zone Edwards aquifers and because of unique geological formations in the middle reaches. Seven mainstem sites, two tributary sites, and two seep sites were sampled qualitatively and quantitatively within the Blanco River drainage seasonally from October 2003 through July 2005. In addition, 24-h drift samples were taken in spring, summer and fall from three sites. Ephemeroptera, Trichoptera and Diptera were the most abundant taxa in benthic and drift samples, although riffle beetles (Coleoptera) and *Argia* (Odonata) were among the most ubiquitous. Habitat, site, and season explained 33% of community variation in the drainage (F = 1.35, P < 0.01). Current velocity and substrate were primary habitat factors associated with taxa occurrence and distribution. Adjacent communities differed (analysis of similarity: R = 0.086, P = 0.02) among mainstem sites suggesting local habitat factors were more important than spatial factors in determining community structure. Tributary and seep communities were similar through time and provided habitat for several taxa not found in the mainstem and habitat for source populations for many mainstem taxa. Biodiversity of the Blanco River watershed is dependent upon the diversity and persistence of mainstem, tributary, and seep habitats. However, structure and function of the macroinvertebrate communities and their habitats are susceptible to degradation by increasing surface and groundwater withdrawals, urban development, and water detention devices such as low-head dams.

CHAPTER I

INTRODUCTION

Aquatic macroinvertebrate communities are often described in the framework of the four dimensional lotic ecosystem: longitudinal, vertical, lateral and temporal (Vannote et al. 1980, Ward 1989, Boulton et al. 1998). Within each dimension are many temporal scales (e.g., seasonal and daily) across which benthos organize (Minshall 1988, Townsend and Hildrew 1994). Within a drainage, tributaries might contain taxa absent in the mainstem, thus increasing basin diversity. They can also be a refuge for taxa during mainstem flooding and increase the rate of recovery by providing new colonists for scoured systems (Sagar and Glova 1992, Cellot 1996, Shearer et al. 2002). Seeps, with their cool, constant flow can maintain populations of both crenophilic and cosmopolitan taxa making them potential sources of high taxonomic diversity, especially during low flows in the mainstem (Mattson et al. 1995, Lindegaard et al. 1998, Hoffsten and Malmqvist 2000). At the scale of geomorphic units, riffle habitats generally possess higher densities and richness of macroinvertebrates than pools and runs (Barbour et al. 1999). Within microhabitat scales, drifting insect assemblages may be structured differently from benthic communities and lend further insight into the function of the total assemblage (Müller 1974, Kohler 1985, Smock 1996, Pringle and Ramirez 1998). Distribution patterns within these dimensions and scales develop in the context of the

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habitat template (Poff and Ward 1990, Townsend and Hildrew 1994), in particular, climate, geology, substrate heterogeneity, chemistry, and hydrological and disturbance regimes (Pringle et al. 1988, Feminella 1996, Cannan and Armitage 1999, Ward et al. 2002, Effenberger et al. 2006).

In non-impacted, longitudinally connected streams, macroinvertebrate assemblages are known to change predictably with habitat on a gradient of downstream distance (Vannote et al. 1980, Vannote and Sweeney 1980, Grubaugh et al. 1996). In the classic River Continuum Concept (RCC; Vannote et al. 1980), shredders and gatherers dominate the functional feeding groups in upstream reaches as they take advantage of greater amounts of coarse particulate organic matter (CPOM; leaves, twigs) retained in coarser cobble/boulder substrates. Midstream reaches should possess more scrapers as stream width increases to allow light penetration and increased autotroph production. Collector-gatherers are expected to be a considerable portion ($\sim 50\%$) at all sites and increase, with filterers, to high dominance at downstream sites ($\sim 70\%$) as they take advantage of the fine particulate organic matter (FPOM) leaked from upstream reaches. Alterations to the RCC can occur in streams where impoundments and natural hydrogeological breaks disrupt the transport of organic matter (Ward and Stanford 1983, Lake 2000, Wright and Li 2002). Intermittent streams are especially susceptible to longitudinal disconnectedness as hydrological connection between reaches is frequently broken by drought (Resh et al. 1988, Stanley et al. 1994, Meyer and Meyer 2000, Bonada et al. 2006). Vannote et al. (1980) speculated that xeric streams could resist conformity to the RCC because of reduced allochthonous inputs from the riparian zone.

Within the temporal dimension, depressed seasonality in the sub-tropics obfuscates seasonal trends in insect life cycles (Brown and Fitzpatrick 1978, Gray 1981). This is demonstrated in southern gulf-slope drainages, where Ephemeropteran and Trichopteran taxa exhibit voltinism that differs from their congeneric relatives in more temperate climates (Stanley and Short 1988, Tiemann and Arsuffi 1991).

Central Texas borders the southern gulf slope where summers are hot (N of days > $32^{\circ}C = 111$), winters are mild (average temperature: $11^{\circ}C$) and mean annual precipitation is 812 mm. Flash floods are common because many streams in this region flow over the limestone bedrock of the Edward's Plateau where shallow soils predominate and rainfall events are brief and intense. The Blanco River lies on the eastern border of the Edwards Plateau and is fed partly by the hardwater springs and seeps that flow from the Trinity and Edwards Balcones Fault Zone aquifers. The karst geology of the Blanco River drainage disrupts flow continuity and annually causes stretches of river bed to go dry for several kilometers when precipitation is low. However, rainfall is sufficient to maintain longitudinal connectedness throughout the river's 120 km length for much of the year. During periods of intense precipitation, discharge can increase by several orders of magnitude and quickly return to pre-spate flows. In October 2004, discharge increased by two orders of magnitude and returned to near pre-spate flows within a 48-hour period (A 1). Frequent spates, drought and depressed seasonality disrupt the spatio-temporal trends by which macroinvertebrates are traditionally studied. Consequently, the Blanco River watershed offers a unique opportunity to investigate macroinvertebrate community patterns in a highly variable system. Furthermore, the Blanco River is within a region of the Edwards Plateau known to support a rich macroinvertebrate community, including

many endemics (Longley 1981, Bowles and Arsuffi 1993), yet drainage-wide surveys of Blanco River macroinvertebrates are lacking. Therefore, the objectives of this study were to quantify the occurrence and abundance of macroinvertebrate taxa among mainstem, tributary, and seep macrohabitats, within a longitudinal gradient, and to determine the influence of site (macrohabitat and longitudinal gradient), season, and habitat parameters on the macroinvertebrate community.

CHAPTER II

METHODS

Seven sampling sites were selected in the upper, middle, and lower reaches of the Blanco River (A 2). Two tributary sites, the Little Blanco River and Cypress Creek, were selected about 1 km upstream from their confluence with the Blanco River. Two seep sites were selected: one near Site 1 (Hammond Seep) and the other near Site 4 (Narrows Seep). All mainstem, tributary and seep sites were sampled qualitatively every 3 months from October 2003 through July 2005 with the exception of Site 3, which was only sampled from October 2004 through July 2005. Within each site, geomorphic units (i.e. pools, runs, and riffles) were sampled with a d-net and handpicking in proportion to their availability (Barbour et al. 1999). Specimens were sorted in the field and preserved in 90% ethanol for identification in the lab. In addition to qualitative sampling at sites 2, 6 and 7, one quantitative sample was taken with a Hess sampler in riffles with gravel and cobble substrate. Substrate within the Hess sampler was disturbed by hand to a depth of 8 cm for two minutes. Entire samples, including invertebrates and detritus were preserved in 90% ethanol and returned to the lab for sorting and identification. Excessive buildup of $CaCO_3$ prevented quantitative sampling at Site 3 in October 2003, January 2004, and July 2005. High flows prevented quantitative sampling at sites 6 and 7 in April 2004.

A 250-µm-mesh drift net was set at sites 1, 4 and 7 for one 24-h period in the spring (27 May through 3 June), summer (23 through 26 July) and fall (18 September through 1 October) of 2004 to supplement macroinvertebrate occurrence information. The catch was emptied every three hours (Allan and Russek 1985, Ramirez and Pringle 2001). Average flow through the net was calculated from depth and current velocity measurements taken at the beginning and end of each 3-h period (Matzinger and Bass 1995). Nets were at least 8 cm above the substrate on all occasions (Allan and Russek 1985, Smock 1996) and checked often to prevent clogging. Samples were preserved in 90% ethanol.

At each site and for each drift sample, water temperature (°C), dissolved oxygen (DO; mg I^{-1}), pH, and specific conductivity (μ S cm⁻¹) were measured. Depth (m), current velocity (m/s), percent substrate, percent vegetation, length, and width of each geomorphic unit were measured. Habitat measures of geomorphic units were averaged by areal coverage (length x width) of each geomorphic unit to calculate mean depth, mean current velocity, percent substrate, percent vegetation for each site. Stream discharge was obtained from a USGS gauge (Kyle, Texas; 08171300), located between sites 5 and 6.

In the laboratory, macroinvertebrate samples were washed in a 70-µm sieve to remove fine silt. In Hess and drift samples, specimens longer than 1 cm were placed in a vial and counted as part of the sub-sample (Courtemanch 1996, Vinson and Hawkins 1996, King and Richardson 2002). Debris larger than 1 cm were washed rigorously into the sieve, inspected for macroinvertebrates and discarded. Remaining mix of detritus and organisms were sub-sampled by dividing each collection into fourths and randomly choosing one of the quarters for picking under a stereoscope (Wrona et al. 1982, Allan and Russek 1985, Delucchi 1989). Remaining three quarters were saved for future reference. Taxonomy followed Merritt and Cummins (1996), Lugo-Ortiz and McCafferty (1998), Wiggins (1998), Thorp and Covich (2001), and others as needed. Insects were keyed to the lowest practical taxon, generally to genus. Non-insects were keyed to the lowest practical resolution ranging from phylum (e.g. Nematoda) to species (e.g. the blind Amphipod *Stygobromus russelli*).

Statistical Methods

Taxa richness, Shannon-Weiner diversity (H'; log₂) and percent dominance were calculated to quantify community structure. All taxa were classified into one of the following functional feeding groups: shredder, scraper, gatherer, filterer and predator (Cummins and Klug 1979, Merritt and Cummins 1996, Scoggins 1996, Mackie 2004). For taxonomically rich groups (e.g. Chironomidae), the "value" of the feeding niche for that organism was divided equally among the number of groups it encompassed. For example, one Chironomidae specimen lent 0.2 to each of the five feeding groups because its members cover all the groups delineated in this study. Percent abundance of each functional feeding group was calculated for site and season. Macroinvertebrates were sorted as "rare" and "common", defined as appearing in at least 2% of the 167 total samples including d-net, Hess and drift.

Spatial and temporal habitat differences between sites were assessed with Principal Components Analysis (PCA). Macroinvertebrate associations with site, season and habitat were accomplished with Canonical Correspondence Analysis (CCA; ter Braak 1986). Site comparisons across the drainage were done with ANOSIM and longitudinal trends in the mainstem were examined with cluster analysis and multidimensional scaling (MDS; Clarke and Gorley 2001). Seasonal turnover was measured with the Renkonen Similarity Index (RSI). Monte Carlo simulations estimated the significance of habitat variables in the partial CCA analyses (ter Braak and Smilauer 2002). Variance partitioning technique (VPT; Borcard et al. 1992, Magnan et al. 1994, Williams et al. 2002) provided the percent variance in assemblage structure attributable to each of three variables: site, season and habitat.

CHAPTER III

RESULTS

Habitat

Mainstem, tributary and seep macrohabitats formed three distinct groups based on habitat characteristics. Principal component Axis 1 explained 26% of the habitat variation and described a substrate, depth, and current velocity gradient (A 3). Principal component Axis 2 explained 18% of the habitat variation and also described a gradient of substrate, depth and current velocity. Mainstem habitats had swifter current velocity [mean $(\pm SE)$; m/s] 0.34 (0.04), moderate depths (m) 0.47 (0.03), and predominately bedrock substrate 40% (5%). Tributary habitats had moderate mean current velocities (0.13 - 0.25 cm/s) and greater depths (0.35 - 0.87 m), and generally greater amounts of vegetation (5-41%) and detritus (11-19%). Seep habitats were the shallowest among the three habitat types sampled (0.03 - 0.15 m) with predominately sand substrate over bedrock and with negligible flow. A CaCO₃ layer up to 5-mm thick was observed on most benthic substrates, organic and inorganic, at all sites and seasons except at the Little Blanco River and only in low amounts at Site 7 on the mainstem. Means $(\pm 1 \text{ SE})$ and ranges for water quality measures in the Blanco River basin were water temperature 21.0 °C (0.5) (range 9.1 – 30.8 °C), pH 7.9 (0.0) (7.3 – 8.2), dissolved oxygen DO 8.9 mg/l

(0.1) (5.7 – 13.7 mg/l), specific conductivity 441 μ S/cm (4) (280 – 562 μ S/cm) and alkalinity 4.0 meq/l (0.1) (2.7 – 5.2 meq/l). Spatial, temporal, and diel patterns in water quality measures within the basin were assessed in a concurrent study and reported elsewhere (Cave 2006).

Benthic Community

A total of 30,071 macroinvertebrates and 181 taxonomic groups, representing 25 orders including 11 orders and 64 families of insects, were collected from the Blanco River drainage (B 4). Insects, primarily Ephemeroptera, Diptera, and Trichoptera, were 87% of the total number of macroinvertebrates collected. Non-insects (i.e., Acari, Crustacea, and Mollusca) were 12%. Among the 185 taxonomic groups identified, 117 taxa were common, representing 99% of the total number collected, and 64 taxa were considered rare. The most common macroinvertebrates were Chironomidae (found in 81% of samples), Simuliidae (69%), *Chimarra* (57%), *Camelobaetidius* (56%) and Acari (54%). Rare taxa included nine Coleoptera and five Hemiptera genera.

Collectively, the macroinvertebrate community contained several abundant taxa, a few ubiquitous taxa, one exotic invasive taxon, and one taxon previously not described in central Texas. The seven most relatively abundant insects were Chironomidae (11%), Simuliidae (9%), *Hydroptila* (6%) and *Tricorythodes* (5%), *Chimarra* (5%), *Baetodes* (4%) and *Camelobaetidius* (4%). Riffle beetles (Elmidae and Dryopidae) were the most abundant coleopterans collected (84%) and along with the damselfly *Argia* (Coenagrionidae) were the most ubiquitous taxa across sites and seasons. The exotic invasive clam *Corbicula fluminea* was captured in 28% of the samples with an overall

relative abundance of 1.5%. It was found throughout the watershed although 90% of the total number of *C. fluminea* were collected at sites 6 and 7. Two specimens of the endemic blind cave amphipod, *S. russelli*, were captured in the Little Blanco River in January and April 2004 suggesting a possible persistent population. One riffle beetle *Dryops arizonensis* (Dryopidae: Coleoptera) was captured at Site 2 in October 2003. Prior to this collection, *D. arizonensis* was reported only west of the Trans-Pecos region in West Texas (Brown 1972). This is a new record for Blanco County and extends the range of *D. arizonensis* eastward.

Mean taxonomic richness at each site varied considerably by system and sampling method (B 1). The range of richness (\pm SE) in mainstem qualitative samples was 11.6 (2.3)-22.5 (2.7). The tributaries were moderate, ranging between 15.0 (2.2)-18.1 (2.3) taxa per sample. Seeps had comparatively low sample richness: 7.5 (1.5)-11.1 (2.1). Richness in quantitative samples ranged from 16.8 (1.5) in Site 4 drift, to 28.6 (5.6) in Site 7 Hess samples. Sixteen taxa were exclusive to the mainstem samples and eight of these were collected only at Site 7. Tributaries and seeps each contained taxa not found in the mainstem (B 2). The Little Blanco contributed 4 unique taxa. The seeps were low in diversity (1.8 – 2.0), yet contained several taxa found only in the seeps (i.e., *Archilestes, Helicopsyche* and *Phylloicus*). The seeps also had higher dominance (0.20 – 0.23) than most other sites in the mainstem and tributaries.

Among functional feeding groups, gatherers (31%) were the most common, followed by scrapers (26%), filterers (25%), predators (18%), and shredders (<1%) (B 3). Gatherer and filterer taxa in the mainstem and tributaries were attributed to the abundance of Hydropsychidae caddisflies and Simuliidae. Ephemeroptera, Trichoptera and Coleoptera contributed the most scraper taxa. Odonates were the dominant predators in the mainstem and tributaries whereas Hemipterans and diving beetles were the more common predators in the seeps. The high abundance of shredders at the Narrows Seep (19%) was attributable to the crenophilic Trichopteran shredders, *Phylloicus* and *Marilia* and several Dipterans.

Site, Season, Habitat Effects

Site, season and habitat explained 33% of the taxonomic variation within the drainage in CCA analysis (F = 1.35, P < 0.01) (A 4). Habitat effects explained 17% (F = 1.5, P < 0.01) and season effects explained 6% (F = 2.0, P < 0.01). Site explained 9% and was not significant (F = 0.91, P = 0.67). Axis 1 explained 13% and described a gradient of season, current velocity and substrate [winter (0.24), velocity (0.24), summer (-0.29), silt (-0.23)]. Axis 2 explained 7% and described a gradient of season, substrate and vegetation [Cobble (0.29), gravel (0.18), summer (0.18), bedrock (-0.28) and vegetation (-0.21)]. Ephemeropteran and Trichopteran abundance were associated with summer, silt, and slower current velocity. Crustaceans, mollusks, and minor insect orders were associated with the winter and higher current velocity. Dipteran abundance was associated with cobble and gravel and site 2. Megalopteran abundance was associated with sand substrate, vegetation, slower current velocity, and the Narrows seep. Odonate abundance was associated with bedrock substrate and fall. Although site effects did not explain a significant portion of the total taxonomic variation, tributaries and seeps tended to have higher abundances of less common taxa such as Plecoptera, Hemiptera,

Lepidoptera, Orthoptera, Neuroptera, Collembola, Nematoda, Turbellaria, Oligochaeta, and Hirudinea.

Longitudinal patterns in the mainstem were not detected in habitat, taxonomic and functional feeding group analyses. Analysis of similarity and MDS paired non-adjacent sites according to habitat (A 5), departing from the expected pairing of sites 1 and 2, 2 and 3, etc., if a gradient were present. In contrast to CCA results for site analysis across the drainage, site differences among mainstem assemblages from qualitative samples alone were significant in ANOSIM tests (R = 0.086, P = 0.02). Non-adjacent sites showed greater taxonomic similarity than adjacent sites (A 6). Shredders were almost absent in the Blanco River, contrary to the expected abundance in upstream sites (B 3, A 7). Scrapers consistently measured 20% at every site. Gatherers and filterers were prominent at every site (45-63% combined) and showed a slight increase in downstream sites. Predators averaged one-quarter of each site except at sites 6 and 7 where they were replaced by filterers.

Drift

A total of 13,221 invertebrates representing 122 taxa were collected as drift. Among these, 45 taxa were not captured during the benthic surveys. Drifting community consisted of insects (83%), primarily Ephemeroptera, Trichoptera, Coleopteran and Diptera, and non-insects (12%). Overall, most abundant taxa were *Tricorythodes* (12%), Simuliidae (10%), Chironomidae (8%) and *Baetodes* (7%). Drift richness and densities were highest at post-dusk and pre-dawn hours (A 8). Most taxa drifted at night; only 11 taxa did not and these combined to 2% of all drifting macroinvertebrates in this study. Abundant drifters with the most pronounced periodicity (night : day drift density ratios) were *Procloeon* (34), *Neoelmis* (adult; 22), *Tricorythodes* (15) and *Chimarra* (12). Even Acari (water mites), which were 12% of all drifting invertebrates and are cited in some studies as day-drifters (Elliott and Minshall 1968; Allan 1995), had night : day ratios over 7. Sites sampled with drift nets in addition to benthic collection methods (sites 1, 4, and 7) had greater numbers of taxa than those not sampled with drift nets. Some taxa were captured only in the drift including several Baetid mayflies and surface dwelling Hemipterans and Coleopterans. Likewise, some taxa common in the benthic samples were absent in the drift, most notably Odonates, Plecopterans (which were low in abundance in the watershed) and *C. fluminea* which was 5x more abundant in benthic samples than in the drift.

Bray-Curtis similarity and multi-dimensional scaling (Figs. 9 and 10) show that samples from the same site were more similar than samples from the same season. ANOSIM pairwise comparisons of drift samples were marginally significant for site differences (P = 0.10) but not significant for season (P > 0.5). Drift density and taxa richness differed primarily among sites but also among seasons. Highest density was at Site 7 (1077 organisms per 24 h) followed by Sites 1 (981) and 4 (862). Mean richness (\pm 1 SE) also was highest at Site 7 [25.0 (2.33)] followed by sites 1[19.5 (2.3)] and 4 [16.8 (1.5)]. Mean percent similarity in assemblage structure was 0.43 (0.09) between Sites 1 and 4, 0.35 (0.08) between sites 4 and 7, and 0.34 (0.08) between Sites 1 and 7. Differences among sites were attributed to a much higher relative abundance of Acari 25.7 (12.7) at Site 1, Simuliidae at Site 4 [26.9 (8.0)] and Tricorythidae [18.9 (2.4)] at Site 7. Seasonally, highest density was during the summer (1441) followed by fall (832) and spring (637). Correspondingly, mean richness was highest during the summer 22.7 (2.4), followed by fall 22.7 (1.7) and spring 15.5 (1.7). Mean percent similarity among season was 0.49 (0.02) for spring-summer, 0.53 (0.04) for summer-fall, and 0.53 (0.83) for spring-fall.

CHAPTER IV

DISCUSSION

The Blanco River watershed is in a region of karst bedrock with shallow soils and is subjected to unpredictable, sometimes torrential, rainfall followed by extended periods of drought. The mainstem provides habitat suitable for invertebrates adapted to hydrologic variability whereas the tributaries and seeps offer alternative substrates and hydrologies that shelter rare and endemic taxa from the harsh climate and hydrogeology of the region.

Longitudinal connection between sites in the Blanco River mainstem was broken several times by drought during this study. On some occasions, many kilometers of river bed became disconnected pools, runs and shallow riffles. Low-head dams (> 80) are scattered on the river's 140 kilometer length and exacerbate the natural longitudinal discontinuity (Ward and Stanford 1983). The generally impermeable river bed limited interstitial exchanges and intensified the scouring effects of the river's flash floods on the shallow, sparse beds of cobble that would otherwise have retained organic matter swept in from the riparian zone during flood stage (Junk et al. 1989, Hoover et al. 2006), thus limiting vertical and lateral exchanges.

Differences between mainstem site assemblages (A 6) might be attributable to local geomorphologies. Sites 1, 4 & 5 formed one group while sites 2, 6 & 7 formed a

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second group and Site 3 was most dissimilar from all others. The first group of sites was distinguished by greater width, more bedrock substrate and almost no canopy cover. The second group of sites was narrower, contained more cobble and had more canopy cover than any other sites. Site 3 was surrounded on both sides by sheer limestone cliffs 15m high and it's assemblage was influenced by taxa from the adjacent Narrows Seep that flowed into the mainstem.

Shredder abundance was likely inhibited by low riparian shading, low leaf retention in the river channel and regionally low abundances of shredder taxa (Bayer et al. 1992). Scraper abundances were somewhat higher in response to greater autotrophic production associated with wide, shallow, exposed flows. Gatherer and filterer taxa abundances did conform somewhat to the RCC model since they accounted for 50% of the population at nearly all mainstem sites and increased slightly at downstream sites 6 and 7. In general, discrepancies between the Blanco River (a 2^{nd} order stream) and the expectations of the RCC model for small-order streams is likely a function of geomorphology and riparian productivity. Nearly all of the sampling sites in the Blanco River were wide (4 - 30 m) and shallow (0.4 - 0.6 m) with predominately bedrock substrate. Most sites had minimal canopy cover (less than 5% of the streambed was shaded at all sites) and the riparian at Sites 1, 2, 4, 5 and 6 was partially cleared for ranching and/or recreation, thus limiting allochthonous inputs. Furthermore, limited cobble/gravel substrate and frequent flash-flooding can hamper leaf-litter retention (Dobson et al. 1992, Richardson 1992, Ruetz et al. 2006).

Tributaries and seeps provided habitat not found in the mainstem and this is reflected in the diversity and ecology of the taxa they contributed to the drainage. The

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Little Blanco River site was more structurally heterogeneous than most mainstem sites at the geomorphic unit and microhabitat scale and this may partly explain the more diverse macroinvertebrate assemblage (Downes et al. 1998, Minshall and Robinson 1998). Lentic flows, cobble substrate and low CaCO₃ precipitation at the Little Blanco River site enabled greater macrophyte abundance and hyporheic exchange, indicated by a persistent population of *S. russelli*. Such hyporheic interactions are the exception in the Blanco River watershed according to our data. Seep assemblages also contained several unique taxa (B 2). Some were found consistently at the seeps though they appeared rarely or not at all at other sites including *Helicopsyche* and *Caloparyphus*. The seeps enjoyed relatively consistent, cool flows even when precipitation was low, suggesting that taxa exclusive to the seep sites were crenophilic taxa intolerant of the more stochastic riverine environment of the mainstem.

The proximity of Site 7 to the San Marcos River (6 km from the confluence; A 2) may explain the high total taxa, richness and unique taxa found there (Sagar and Glova 1992, Cellot 1996, Shearer et al. 2002). Higher dominance at Site 7 suggests that many taxa were transient and never formed a large contribution to this downstream community. Taxa originating in the San Marcos River might be attempting to disperse into the Blanco River but are blocked by a low-head dam 500m above Site 6. Interestingly, Sites 6 and 7 supported the Blanco River's largest colony of *C. fluminea* and the San Marcos River is known to support populations of the exotic invasive clam (Howells et al. 1996). However the low abundance and frequent presence at the upstream sites (1-5) indicates that proximity to the San Marcos River is less likely an explanation of their distribution than the Blanco River's hydrogeology. The bedrock substrate and intermittency may

dampen the invasive strength of the clam by limiting its upstream movement and reproduction in the often-dry, yet regularly scoured, bedrock river channel.

Comparisons with other studies indicate that macroinvertebrate diversity in Edward's Plateau streams is higher than previously reported. In 1988, 52-59 taxa were collected by Bayer et al. (1992) in a survey of least-disturbed streams in the eastern Edward's Plateau. The Little Blanco River was the only stream in the Blanco River drainage studied by Bayer et al., yet several other streams were within 20 km of the watershed:. Onion Creek, Hays Co.; Carper's Creek, Comal Co.; and Little Barton Creek, Travis Co. One riffle from each stream was sampled during low-flow with 3 composited square-foot surber samples. Many taxa were not shared between the drainages in Bayer et al. (1992) and the current study. Amazingly, only 13 taxa were held in common between the assay of Bayer et al. and the current study of the Little Blanco River. Furthermore, 19 genera from the Little Blanco River in Bayer et al. were absent from the entire Blanco River drainage in the current study. These facts suggest that individual assays have strongly underestimated the contribution of the Blanco River watershed to the aquatic macroinvertebrate diversity in the Edward's Plateau.

The majority of unique taxa listed in this study were represented by only one individual; however, those captured only once or in low abundance should not be overlooked. For instance, Resh et al. (2005) found that in a California stream, "rare" taxa, in sum, were major portions of each sample and over large time scales quite common. In the Blanco River, some taxa were common at only one site (e.g. *Phylloicus*, Narrows Seep) and thus reveal their contribution to the watershed only at smaller spatial scales such as reach. Some taxa were also exclusive to the drift (e.g. *Polycentropus* and *Oxyethira*) and would have been under-represented except for the added effort of drift sampling (e.g. Hemiptera). Central Texas is a region known to possess a high number of rare and endemic species of aquatic macroinvertebrate taxa (Brown 1972, Edwards 1973, Longley 1981, Bowles and Arsuffi 1993). Based on our data and comparisons with Bayer et al. (1992), robust assessment of the abundance and distribution of rare and endemic species in the Edward's Plateau requires diversified sampling approaches including drift and benthic sampling.

Drift dominance by Ephemeropteran, Trichopteran and Dipteran taxa is consistent with studies in temperate, alpine and equatorial streams (Allan 1995, Matzinger and Bass 1995, Schreiber 1995, Jacobsen and Bojsen 2002, Hieber et al. 2003). Likewise, drifting invertebrate density peaks at post-dusk and pre-dawn (the "bigeminus" pattern; Müller 1965) is common to previous studies (Müller 1974, Bergey and Ward 1989, Smock 1996, Ramirez and Pringle 1998) and was similar across the three dates and seasons (A 9), suggesting that even in karst streams, during low flow, invertebrates drift in predictable cycles.

Diel drift has been associated with acquisition of and competition for resources (Delucchi 1989, Richardson 1991, Dobson and Hildrew 1992, Siler et al. 2001), as well as predator avoidance (Skinner 1985, Allan 1995). Vannote et al. (1980) postulated that organic matter in streams of the southwest United States is limited relative to streams in the northeast United States. This assumption is supported by seasonal shifts in drift densities for some Baetid mayflies in the Blanco River. The density of night drifting *Baetodes* and *Procloeon* increased with an increase in overall densities for those genera (A 11), suggesting density dependant drift behavior. In contrast, the density of night drift

in *Camelobaetidius* was the converse of overall *Camelobaetidius* densities perhaps indicating greater use of darkness by an older, larger population to avoid predation. Allan (1978) and Skinner (1985) found that larger size classes of *Baetis* were more prone to drift than smaller size classes and both hypothesized this was the result of predatoravoidance since larger larvae are more vulnerable to drift-feeding fish. Thus, seasonal shifts in drift density patterns among these 3 Baetidae genera in the Blanco River might stem from fluctuations in size-class ratios and vulnerability to predation.

Seasonal patterns in aquatic macroinvertebrates from intermittent streams are distinguishable, despite asynchronous life cycles in some common central Texas aquatic insects (Stanley and Short 1988, Tiemann and Arsuffi 1991), because of adaptations to the local climatic and hydrologic context (Robinson et al. 1993, Meyer and Meyer 2000, Bunn and Arthington 2002). For instance, minor insect orders (Plecoptera, Hemiptera, Lepidoptera, Orthoptera, Neuroptera, Collembola) were associated with winter (January) samples taken during periods of relative hydrologic stability (at least 5 weeks post-spate; A 1). It appears uncommon taxa are able to recolonize the drainage during times of hydrologic stability whereas periods of higher spate frequency favor the resilient taxa most adapted to hydrologic disturbance (Feminella 1996, Smith et al. 2003). Thus shifts from "summer" to "winter" taxa may be understood as shifts from "wet" season to "dry" season taxa.

The Blanco River is spatio-temporally disconnected and has a hydrogeology that limits available organic matter in the river channel. Yet, for the aquatic macroinvertebrates living in its waters, it is stable because it is the hydrogeological context to which they are adapted. The majority of macroinvertebrates in the Blanco River watershed are R-selected organisms with relatively brief life-spans, such as Simuliidae and Chironomidae, making them resilient to the variable flow conditions in the region. Uncommon, rare and endemic taxa, however, were more abundant in tributary and seep habitats and occupied the mainstem in greater numbers during periods of relative hydrologic stability (January). The karst geology of the drainage also provides habitat for endemic groundwater fauna that interact with surface waters in those regions of the watershed where hyporheic exchange is possible. The biotic diversity within the Blanco River watershed is clearly tied to habitat diversity: stable and unstable habitats, surface and subsurface flows and close proximity to taxonomically rich aquatic habitats (i.e. the San Marcos River). This template is common in the Edward's Plateau because its streams lie on the same karst geology and are subjected to weak climatic seasonality and precipitation patterns that favor invertebrate assemblages adapted to hydrologic variability.

Aquifer draw-down, urbanization and water-retention devices threaten to alter the natural hydrologic patterns of the Blanco River drainage. Conservation of biotic diversity in the watershed should begin with preservation of the physical diversity found within mainstem, tributary and seep habitats.

APPENDIX A FIGURES

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A 1. Historical and recent flows (m3/s) from USGS gauge station in Kyle, Texas (between Sites 5-6). Drift and benthic samples indicated by gray and black arrows. Between Oct 22 and Oct 24 2004 the Blanco River demonstrated its flashiness when flows increased from 1.2 to 169.0 CMS and back to 26.2 CMS in 48 hrs.



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A 8. Diel drift densities (no./m³) and richness for Sites 1, 4 & 7 for the spring, summer and fall sampling dates. Bars represent day and night sampling hours. Note peaks at post-dusk and pre-dawn hours. Density was unavailable for Site 4 in Sept for lack of flow data.



A 9. Multidimensional scaling of drift samples grouped by site (A) and season (B).



A 10. Bray-Curtis similarity of drift samples showing site groups. The May sample at Site 7 was the most dissimilar from all other sites and dates perhaps because it was placed at the end of a long pool whereas subsequent samples were placed at the end of riffles. It is grouped with other Site 7 samples for graphical considerations.



A 11. Densities and night : day drift ratios for selected Baetidae (Ephemeroptera).

APPENDIX B

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	Total											Total
System	Taxa	Unique		Richness			H'			Dominance		Samples
	_		Qual	Drift	Hess	Qual	Drift	Hess	Qual	Drift	Hess	
Blanco	167											140
1	108	3	17.5 ± 3.8	19.5 ± 2.3		2.3 ± 0.2	2.1 ± 0.1		0.17 ± 0.04	0.22 ± 0.03		32
2	67	1	22.5 ± 2.7		20.2 ± 1.8	2.7 ± 0.1		2.5 ± 0.1	0.10 ± 0.02		0.13 ± 0.03	13
3	34	1	12.5 ± 3.7			2.2 ± 0.4			0.19 ± 0.09			4
4	93	3	11.6 ± 2.3	16.8 ± 1.5		1.9 ± 0.2	2.2 ± 0.1		0.25 ± 0.06	0.17 ± 0.01		31
5	59	1	21.8 ± 1.7			2.5 ± 0.2			0.14 ± 0.03			8
6	80	1	15.5 ± 2.9		25.3 ± 2.2	2.2 ± 0.2		2.2 ± 0.1	0.16 ± 0.03		0.17 ± 0.03	15
7	115	8	18.7 ± 2.1	23.4 ± 2.3	28.6 ± 5.6	2.2 ± 0.3	2.4 ± 0.1	2.1 ± 0.2	0.21 ± 0.09	0.14 ± 0.01	0.26 ± 0.08	37
Little Blanco	67	4	18.1 ± 2.3			2.5 ± 0.1			0.11 ± 0.01			8
Cypress Creek	45	2	15.0 ± 2.2			2.2 ± 0.1			0.17 ± 0.02			8
Hammond Seep	23	2	7.5 ± 1.5			1.8 ± 0.2			0.20 ± 0.03			4
Narrows Seep	37	2	11.1 ± 2.1			2.0 ± 0.2			0.23 ± 0.01			7
Drainage Total	181											167

B 1. Taxonomic richness, diversity and dominance in the Blanco River drainage. Unique taxa are those found only at that site. Means ± 1 standard error are provided.

	Blanco River		Tributaries	Seeps	
Site 1	Site 4	Site 7	Little Blanco River	Hammond	
Helobata	Didymops	Anagapetus	Brachymesia	Libellula	
Laccophilus	Gelastocoris (Kirklady)	Atrichopogon (Kieffer)	Leptophlebia	Rhantus	
Neotrichia Gyrinus Ceratopogon (Meiger		Ceratopogon (Meigen)	Myxosargus (Brauer)		
		Dolichopodidae	Stygobromus	Narrows	
Site 2	Site 5	Mallochohelea		Crambus	
Dryops	Curicta	Pleuroceridae	Cypress Creek	Enochrus	
		Potamyia	Archips		
Site 3	Site 6	Psephenus	Buenoa		
Metrichia	Pelonomus				

B 2. Unique taxa for each site were found in no other sites within the Blanco River drainage during the two year study.

System	Shredder	Scraper	Gatherer	Filterer	Predator	n
Blanco	0.4 ± 0.1	20.0 ± 0.9	28.8 ± 1.0	26.1 ± 1.5	24.7 ± 1.3	140
1	0.9 ± 0.2	18.5 ± 1.8	32.8 ± 1.8	12.0 ± 1.5	35.8 ± 3.1	32
2	0.2 ± 0.2	17.4 ± 2.5	26.5 ± 2.7	31.8 ± 3.5	24.0 ± 3.8	13
3	1.7 ± 1.7	12.5 ± 5.4	31.9 ± 6.2	14.9 ± 9.2	39.1 ± 8.7	4
4	0.2 ± 0.1	22.5 ± 1.6	20.1 ± 1.4	32.5 ± 3.0	24.6 ± 2.6	31
5	0.2 ± 0.2	15.7 ± 3.1	21.9 ± 3.4	38.3 ± 5.2	23.9 ± 4.4	8
6	0.0 ± 0.0	17.1 ± 2.1	25.4 ± 2.9	37.6 ± 5.7	19.9 ± 4.2	15
7	0.2 ± 0.1	22.8 ± 2.0	36.0 ± 2.0	25.0 ± 2.4	16.1 ± 1.6	37
Little Blanco	7.3 ± 1.9	10.4 ± 2.1	24.6 ± 2.8	22.9 ± 6.6	34.8 ± 5.4	8
Cypress Creek	0.1 ± 0.1	15.3 ± 2.6	19.2 ± 4.7	37.9 ± 4.1	27.5 ± 5.8	8
Hammond Seep	0.8 ± 0.8	12.1 ± 4.4	29.0 ± 9.7	6.0 ± 4.8	52.1 ± 7.4	4
Narrows Seep	25.2 ± 8.1	7.7 ± 2.6	27.0 ± 9.7	5.2 ± 1.9	34.9 ± 4.2	7
Drainage Total	1.8 ± 0.6	18.6 ± 0.9	28.1 ± 1.1	25.2 ± 1.5	26.4 ± 1.4	167

B 3. Functional feeding group distributions for the Blanco River, Little Blanco River, Cypress Creek and Hammond and Narrows Seeps October 2003 – July 2005. Means ± 1 SE are provided.

Taxa	System
Insecta	
Ephemeroptera	
Ephemeridae	
Hexagenia	B LB
Tricorythidae	
Tricorythodes	B LB CC
Leptohyphes	B LB CC
Caenidae	
Caenis	B LB
Brachycercus	В
Heptageniidae	
Stenonema	B LB CC N
Isonychiidae	
Isonychia	B LB CC
Leptophlebiidae	
Neochoroterpes	B LB
Paraleptophlebia	В
Thraulodes	B LB N
Choroterpes	В
Traverella	В
Leptophlebia	LB
Farrodes	В
Baetidae	
Fallceon	B CC N
Procloeon	B CC
Camelobaetidius	B LB CC
Paracloeodes	B LB
Baetodes	B CC
Acentrella	В
Centroptilum	В
Apobaetis	В
Barbaetis	В
Plauditus	B LB
Baetis	В
Labiobaetis	В
Americabaetis	В
Callibaetis	B LB H N
Plecoptera	
Perlidae	
Perlesta (Banks)	B LB N
Attaneuria (Ricker)	B CC
Neoperla	В
Leuctridae	
Zealeuctra	B LB

B 4. Taxa collected in the Blanco River (B), Little Blanco River (LB), Cypress Creek (CC), Hammond Seep (H) and Narrows Seep (N) from qualitative, Hess and drift samples October 2003 – July 2005. Taxa represented by only one specimen are noted with an asterisk.

Taxa	System
Trichoptera	
Philopotamidae	
Chimarra	B LB CC N
Polycentropodidae	
Polycentropus	B CC N
Polyplectropus	В
Neureclipsis	В
Cernotina	В
Nyctiophylax	В
Glossosomatidae	
Anagapetus	В
Hydroptilidae	
Hydroptila	B N
Ochrotrichia	B N
Oxyethira	В
Neotrichia	В
Mayatrichia	В
Ithytrichia	В
* Metrichia	В
Hvdropsychidae	
Cheumatopsyche	B LB CC
Hydropsyche	B LB
Smicridea	 B
* Potamvia	В
Leptoceridae	2
Nectonsyche	В
Oecetis	BLB
Helicopsychidae	
Helicopsyche	B N
Hydrobioscidae	
Atonsyche	В
Calamoceratidae	
Phylloicus	H N
Odontoceridae	
Marilia	B N
Ecnomidae	
Austratinades	В
Dintera	d
Chironomidae	BIBCCHN
Simuliidae	B LB CC N
Tabanidae	b Lb cc N
Tabanus	R I R
Stratiomuidaa	D LD
Strationus (Cooffron)	
Funammhus (Constaaker)	
Calor armhua	
Catoparypnus	
toxycera	вссп
* Myxosargus (Brauer)	LB

B 4. CONTINUED

Tava	System
Taxa	System
* Anophalas	CC
Ceretopogonidas	
Dasyholog (Kieffer)	В
Busyneieu (Kieffer)	B
Bezziu (Klejjel) * Mallochohalaa	B
Manahalaa	D
* Atrichopogon (Kieffer)	D
Culicoides	
* Caratonogon (Maigan)	D LD IN
Brohozzia (Kieffen)	B B N
Tipulidae	B N
Holomusia	D N
Houstonia	B N
<i>Hexuloma</i>	В
Chaliford	P
Chelijera Homorodromia	D
nemeroaromia Athoricidae	D
	BCC
	В
Odonata	В
Calopterygidae	
Hetaerina	B LB
Coenagrionidae	
Argia	B LB CC H N
Enallagma	B LB
Amphiagrion	В
Lestidae	
Archilestes	CC H N
Gomphidae	
Hagenius	B LB CC
Gomphus	B LB CC
Phyllogomphoides	B LB
Erpetogomphus	B LB N
Dromogomphus	В
Libellulidae	
Macrothemis	B LB
Dythemis	B LB
Brechmorhoga	B CC N
* Brachymesia	LB
Leucorrhinia	LB CC
* Libellula	Н
Corduliidae	
Epitheca	B LB CC
Macromia	B LB
Neurocordulia	В
* Didymops	В
Aeshnidae	
Basiaeschna	В

B 4. CONTINUED

Taxa	System	
Coleoptera		
Elmidae		
Macrelmis A	B CC	
Macrelmis L	B CC	
Neoelmis A	В	
Neoelmis L	В	
Stenelmis A	B CC	
Stenelmis L	В	
Microcylloepus A	В	
Microcylloepus L	В	
Hexacylloepus A	В	
Hexacylloepus L	В	
Dubiraphia A	В	
Dubiraphia L	В	
Cylloepus A	В	
Heterelmis A	В	
Heterelmis L	В	
Ordobrevia A	В	
Ordobrevia L	B N	
Phanocerus A	В	
Phanocerus L	В	
Dryopidae		
* Dryops arizonensis A	В	
Postelichus A	В	
Helichus A	В	
* Pelonomus A	В	
Lutrochidae		
Lutrochus A	B LB CC	
Lutrochus L	B CC	
Gyrinidae		
Dineutus A	В	
Gyretes A	В	
Gyretes L	В	
Gyrinus A	В	
Haliplidae		
Peltodytes A	B LB	
Haliplus A	B LB	
Dytiscidae		
Agabus L	LB CC	
Celina A	В	
Derovatellus A	B LB	
* Laccophilus A	В	
* Rhantus A	Н	
Liodessus A	B H N	
Psephenidae		
Psephenus L	В	
Scirtidae		
Scirtes L	В	

B 4. CONTINUED

Таха		S	vsten	n	
Hydrophilidae		2	<u></u>		
Berosus A	В	LB		Н	
Berosus L	В			-	
Tropisternus A	В	LB		Н	Ν
Tropisternus L	В				Ν
* Helobata A	В				
* Enochrus A					Ν
Hemiptera					
Corixidae					
Trichocorixa (Kirkaldy)	В				
Belostomatidae					
Belostoma	В	LB			
Naucoridae					
Ambrysus (Stal)	В	LB			Ν
Cryphocricos	В				Ν
Notonectidae				Н	
Buenoa	В		CC		
Veliidae					
Rhagovelia (Mayr)	В	LB	CC	Η	
Microvelia	В	LB		Н	
Mesoveliidae					
Mesovelia	В	LB	CC		
Hebridae					
Merragata	В				
Macroveliidae					
Macrovelia (Uhler)	В				
Saldidae					
Pentacora (Reuter)	В				
Gerridae					
Neogerris	В				
Metrobates (Uhler)	В		CC		
Trepobates (Uhler)	В	LB			
Rheumatobates (Bergoth)	В				
Aquarius (Schellenberg)	В	LB	CC	Η	
Limnoporus (Stal)		LB	CC		
Gelastocoridae					
* Gelastocoris (Kirklady)	В				
Nepidae					
* Curicta	В				
Megaloptera					
Corydalidae					
Corydalus	В	LB	CC		
Lepidoptera					
Pyralidae					
Petrophila	В		CC		
* Crambus					Ν
Tortricidae					
* Archips			CC		

B 4. CONTINUED

Taxa	System	
Neuroptera		
Sisyridae		
Climacia (McLachlan)	В	
Orthoptera	LB	
Tridactylidae		
Ellipes minuta (Sudder)	В	
Collembola		
Entomobrvidae	В	
Nematoda	B N	
Turbellaria	B CC N	
Oligochaeta	B IB CC H N	
Himidinge		
Arachnida	D LD II	
Aracimida		
Acall	B LB CC	
Perycypoda		
veneroida		
Corbiculidae		
<i>Corbicula fluminea</i>	B LB CC H	
Gastropoda		
Neotaenioglossa		
* Pleuroceridae	В	
Hydrobiidae	В	
Basommatomorpha		
Lymnaeidae	B H	
Fossaria	В	
Planorbidae^	B CC	
Menetus	B LB CC H	
Gyraulus	B LB	
Physidae	B LB CC H N	
Malacostraca		
Amphipoda		
Crangonyctidae		
Stygobromus russelli	LB	
Hvallelidae		
Hvallela	B LB	
Decapoda		
Cambaridae	BIBCCH	
Isopoda	B	
Ostracoda	D	
Bedesenide	D N	
r ouocopida Dranchionada	D IN	
	D	
	В	
Chydoridae		
Alona	R TR	
Bosminidae		
Bosmina	LB	

B 4. CONTINUED

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B 4. Continued

Taxa	System	
Daphniidae		
Ceriodaphnia	B LB	
Maxillopoda	В	Ν
Cyclopoida	В	

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VITA

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