DISSERTATION

A SURVEY OF COLORADO PLATEAU STREAM INSECT COMMUNITITES: THE ROLES OF RIPARIAN LEAF LITTER AND HYDROLOGIC VARIATION ON SPECIES GROWTH AND COMMUNITY STRUCTURE

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY ANGELA B. MOLINE ENTITLED A SURVEY OF COLORADO PLATEAU STREAM INSECT COMMUNITITES: THE ROLES OF RIPARIAN LEAF LITTER AND HYDROLOGIC VARIATION ON SPECIES GROWTH AND COMMUNITY STRUCTURE BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

A SURVEY OF COLORADO PLATEAU STREAM INSECT COMMUNITITES: THE ROLES OF RIPARIAN LEAF LITTER AND HYDROLOGIC VARIATION ON SPECIES GROWTH AND COMMUNITY STRUCTURE

Non-native saltcedar (*Tamarix* sp.) and Russian olive (*Elaeagnus angustifolia*) are now among the most common trees in western riparian zones, yet their effects on the growth of stream detritivores and the benthic community is largely unknown. I examined *Tipula* sp. growth on native (*Populus*) and non-native leaf litter in a laboratory experiment. *Tipula* larvae fed *Tamarix* were 1.7 and 2.5 times heavier than larvae fed *Elaeagnus* and *Populus*, respectively (Chapter 2).

The Colorado Plateau of Utah, Arizona, Colorado and New Mexico is remote and one of the least studied regions in the USA from the perspective of stream ecology. I compared the ability of environmental and biological variables to explain the variance in benthic insect and riparian vegetation communities at 25 Plateau streams. Median particle size and the number of flood-free days were strong predictors of insect density and richness, but periphyton and leaf litter abundance were not. non-metric multidimensional scaling revealed three stream types (mountain, valley, and canyon streams) based on riparian species composition (Chapter 3).

The hydrologic diversity of the Colorado Plateau makes it well suited to tests of habitat template theory; however, the stream hydrology of the region has not been characterized in an ecologically-meaningful way. I developed a conceptual model and classification system of unregulated Colorado Plateau streams based on two ecologically-relevant flow

axes: flow permanence and flood regime. I was able to correctly classify streams into four classes (perennial-snowmelt, non-perennial-snowmelt, perennial-rain-driven, and non-perennial-rain-driven streams) based on ecologically-relevant hydrologic metrics and GIS-derived landscape variables with approximately 85% accuracy (Chapter 4).

I addressed habitat template theory by testing the hypothesis that hydrologic disturbances (floods and droughts) are the major drivers of stream insect communities on the Colorado Plateau. I used family-level community metrics and six evolutionarily labile functional traits to test differences in the insect community assemblages in four stream classes. I found that disturbance-adapted taxa were common at all Colorado Plateau stream sites, but some insect traits (semi/univoltine, rare in drift, medium/large size) were more common in snowmelt-driven streams. I was able to predict snowmelt stream types from insect functional traits with 61% accuracy (Chapter 5).

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CHAPTER 1

INTRODUCTORY COMMENTS

CHAPTER 1

If there is a thread that ties this dissertation together it is my love of the Colorado Plateau, which is that "elevated, northward-tipping saucer" that occupies the four corners of Utah, Arizona, New Mexico, and Colorado (Rigby 1976). It is no secret that I have studied the Plateau for the past five years because it is a fascinating, beautiful, magical place. I am fortunate to have had the opportunity to scurry around the region wading streams, collecting bugs, counting trees, and sharing time with wonderful friends who served as field assistants. I am also fortunate to have discovered some things about the Colorado Plateau that further our understanding of the region and may possibly pique scientific and conservation interest in the area.

I started my dissertation with a very firm idea about how *Tamarix* is affecting western stream communities. I thought that *Tamarix* was very bad. I had experienced the dense saltcedar thickets of Grand Gulch, Utah and decided that anything exotic that was as abundant as saltcedar couldn't be good for the natives. This very firm idea was supported by research that my friend Ted Kennedy conducted while I was at the University of Minnesota (Kennedy 2002) and that my friends Joe Bailey and Jen Schweitzer conducted while I was at Northern Arizona University (Bailey *et al.* 2001). Both studies found evidence to suggest that saltcedar invasion is negatively affecting native stream biota. In order to test the hypothesis that "*Tamarix* is bad", I designed two experiments that are reported here. In the first experiment (Chapter 2), I compared the growth of an aquatic shredder (*Tipula* sp.) on diets of native *Populus* and non-native *Tamarix* and *Elaeagnus* leaf litter in the laboratory. The foundation of my very firm idea

began to crack during the pilot study for this experiment in the spring of 2004 when I found that an aquatic shredder grew significantly larger on *Tamarix* than *Populus*.

The second *Tamarix* experiment was a "natural experiment" (sensu Diamond 1986), in which I surveyed aquatic insect communities in unregulated streams along a saltcedar invasion gradient on the Colorado Plateau. Despite my expectation that *Tamarix* dominates the riparian zones of the Plateau, which was based on experience in the thickets of Grand Gulch, I found relatively little saltcedar on the Plateau. *Tamarix* was only present at 54.4% of the points sampled at my most abundant site (Lower Indian Creek). The preliminary data that came out of my first field season (fall 2004) on the Colorado Plateau caused me to reconsider the importance of riparian vegetation, and all biological variables, to the stream invertebrate communities in arid regions. On the Plateau, the periphyton and in-stream leaf litter abundances were much lower than I expected and the habitat heterogeneity, specifically the channel morphology and stream hydrology, was much greater than I expected. Prior to my second year of field work, I spent some time reading about the relative importance of biotic and abiotic factors to stream invertebrate communities in the West (Minshall 1978; Fisher *et al.* 1982; Schade and Fisher 1997; Lewis 1998). Chapter 3 is an attempt to quantify and describe my transition from "*Tamarix* is bad" to "maybe *Tamarix* isn't so important after all".

My more recent research has focused on characterizing hydrologic variability on the Colorado Plateau and assessing the relationship of aquatic invertebrates to streamflow. As evidenced by frequent citations to his work, this work builds on work done by my advisor, LeRoy Poff. For this research, I looked at the Colorado Plateau as a whole to determine which aspects of the physical environment affect stream insect

communities. I hypothesized that hydrologic disturbances were a major driver of lotic communities on the Plateau and that the stream insect assemblage should differ in streams with distinct flow regimes (Chapter 4). The conceptual typology of Colorado Plateau streamflow was borne out of the time that I spent in the field and conversations that I had with people who have spent more time in the field than I have. Briefly, the typology separates Plateau streams along "flood predictability" and "flow permanence" axes, which results in four stream types: perennial-snowmelt, non-perennial-snowmelt, perennial-rain-driven, and non-perennial-rain-driven streams. Although the stream classification system that I developed for the Colorado Plateau contains the uncertainty common to all statistical models and classification systems, I believe that it will provide a useful framework for future scientific research and conservation in the region.

Finally, I tested the relevance of the streamflow typology to the aquatic insect community on the Colorado Plateau. I approached this task from the perspective of insect functional traits, which have provided a lively topic of conversation in our lab meetings in recent years (see Poff *et al.* 2006 for details). I found that disturbance-adapted insect taxa, such as Chironomidae, Baetidae, and Simuliidae, are dominant on the Colorado Plateau; however, several insect families, which tend to be semi/univoltine, rare in the drift, and medium/large bodied, serve as indicator taxa for snowmelt streams (Chapter 5). It is unclear from my research whether the snowmelt-adapted insect assemblage is a result of local adaptation, regional biogeography, or environmental filtering (sensu Poff 1997), but I hope that it will provide the foundation for future Colorado Plateau stream studies.

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CHAPTER 2

AQUATIC INVERTEBRATE SHREDDER GROWTH ON NATIVE (*POPULUS*) AND NON-NATIVE (*TAMARIX, ELAEAGNUS*) LEAF LITTER

CHAPTER 2

Abstract

Non-native saltcedar (*Tamarix* sp.) and Russian olive (*Elaeagnus angustifolia*) are now among the most common trees in western riparian zones (Friedman *et al.* 2005), yet their effects on the growth of stream detritivores and the benthic community is largely unknown. The aim of this study was to compare the growth of aquatic crane fly larvae (Diptera: Tipulidae) on native *Populus* and non-native *Tamarix* and *Elaeagnus* leaf litter in the laboratory. We also sought to relate *Tipula* larvae growth to leaf morphology and chemistry.

Tipula was able to grow on leaf litter of all three species. After seven weeks, crane fly larvae showed the greatest growth on *Tamarix* leaf litter; larvae fed *Tamarix* were 1.7 and 2.5 times heavier than larvae fed *Elaeagnus* and *Populus*, respectively. *Tipula* survival was highest on *Populus*, intermediate on *Tamarix*, and lowest on *Elaeagnus*. Our results indicate that *Tamarix* may produce the highest crane fly larvae growth because of its favorable leaf chemistry (high nitrogen and low structural carbon). Although *Tamarix* leaf litter provided the best food for *Tipula* larvae in the lab, *Tamarix* litter appears to be rare in western US streams.

2.1.0. Introduction

Non-indigenous species invasions threaten native species (Wilcove *et al.* 1998) and are a major component of anthropogenic global change (Lodge and Shrader-Frechette 2003). Stream and river floodplains are particularly susceptible to non-native invasion because they are subject to natural disturbances and anthropogenic alteration of natural disturbance regimes, both of which provide opportunities for invasion (Hood and Naiman 2000). Non-native trees are replacing native riparian forests along streams and rivers around the world (Rood and Mahoney 1990; Pysek and Prach 1994; Friedman *et al.* 2005). Some non-native tree species were deliberately introduced to riparian areas as forest plantations (Abelho and Graça 1996; Valdovinos 2001; Thompson and Townsend 2003), while other shrubs and trees became naturalized in riparian areas after escaping cultivation (Schulze and Walker 1997; O'Connor *et al.* 2000; Decruyenaere and Holt 2005).

The occurrence of non-native vegetation in riparian zones, and the subsequent introduction of non-native leaf litter to streams, has implications for energy flow and aquatic invertebrate communities in streams. Riparian vegetation influences several aspects of stream energy budgets including light availability, dissolved nutrient inputs, particulate organic matter input, and organic matter retention (Gregory *et al.* 1991; Sweeney 1993). Leaf litter serves an important role in stream ecosystems as it provides food and habitat for aquatic invertebrates (Cummins *et al.* 1989). Allochthonous litter inputs can provide up to 98% of the energy budget of small headwaters streams (Vannote *et al.* 1980) and leaves make up 49-98% of allochthonous litter inputs to streams (Abelho 2001). Experimental manipulations have shown that leaf litter addition increases

macroinvertebrate abundance in streams (Dobson *et al.* 1992) and that litter exclusion reduces abundance (Wallace *et al.* 1997), especially for shredder taxa . Shredders facilitate energy and nutrient cycling in streams by consuming and fragmenting allochthonous leaf litter (Cummins *et al.* 1989) and their life cycles may be tied to the timing and decomposition rate of leaf litter input (Cummins 1974). Therefore, a change in riparian vegetation may alter aquatic invertebrate population dynamics (Basaguren and Pozo 1994) and could potentially change energy flow and nutrient cycling.

Previous research has shown that non-native riparian invasion can have deleterious effects on aquatic insect communities. For example, studies of exotic eucalyptus (*Eucalyptus globulus*, Labill.) plantations in Portugal have revealed that streams in eucalyptus forest support fewer taxa and lower invertebrate abundance than streams in native chestnut (*Castanea sativa*, P. Mill.) forest (Abelho and Graça 1996). Eucalyptus also decomposes more slowly than native alder (*Alnus glutinosa*, L.) and chestnut (Basaguren and Pozo 1994) and a native shredder (*Tipula lateralis)* has reduced growth and survival on eucalyptus compared to the two natives (Canhoto and Graça 1995). In South America non-native Ponderosa pine (*Pinus ponderosa*, Lawson) decomposes more slowly than native leaf litter (Valdovinos 2001) and native shredders do not appear to feed on pine needles (Albarino and Balseiro 2002). The lack of palatability and decomposability of both pine and eucalyptus was attributed to leaf chemistry, including structural carbon and polyphenols.

Non-native saltcedar (*Tamarix* sp., L) and Russian olive (*Elaeagnus angustifolia*, L) are the third and fourth most frequently occurring trees in riparian zones of the western United States (Friedman *et al.* 2005). *Tamarix* and *E. angustifolia* were

introduced from Eurasia in the mid-1800s and both have become naturalized in the western US (Katz and Shafroth 2003; Shafroth *et al.* 2005). *Tamarix* tends to occur in the warmer, drier south, whereas *Elaeagnus* dominates in the cooler, wetter north (Friedman *et al.* 2005). The effect of *Tamarix* invasion (Shafroth *et al.* 2005) on stream-riparian communities has received considerably more attention than *Elaeagnus* invasion (Katz and Shafroth 2003) and almost all of this research has focused on terrestrial species and food webs (e.g., (Ellis 1995; Ellis *et al.* 1997; Yard *et al.* 2004; Wiesenborn 2005).

Limited research suggests that *Tamarix* and *Elaeagnus* leaf litter are colonized by aquatic insects at lower rates than native *Populus* litter. Bailey, Schweitzer, and Whitham (2001) found that *Tamarix* leaf packs supported significantly lower invertebrate abundance than *Populus* leaf packs after three weeks in a northern Arizona stream. Bailey *et al.* (2001) suggested that this difference was due to the rapid decomposition rate of *Tamarix* foliage. Royer, Monaghan, and Minshall (1999) found a non-significant trend towards lower invertebrate abundance in *E. angustifolia* leaf packs than in *P. trichocarpa* leaf packs after 30 days in an Idaho stream. Bailey *et al.* (2001) and Royer *et al.* (1999) concluded that the non-native vegetation not only provided poorer habitat for aquatic invertebrates than native *Populus* but also lower food quality. However, neither study examined the value of native and non-native leaf litter as food or measured growth rates or diet preferences. A comparison of the stable isotope signatures in invertebrates inhabiting *Tamarix* and *Populus* leaf litter indicated that invertebrates did not use the litter as food (Pomeroy *et al.* 2000) because the two litter types had distinct isotopic signatures, but the invertebrates inhabiting *Tamarix* and *Populus* leaf packs did not. Pomeroy *et al.* (2000) suggested that invertebrates in *Tamarix* and *Populus* had the same

isotopic signature because they consumed the biofilm on the leaves rather than leaf material itself.

In order to understand how *Tamarix* and *Elaeagnus* are affecting stream invertebrate communities in the western USA, information on the value of these species as food for aquatic detritivores is needed. In this study, we experimentally tested whether a common invertebrate shredder would grow faster on native or non-native leaf litter over a seven-week period. We compared the growth of crane fly larvae (Diptera: Tipulidae) on pre-conditioned *Populus*, *Tamarix* and *Elaeagnus* leaf litter in a controlled lab setting.

2.2.0. Methods

2.2.1. Invertebrate Growth

We compared the relative growth of crane fly larvae (*Tipula* sp.) on *Populus deltoides* subsp. *monilifera*, *Elaeagnus angustifolia* and *Tamarix* sp. In the fall of 2004, senescent leaf litter was collected from trees, air-dried, and stored at ambient temperatures in the lab until needed. *Populus* and *Elaeagnus* leaf litter was collected from the Cache la Poudre River in Fort Collins, Colorado and *Tamarix*, which is uncommon along the Poudre River, was collected from the Dolores River near Egnar, Colorado. The carbon:nitrogen values of the unconditioned leaf litter used for the experiment fell within the range observed for *Populus*, *Tamarix*, and *Elaeagnus* in riparian forests in southern Utah (Table 2.1). To minimize differences in the biofilm colonizing the three treatments, the leaves were conditioned in a common aquarium of aerated Poudre River streamwater for two weeks prior to the start of the experiment.

We used *Tipula* (*Sinotipula*) sp. (*commisicibilis* group), hereafter *Tipula*, for this experiment. We collected larvae from the Poudre River in February 2006 and allowed them to acclimate in the lab for 3-5 days prior to the experiment. *Tipula* sp. is a large insect shredder commonly found in western streams, where it can constitute the greatest biomass in some locations (Gelhaus 1986). We chose *Tipula* for this experiment because members of the genus are commonly used as model shredders (Sinsabaugh *et al.* 1985; Findlay *et al.* 1986; Canhoto and Graça 1995; Rong *et al.* 1995), are easy to collect from the field, and are robust enough to maintain in the lab.

Crane fly larvae were maintained in separate mini-aquaria and fed *ad libitum* on a diet of a single species of pre-conditioned leaves. There were 20 replicates per leaf species treatment for a total of 60 *Tipula* larvae in 60 separate containers. The experiment was carried out in an incubator at a constant temperature (12.5°C) and under a 12L:12D photoperiod. Crane fly larvae were housed in 500-ml containers with aerated water from the Poudre River, sand that had been sterilized in a muffle furnace, and leaf litter. Streamwater and leaf litter were replaced every two weeks with fresh water from the Poudre River and new leaves were added from the incubation tank. At that time, the sand in the aquarium was thoroughly rinsed to remove fecal matter and detritus. Each week crane fly larvae were blotted dry and weighed to the nearest 0.001g on a Sargent-Welch SWT-104 balance (Buffalo, NY, USA). At the end of the 7-week experiment, larvae were also dried at 60°C and weighed.

2.2.2. *Leaf Chemistry*

Lignin analysis, also called carbon fraction analysis, (Ryan *et al.* 1990) was conducted on unconditioned leaves at the Center for Water and the Environment (Natural Resources Research Institute, University of Minnesota, Duluth, MN, USA). Carbon fraction analysis (Ryan *et al.* 1990) reveals the structural carbon content of leaf material. The relevant structural components are lignin and the acid-soluble fraction, which includes cellulose and hemicellulose.

Carbon and nitrogen analyses were conducted on unconditioned and conditioned *Populus*, *Elaeagnus,* and *Tamarix* leaf samples that had been air dried and ground in a coffee grinder. Samples were analyzed for carbon and nitrogen content on a LECO CHN1000 auto-analyzer (LECO Corporation, St. Joseph, MI, USA). All leaf chemistry samples (lignin analysis and carbon/nitrogen content) were run in duplicate and the values averaged. Carbon to nitrogen (C:N) ratios were calculated from dry mass by dividing the carbon fraction (%C) by the nitrogen fraction (%N).

2.2.3. *Statistical Methods*

All statistical analyses were conducted using wet larval mass of *Tipula*. Prior to analyzing the data we tested weekly *Tipula* mass for each treatment for normality and homogeneity of variance and untransformed data were used (Shapiro-Wilk, $p > 0.1$; Levene, $p > 0.1$). In order to test for differences in mean larval mass among treatments at the start of the experiment, we used a one-way ANOVA with leaf species treatment as the independent variable and initial larval mass as the dependent variable.

We analyzed differences in *Tipula* wet mass over time and leaf species with a repeated measures analysis of covariance (RMANCOVA). The RMANCOVA tested for significant differences in larval mass over time, in treatment (leaf species), and in the time x treatment interaction. The RMANCOVA model included initial crane fly wet mass as a covariate; treatment error was not included in the RMANCOVA. Tukey's HSD post-hoc test was used to test for significance of the time x treatment term among the treatments. We conducted the RMANCOVA with all individuals that started the experiment (n = 60). Individuals that died during the experiment were dropped from the analysis in the weeks after their death. The RMANCOVA analysis was conducted in SAS 9.1 (SAS Institute 2007).

We estimated larval growth for each treatment with linear regression. We conducted the regression on the raw data, rather than natural-log transformed data (Canhoto and Graça 1995), because it provided a better fit. We used average *Tipula* wet weight (grams) as the independent variable and time (days) as the dependent variable (n = 8). At the end of the experiment, we constructed a regression of *Tipula* wet mass to dry mass to facilitate comparison of our data to the literature. All statistical analyses were conducted with Statistica software (StatSoft, Inc., Tulsa, OK, USA).

2.3.0. Results

Initial mean *Tipula* wet mass was not significantly different among treatments ($F = 0.54$; d.f. = 2; $p = 0.58$, see Figure 2.1). There was a significant change in *Tipula* mass over time (RMANCOVA; $F = 64.0$, d.f. = 7, $p < 0.001$), leaf species treatment ($F = 196.2$, d.f. = 2, $p < 0.001$), and in the time x treatment interaction term ($F = 10.6$, d.f. =

14, $p < 0.001$). Mean larval weight in *Tamarix* was significantly greater than *Populus* (Tukey HSD; $p = 0.012$) by week 2 and *Elaeagnus* (Tukey HSD; $p < 0.01$) by week 3. The *Populus* and *Elaeagnus* treatments had approximately the same mean larval weight until week 5, when larvae in *Elaeagnus* were significantly heavier than larvae in *Populus* (Tukey HSD; $p = 0.024$). By the end of the experiment (week 7), crane fly larvae fed *Tamarix* were 1.7 and 2.5 times the average wet weight of larvae fed *Elaeagnus* and *Populus*, respectively. Larval wet mass (**x**) was a good predictor of dry mass (**y**) for the *Tipula* used in this study: $\mathbf{y}=0.0644\mathbf{x} - 0.00078$ ($r^2 = 0.895$, $p < 0.01$).

Twenty-eight percent of the 60 *Tipula* larvae that started the experiment died over the course of the 7 week experiment. Most of the mortality (88%) occurred within the first two weeks. At the end of the experiment, *Tipula* survival was highest in the *Populus* treatment (90% surviving), intermediate in the *Tamarix* treatment (70%), and lowest in the *Elaeagnus* treatment (55%).

2.3.1. Leaf Chemistry

Populus, *Tamarix* and *Elaeagnus* leaf litter differed in their chemical composition (Table 2.1). Lignin analysis revealed that unconditioned *Populus* contained the lowest amount of structural carbon (35%) of the three species, as indicated by the combined lignin and acid-soluble fractions. *Elaeagnus* contained the most structural carbon (57%) and *Tamarix* was intermediate (42%).

Nutrient chemistry was analyzed for both unconditioned and conditioned leaf litter. Unconditioned *Populus* leaf litter had approximately half the nitrogen content of *Tamarix* and *Elaeagnus* litter, which were similar (Table 2.1). The C:N ratio for

unconditioned *Populus* leaf litter was the highest C:N (70:1), followed by similar values for *Tamarix* (30:1) and *Elaeagnus* (30:1).

All three leaf species gained nitrogen and carbon during the conditioning process due to microbial colonization. *Populus* leaf litter gained proportionately more nitrogen than *Tamarix* or *Elaeagnus* during conditioning, which greatly reduced the difference in C:N values among the three species, but conditioned *Populus* leaf litter still had the highest C:N value of the three species (Table 2.1). Conditioned *Elaeagnus* had the lowest C:N ratio and *Tamarix* was intermediate.

2.4.0. Discussion

Tipula larvae were able to grow and survive on *Tamarix*, *Populus* and *Elaeagnus* leaf litter. In other systems, researchers have found that *Tipula* cannot extract enough energy from some non-native species of leaf litter to survive and grow, even when fed *ad libitum*. For example, Canhoto and Graça (1995) observed 100% *Tipula* mortality on diets of *Eucalyptus globulus* and *Quercus faginea,* Lam. For *Lepidostoma* sp. caddisflies, Going and Dudley (T. Dudley, Marine Science Institute, UC Santa Barbara, *unpub. data*) observed 80% mortality when larvae were fed *Arundo donax*, L. leaf litter. Both studies suggested that leaf structure was partially responsible for poor growth; specifically, the thick cuticles of *Eucalyptus* and *Quercus* and the tough silicaceous *Arundo* leaves made consumption difficult for invertebrates.

Contrary to our expectations, crane fly larvae had the highest growth on *Tamarix* leaf litter. *Tipula* larvae grew two times faster on *Tamarix* than *Elaeagnus* and almost three times faster on *Tamarix* than *Populus*. Other researchers have found mixed results

when looking at insect growth on *Tamarix* relative to other types of leaf litter. Going and Dudley (T. Dudley, *unpub. data*) found that the relative growth of caddisfly larvae on conditioned, senescent alder, *Tamarix* and *Salix* leaf litter varied among caddisfly genera. *Gumaga* sp. caddisflies grew better on alder litter and worse on *Salix* than they did on *Tamarix*. *Lepidostoma* sp., however, exhibited approximately the same level of growth on all three leaf species.

We have two hypotheses for why *Tipula* exhibited greater growth on *Tamarix* than on *Elaeagnus* or *Populus*. First, *Tamarix* leaf litter may be easier for *Tipula* to ingest than *Populus* or *Elaeagnus* leaf litter because of its morphology. *Tamarix* is also known as salt cedar because of its scaly, overlapping leaves that resemble the leaves of a cedar tree (unlike cedar, *Tamarix* is an angiosperm). *Tamarix* is very different from *Elaeagnus* and *Populus*, which have typical deciduous leaves with long petioles and a single expanded blade rather than overlapping scales. Although we did not measure leaf consumption, it is possible that *Tipula* grew better on *Tamarix* because the long, thin *Tamarix* leaves were easier to consume than the broad, flat *Elaeagnus* and *Populus* leaves.

Second, *Tamarix* leaves may be more palatable or more easily assimilated because of leaf nutrient and/or structural chemistry. Aquatic insects are known to preferentially consume leaves that are high in nitrogen and have low amounts of structural carbon (Canhoto and Graça 1993; Rincon and Martinez 2006). Nitrogen is generally considered a limiting nutrient for primary consumers (Cross *et al.* 2005); therefore, leaves with low C:N values are considered high quality food (Chapin *et al.* 2002). *Tipula* can convert as much as 61% of ingested nitrogen into larval biomass

(Martin *et al.* 1980). Although no literature on crane flies exists, caddisflies exhibit higher growth and survivorship on leaf litter that is high in nitrogen (Anderson and Cummins 1979; Canhoto and Graça 1995). The C:N of the *Populus* leaf litter used for this experiment (70:1) is comparable to values that we observed in the field (Table 2.1) and values published in the literature (Royer *et al.* 1999; Tibbets and Molles 2005). However, *Populus* had the highest C:N value of the three species used for this experiment. The low nitrogen content of the *Populus* litter used in the experiment may explain the relatively poor growth on *Populus*.

Poor insect growth on oak and eucalyptus leaves has been attributed to leaf structural chemistry, including cellulose and lignin (Canhoto and Graça 1995). In our study, *Elaeagnus* had the most combined structural carbon (acid soluble + lignin fractions) of the three species (Table 2.1). *Tipula* is generally thought to be a poor processor of cellulose (Sinsabaugh *et al.* 1985) as cellulytic activity in *T. abdominalis* is very low in natural populations. In a ^{14}C-label study, *T. abdominalis* assimilated only about 18% of the carbon in consumed cellulose (Sinsabaugh *et al.* 1985). Although crane fly larvae are known to digest and assimilate cellulose, their digestion is inhibited by tannins and nutritional needs are probably met from the fungi that colonize leaf detritus in streams (Martin *et al.* 1980). The *Tipula* used in this experiment grew well on *Tamarix*, which contained the most tannin of the three leaf types, so tannin concentration does not appear to have been the major factor regulating crane fly growth. *Tamarix* leaf chemistry appears to be the best balance between high nitrogen and low structural carbon of the three leaf species.

Although our results from the lab suggest that non-native tree species support increased (*Tamarix*) or equal (*Elaeagnus*) growth by shredders than native *Populus* trees, the broader ecological implications of riparian invasion by these species in natural streams of the western US will depend not only on leaf chemistry and invertebrate assimilation but also on the availability of leaf litter in streams. The retention of leaves on the streambed, and thus their availability to consumers is expected to vary considerably among these species as a function of their morphology. For example, we collected leaf litter from three ½m-wide stream cross sections at each of 21 streams on the Colorado Plateau and found approximately five times more *Populus* litter (mean ± SD: 0.78 $g/m^2 \pm 0.21$, n = 20) in the stream channel than *Elaeagnus* litter (0.16 $g/m^2 \pm$ 0.35, n = 7) and approximately 80 times more *Populus* than *Tamarix* litter (0.01 $g/m^2 \pm$ 0.03, n = 20). We observed *Populus* leaf litter to frequently form leaf packs, but not *Elaeagnus* or *Tamarix*; *Tamarix* leaves, in particular, were not observed to aggregate in the stream and we rarely found more than single leaves. It is also possible that *Tamarix* leaves, which decompose about 1.3X faster than *Populus* leaves (Bailey *et al.* 2001), may simply not persist on the streambed and thus exhibit relative scarcity. Thus, there may be less litter available to shredders in natural settings than in the lab. Because they do not form leaf packs and are easily fragmented, *Tamarix* leaves also may not be retained in flashy systems with fine sediments like on the Colorado Plateau and across the western USA (e.g. (Schade and Fisher 1997).

Our understanding of the role of leaf litter in stream ecosystems has centered on the contribution of allochthonous material to stream energy budgets (Wallace *et al.* 1997), leaf litter decomposition rates (Irons *et al.* 1994), and invertebrate nutrition

(Cummins *et al.* 1989) in heavily forested headwaters streams. In order to understand the impact of non-native riparian leaf litter on stream invertebrate communities in more open-canopied and hydrologically flashy streams such as on the Colorado Plateau, more data are needed on leaf litter retention and persistence in these streams.

2.5.0. Literature Cited

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Table 2.1. Summary of leaf chemistry values for *Populus*, *Tamarix*, and *Elaeagnus*. a) Chemistry of the unconditioned leaf litter used in the *Tipula* growth experiment. b) Carbon and nitrogen chemistry of conditioned leaf litter, which soaked in aerated streamwater for two weeks prior to the experiment. c) Carbon and nitrogen chemistry of conditioned leaf litter, which soaked in aerated streamwater for four weeks. d) Minimum and maximum carbon:nitrogen values of leaf litter collected in autumn from trees on 14 streams on the Colorado Plateau. The leaf litter used for the *Tipula* feeding experiment falls near the midpoint of this range. Water soluble (WS) includes amino acids, simple sugars and soluble phenolics. Acid soluble (AS) includes cellulose, hemicellulose, starch, polypeptides, and nucleic acids.

Litter Chemistry		***Populus***	***Tamarix***	***Elaeagnus***
a) Unconditioned Leaf Litter				
Non-polar Extractable (%)		10.5	13.3	16.2
Water Soluble (%)		54.1	44.3	26.6
WS polyphenols as tannin (%)		5.9	8.9	3.5
WS polysaccharides as glucose equivalents (%)		7.1	13.4	7.0
Acid Soluble (%)		33.6	37.3	49.2
AS polysaccharides as glucose equivalents (%)		16.9	18.7	25.6
Lignin (%)		1.8	5.1	8.0
Ash (%)		16.7	17.8	9.3
Carbon (%)		41.0	35.7	44.4
Nitrogen (%)		0.6	1.2	1.5
Carbon:Nitrogen		70.3	30.1	30.2
b) Conditioned Leaf Litter				
Carbon (%)		44.5	45.8	45.0
Nitrogen (%)		1.1	1.4	1.7
Carbon:Nitrogen		39.8	32.8	26.2
d) Unconditioned Field-collected Leaf Litter				
Carbon:Nitrogen	min	46:1	31:1	15:1
	max	152:1	83:1	30:1

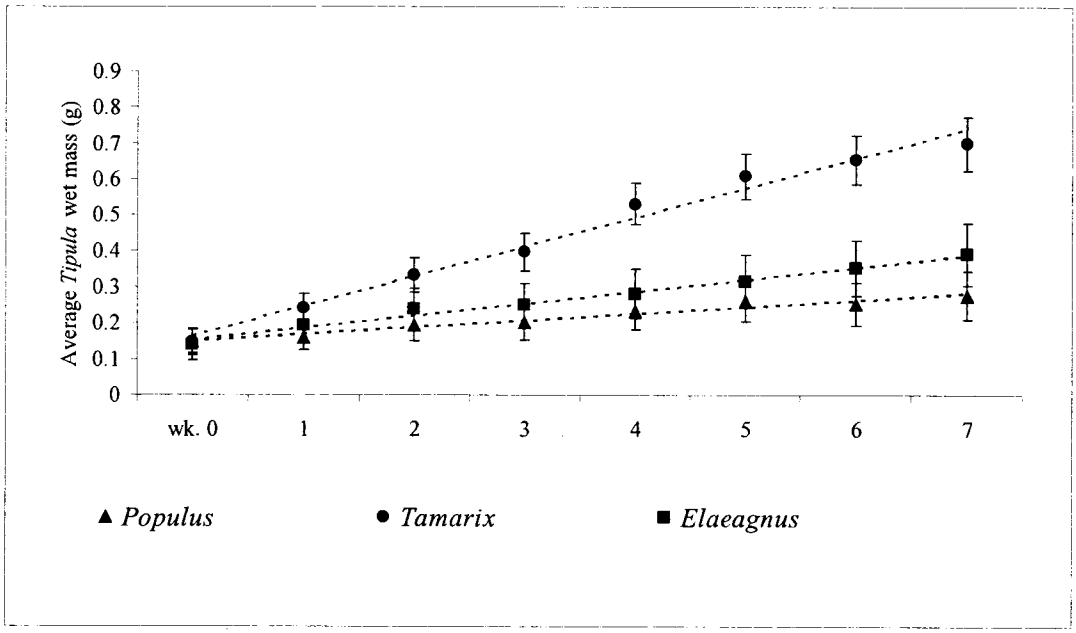

Figure 2.1. Change in *Tipula* mass throughout the seven week experiment. There was no difference in *Tipula* mass among treatments at week 1. Linear regression equations were fitted to each of the treatments to express mean *Tipula* wet mass (grams) in terms of time (days): *Populus* ($y = 0.14 + 0.003x$, $r = 0.97$, $p < 0.001$), *Tamarix* ($y = 0.16 + 0.012x$, $r = 0.99$, $p < 0.001$), and *Elaeagnus* ($y = 0.14 + 0.005x$, $r = 0.99$, $p < 0.001$). Error bars represent 95% confidence intervals.

CHAPTER 3

THE RELATIVE IMPORTANCE OF ABIOTIC AND BIOTIC FACTORS TO COLORADO PLATEAU STREAM INVERTEBRATES

Chapter 3

Abstract

The Colorado Plateau is home to a diverse array of stream types, from ephemeral bedrock washes to productive, high-gradient perennial streams. However, these fascinating systems are among the least well studied streams in the USA. I sampled the aquatic insect community, riparian vegetative community, in-stream organic material, and abiotic environment of 25 perennial, free-flowing streams on the Colorado Plateau in the fall of 2004 and 2005. I examined the relative contributions of environmental versus biological variables in explaining the variance in Colorado Plateau stream insect and riparian vegetation communities. Based on regression analysis, I found that abiotic variables were approximately 20x better at explaining insect density and 3x better at explaining insect richness than biological variables. Median particle size and the number of days since the last flood were the strongest single predictors of insect density and richness.

Second, I examined the correlation between abiotic environmental variables and the riparian community composition with a non-metric multidimensional scaling (NMS) analysis. I found that a 2-dimensional NMS plot could display 88.2% of the variation in the relative abundance of seven riparian tree categories (cottonwood, willow, saltcedar, Russian olive, alder, no vegetation, and other vegetation). The NMS also revealed that these Colorado Plateau streams could be grouped into three functional types based on riparian vegetation: valley, mountain, and canyon streams. Valley streams occur at lower elevations and have higher cottonwood abundances than higher elevation mountain

streams. Canyon streams occur in highly confined canyon bottoms that are characterized by sparse riparian vegetation. Overall, abiotic environmental variables are more highly correlated than biotic variables with Colorado Plateau insect and riparian community assemblages.

3.1.0 Introduction

Colorado Plateau streams have historically been by exotic riparian invasion, flow alteration, overgrazing, and recreational impacts (Tuhy *et al.* 2002), yet they remain among the least studied streams in the USA (Call and Baumann 2002). The Nature Conservancy has suggested that *small, perennial streams* on the Colorado Plateau are most susceptible to diversions, dikes, and exotic invasion (Tuhy *et al.* 2002), but most of the aquatic research on the Colorado Plateau has focused on the Colorado River and its major tributaries (Shannon *et al.* 1994; Stevens *et al.* 1997; Benenati *et al.* 1998; Blinn *et al.* 1998; Childs *et al.* 1998; Jordan *et al.* 1999; Valdez *et al.* 2001; Haden *et al.* 2003). The small streams of the Colorado Plateau are not well studied, perhaps because of the distance between streams, the remoteness of stream sites, and the rugged terrain of the Colorado Plateau (Call and Baumann 2002; Brammer and MacDonald 2003). As foundational literature, I have found four peer-reviewed research papers that examined the aquatic invertebrate community in Colorado Plateau streams (Figure 3.1). All of these papers are recent, which may suggest that the Plateau has recently caught the attention of western aquatic ecologists. This chapter is intended to provide baseline data on perennial Colorado Plateau stream types, examine the relationships between stream biota and the physical environment, and to help scientists and managers better understand the aquatic and riparian ecology of these systems.

Streamflow on the Colorado Plateau is highly variable compared to other regions of the country (Poff and Ward 1989; Poff 1996) because convective thunderstorms produce relatively localized flash floods (Hereford and Webb 1992) and perennial streams in this dry climate are maintained by complex groundwater sources (Weiss 1987;

Robson and Banta 1995). There are some data to support the assertion that streamflow is the major driver of lotic communities on the Colorado Plateau. Oberlin *et al.* (1999) surveyed the macroinvertebrate fauna of ten tributaries to the Grand Canyon. Half of the tributaries originated outside the Grand Canyon, had relatively large drainage areas, and were therefore subject to flood disturbance. The other half of the tributaries were spring-fed and had very small drainage areas (< 300 km^2) so they were not subject to floods. Oberlin *et al.* (1999) found that the spring-fed streams that originated inside the Grand Canyon had significantly more (2x) invertebrate biomass than streams that originated outside the Grand Canyon. They attributed the higher invertebrate biomass to lower stream turbidity, less frequent flooding, and greater food resources. There is also some evidence to suggest that biological variables influence stream invertebrate communities on the Plateau. Baron *et al.* (1998) looked at the invertebrate fauna of intermittent streams (desert rock pools) in Capitol Reef National Park over an 8 month period. They found no variation in insect community composition in pools due to flooding or drought. However, they did find significantly higher insect species richness in rock pools that were surrounded by vegetation than in pools that were barren.

Cottonwood (*Populus deltoides*), willow (*Salix exigua*), saltcedar (*Tamarix* spp.), and Russian olive (*Elaeagnus angustifolia*) are all common in the riparian zones of the western USA (Friedman *et al.* 2005). Riparian vegetation is strongly influenced by water availability and temperature regime (Patten 1998). Many riparian tree species can only germinate in moist alluvial sediments that are available after floods (Mahoney and Rood 1998); therefore, stream hydrology is probably an important abiotic driver of riparian community composition. In addition, western riparian trees cannot survive on ambient

rainfall and must meet their water needs with streamwater or shallow groundwater (Patten 1998). The composition of riparian communities also varies along an elevational gradient, such that cottonwood/willow communities are common at low elevations and alder is more common at higher elevations (Patten 1998).

I had two questions for this research. First, can variation in a set of perennial Colorado Plateau stream insect community assemblages be better explained by environmental or biological variables? More specifically, do stream gradient, discharge, elevation, and substrate size explain a larger portion of the variation in insect density and abundance than the availability of food resources (periphyton, riparian vegetation, and leaf detritus)? Second, can environmental variables (days since last flood, watershed area, estimated annual discharge, gradient, channel width, elevation, particle size, and latitude/longitude) accurately describe the composition and relative abundance of the dominant riparian vegetation?

3.2.0 Methods

3.2.1 Stream Habitat Characterization

I visited 25 stream sites on the Colorado Plateau (Figure 3.2). The sites were located in southern Utah and southwestern Colorado (Table 3.1). Approximately one third of the sites were on National Park Service land (in Canyonlands, Zion, Capitol Reef National Parks, and Glen Canyon National Recreation Area), one third in the Grand Staircase-Escalante National Monument, which is managed by the Bureau of Land Management, and one third on other public lands. All sites were on unregulated streams, although some have upstream water diversion for irrigation and some have downstream

impoundments (Oak Creek, Mill Creek, and Kanab Creek). All of these streams eventually flow into the Colorado River.

Flood disturbances can remove nearly all of the biomass in streams draining arid landscapes (Fisher *et al.* 1982); therefore, I wanted to quantify the number of days that have passed since the last large flood. A couple of the sites have historic daily streamflow data (Indian Creek, North Cottonwood Creek) and three sites have stream gauges downstream of the study sites below impoundments (Kanab Creek, Deer Creek, and Mill Creek). I estimated the number of days since the last flood for all 25 sites from USGS streamflow data for nearby gauged streams (San Miguel River, Escalante River, Paria River, Mill Creek, and the East Fork of the Virgin River); the mean distance from the sample site to the stream gauge was 40 km (range: 2-80 km).

In choosing sites I attempted to control for hydrology, geomorphology, and habitat by choosing streams of similar sizes and by sampling in riffles. However, because the geomorphology of Colorado Plateau streams is highly variable, the sites vary broadly. I attempted to quantify this variation by measuring the substrate particle size distribution, measuring the wetted area of the stream, and documenting sites with photographs. I conducted Wolman pebble counts (Wolman 1954) by randomly sampling 25 points in each of five riffles and measured the intermediate axis of the particles that I encountered (n=125 pebbles). Particles larger than 40 cm and smaller than 0.2 cm were labeled as bedrock and sand, respectively. I calculated the median particle size at each site by ranking the substrate measurements and identifying the median point. I also calculated the variance in particle size across the 125 pebbles at each site to characterize the range of sediment sizes. Pebble counts were not conducted at Hall's Creek, so I

estimated d_{50} by averaging median at 9 other streams dominated by fine sediments (Table 3.1). I also measured three stream cross sections of wetted channel at each site. The cross sections were measured at the downstream end of the 250-m sample reach, 150m upstream from the end, and at the top of the reach. I also measured the stream temperature at each site as a coarse indicator of the water source (cool groundwater or warm surface water) at each site.

After finishing my field sampling, I extracted watershed area, stream gradient, and estimated annual stream discharge from a GIS database that was developed for the entire Colorado River basin (Theobald and Norman 2007). Stream gradient and watershed area were calculated from a 30-m Digital Elevation Model (USGS National Elevation Dataset) and the 1:100k USGS National Hydrography Dataset channel network (USGS 2004). Annual stream discharge was estimated from a regional regression equation (Vogel *et al.* 1999).

3.2.2. Riparian Vegetation & Leaf Litter

I characterized the composition of the riparian vegetation in fall 2004 and 2005 using a green-line approach (Table 3.2). I assessed the relative abundance of the four dominant western riparian trees (cottonwood, willow, Russian olive, and saltcedar; (Friedman *et al.* 2005)) in the riparian zones of the 25 small streams. Riparian species composition was determined along a 250 m stream reach by walking the stream and recording trees that occurred on the right and left stream banks every 1-m interval within 2-3 channel widths of the stream. I also recorded riparian tree presence/absence in six categories (cottonwood, saltcedar, willow, Russian olive, alder, other, and none). I did

have some difficulty differentiating narrow leaf cottonwood and peachleaf willow in the field, so there is some error in the willow and cottonwood coverage estimates. However, the vast majority of the cottonwood that I encountered was the broad-leaved plains cottonwood and the majority of the willow that I encountered was sandbar willow; therefore, I do not believe that this error is large enough to justify combining the cottonwood and willow groups.

Dry leaf litter was collected from as many dominant taxa (plains cottonwood, sandbar willow, saltcedar, and Russian olive) as were present at a given stream. Leaf litter was collected directly from standing trees and maintained in paper envelopes until it could be processed. I conducted carbon and nitrogen analyses on leaf samples that had been air dried and ground in a coffee grinder. Samples were analyzed for carbon and nitrogen content on a LECO CHN1000 auto-analyzer (LECO Corporation, St. Joseph, MI, USA). Leaf chemistry samples were run in duplicate and the values were averaged. I calculated carbon to nitrogen ratios from dry mass by dividing the carbon fraction (%C) by the nitrogen fraction (%N) (Tibbets and Molles 2005).

In-stream leaf litter composition was determined from three leaf litter samples that I collected from the stream bed at 21 sites. I collected wet leaf litter from a 0.5-m wide cross section of the stream at the cross-sectional measurement locations. All litter was visually identified and removed from the stream bottom by hand and preserved in 5% formalin in the field and returned to the lab for processing. Leaf samples were washed, sorted to dominant species (cottonwood, willow, Russian olive, saltcedar, other), air dried, and weighed in the lab.

3.2.3. Stream Invertebrates and Periphyton

Quantitative benthic invertebrate samples were collected from five riffle habitats in each 250-m stream reach. Three to seven modified Hess samples, depending on invertebrate abundance, were collected from each riffle. The modified Hess sampler was constructed from a 2-gallon PVC bucket (0.13 m^2 area) and 500 μm Nytex mesh. Invertebrate samples were preserved in the field in 5% formalin and returned to the lab for processing. In the lab, invertebrates were removed from stream detritus without magnification. Invertebrates were then sorted to order and identified to the lowest feasible taxonomic unit. Most individuals were identified to genus, but Diptera, Hemiptera, and non-insect taxa were identified to family (Merritt and Cummins 1996). Voucher specimens are housed at the C. P. Gillette Museum of Arthropod Biodiversity at Colorado State University.

Quantitative periphyton samples were collected from each site by removing a large cobble from the stream, holding it over a tray, and scrubbing the inside of a PVC tube. At several sites (Kanab Creek, Coyote Gulch, Courthouse Wash) sufficient cobbles could not be found, so a siphon was used to remove a similar area of sand from the stream substrate. The quantitative samples were filtered in the field onto 0.45 micron Whatman GF/C fiberglass filters and allowed to air dry. These samples were returned to the lab and processed for ash-free dry mass (AFDM) according to Steinman and Lamberti (1996).

3.2.4. Statistical Analyses

I conducted multiple linear regression analysis in order to determine whether abiotic or biological variables were better able to describe the variation in insect density and genus-level richness among sites. The abiotic environmental variables included were the number of days since the last flood, stream gradient (m/km), watershed area (km^2), estimated annual stream discharge, the UTM Easting and Northing coordinates, stream elevation, wetted channel width, and median particle size. The biological variables that I used in the analysis were the periphyton AFDM, in-stream leaf litter (dry mass), and the percentage of cottonwood, willow, saltcedar, Russian olive, alder, "other," and "no vegetation" in the riparian zone. Insect density was natural log transformed and genus-level richness was square root transformed to improve normality. Environmental and biological variables were also transformed to improve normality for the regression and the ordination analyses. I used forward stepwise multiple linear regression on the two (abiotic and biological) suites of variables. I conducted the linear regression analysis in Statistica v. 6.0 (StatSoft, Tulsa, OK).

I conducted a non-metric multidimensional scaling (NMS) analysis to calculate the position of each stream site in 'riparian space'. NMS starts with a random configuration of sites in ordination space and gradually adjusts the points in ordination space to minimize the "stress" (McCune and Grace 2002). A useful NMS ordination has minimal "stress" and has as few ordination axes (k) as possible. Stress is the departure from monotonicity between the dissimilarity matrix of the original (riparian) data and the k-dimensional ordination space (McCune and Grace 2002). A perfectly monotonic ordination would have a stress value of zero. I conducted the NMS analysis on a relative

Euclidean distance matrix calculated from the raw percent coverage of cottonwood, willow, saltcedar, Russian olive, alder, other vegetation, and no vegetation at 25 stream sites. I assessed the stability of the final stress with a Monte Carlo test (100 permutations) in PC-ORD (MjM Software, Gleneden Beach, OR). I used Pearson product-moment correlations to measure the similarity between the NMS axes and abiotic variables, which included stream gradient, stream width, watershed area, estimated discharge, median particle size, the UTM coordinates, and elevation of the site (Table 3.1).

3.3.0. Results

3.3.1 Stream Habitat Characterization

Stream sampling took place at the end of the monsoon season (Hereford and Webb 1992; Douglas *et al.* 1993), which typically lasts from mid-June to mid-October. The first year of sampling (2004) was especially rainy, which hindered sampling efforts because of flash floods. Sampling in the second year was much less impacted by floods (Figure 3.2). Despite the differences in the precipitation regime between the two years, the mean number of days that elapsed between a flood and stream sampling was not significantly different between years (t-test: $t = 1.0$, d.f. = 23, $p = 0.33$). The watershed area of the 25 Colorado Plateau streams that I sampled ranged over two orders of magnitude. Birch Creek in Zion NP had the smallest drainage area (7.4 km^2) of the streams that I sampled and the San Miguel River at the Nature Conservancy's Tabeguache Preserve had the largest (3,188 km^2). The streams ranged from high gradient streams with coarse substrates (i.e., Birch Creek, Mill Creek) to low gradient, fine-

grained streams (i.e., Kanab Creek, Hackberry Canyon; Table 3.1). Most of the streams were dominated by coarse substrate (d_{50} = 0.2 - 40 cm) and only three had bedrock channels (d_{50} > 40 cm; Table 3.1).

3.3.2. Riparian Vegetation & Leaf Litter

Willow, cottonwood, saltcedar, and Russian olive were the four most common riparian trees by abundance at the 25 Colorado Plateau sites (Table 3.2). Willow, cottonwood, and saltcedar were present at 92% of the stream sites (23/25) and Russian olive and alder were present at 36% of the sites (9/25). Although I tried to find sites that were as natural as possible, saltcedar and Russian olive are non-native invasive species and often subject to removal projects. Zion National Park, for example, has tried to eliminate saltcedar from within the park boundary. Therefore, the Russian olive and saltcedar abundances that I encountered in the field may be underestimates for the Colorado Plateau as a whole because of mitigation efforts on some streams. In addition, regulated streams have been more severely invaded by these species (Lesica and Miles 1999; Cooper *et al.* 2003). There was a considerable amount of "other" vegetation in the riparian zones of the Colorado Plateau streams, such as rabbit brush (*Chrysothamnus* sp.), juniper (*Juniperus* sp.), ponderosa pine (*Pinus ponderosa*), box elder (*Acer negundo*), and hackberry (*Celtis* sp.). Box elder was especially common at Birch Creek and net-leaf hackberry was common in Hackberry Canyon.

Carbon:nitrogen (C:N) values for the cottonwood, willow, saltcedar, and Russian olive leaf litter that I collected at Colorado Plateau streams were similar to other C:N values published in the literature (Royer *et al.* 1999; Kennedy and Hobbie 2004; Tibbets

2005; Tibbets and Molles 2005). Russian olive, which is able to fix atmospheric nitrogen with the help of symbiotic mycorrhizae (Johnson *et al.* 1997), consistently had the lowest C:N value of the four litter types analyzed (Table 3.3). Cottonwood had the highest C:N values of the four trees and saltcedar and willow were intermediate.

Cottonwood leaf litter was the most abundant type in the Colorado Plateau streams. Cottonwood frequently formed leaf packs in the stream but Russian olive, willow, and saltcedar rarely aggregated. I found approximately seven times more cottonwood leaf litter in the stream channel than willow litter, five times more cottonwood than Russian olive, and approximately 80 times more cottonwood than saltcedar (Figure3. 4). Leaf litter was entrained in the stream in different ways depending on the channel morphology and there was a significant positive correlation between stream gradient and the mass of leaf litter in the stream ($r^2 = 0.43$, $p < 0.05$) but not with median particle size ($r^2 = 0.03$, $p = 0.49$). I encountered leaf litter partially buried in the fine sediments of low gradient streams (i.e. Kanab Creek, Hackberry Canyon) rather than stacked behind cobbles as is common in higher gradient streams (Petersen and Cummins 1974).

3.3.3. Stream Invertebrates and Periphyton

Invertebrate density ranged from very low at some sites to very high at others (Table 3.3). Very low densities tended to occur in low gradient, sandy sites (i.e., Cottonwood Canyon #1 and Kanab Creek) and high densities tended towards bedrock channels (i.e., Deer Creek, Calf Creek), which contained abundant Simuliidae. Insect density was not significantly correlated to the number of days since the last flood ($r^2 =$

0.04, $p = 0.33$), stream size (watershed area: $r^2 = 0.01$, $p = 0.71$; estimated discharge: $r^2 = 0.00$, $p = 0.94$), or stream width ($r^2 = 0.02$, $p = 0.55$).

Nearly all insects (99.9%) were identified to family and approximately half (51%) were identified to genus. The specimens represented 41 insect families and 48 insect genera. Fourteen genera comprised 1% or more of the overall abundance; 35% of the insects identified to genus were *Baetis* (20 sites) and 18% were *Micrasema* (2 sites). Ephemeroptera, Plecoptera, Trichoptera (EPT) taxa were much more common, on average, than Odonata, Coleoptera, Hemiptera (OCH), which comprise a large portion of the stream insect communities in other semi-arid environments especially in perennial pools of intermittent streams (Bogan and Lytle 2007).

3.2.4. Statistical Analyses

The multiple linear regression indicated that abiotic habitat variables described more variation in insect density and genus-level richness than biological variables (Table 3.4). Median particle size, the number of days since the last flood, and watershed area were the strongest abiotic predictors of insect density ($R^2_{adj.} = 0.50$, $n = 24$, $p < 0.01$). Genus level richness was explained by median particle size and the number of days since the last flood ($R^2_{adj.} = 0.51$, $n = 24$, $p < 0.01$). Stream substrate size was a strong predictor of insect density ($r^2 = 0.56$, $p < 0.05$) and richness ($r^2 = 0.44$, $p < 0.05$). Although it appears that this trend is driven by the abundance of Simuliidae (751 ± 631 /m^2) at Calf Creek, the correlations are almost unchanged by the exclusion of this site (density: $r^2 = 0.50$, $p < 0.05$; richness: $r^2 = 0.45$, $p < 0.05$). The linear regressions based on biological variables, including periphyton biomass, riparian composition, and in-

stream leaf litter, did not significantly explain the variation in natural log transformed insect density ($R^2_{adj.} = 0.03$, n = 21, p = 0.21) or genus-level richness ($R^2_{adj.} = 0.32$, n = 21, p = 0.06).

A comparison of three-dimensional and two-dimensional NMS solutions revealed that the solutions accounted for 95% and 88% of the variation in the original riparian data, respectively. I elected to use the two NMS axes (Figure 3.5) because a two-dimensional solution is easy to visualize and the third axis only accounted for 6.5% of the variation in the original data. The final stress of the ordination (Kruskal's stress formula one = 1.28) indicates that the ordination is "fair" and that it corresponds to a usable picture (Clarke 1993). Caution should be used about using stress to gauge the validity of an ordination when the ratio of samples (sites) to descriptive variables (percent cover of riparian trees) exceeds 4:1 (McCune and Grace 2002). However, this analysis had a sample:variable ratio of 3.6:1, so the final stress value should be useful to interpret the quality of the ordination. The first NMS axis can be thought of as an willow-alder axis as it was positively correlated with willow ($r^2 = 0.61$) and alder abundance ($r^2 = 0.56$). The first axis was also positively correlated with median particle size ($r^2 = 0.22$) and the UTM easting coordinate of the stream sites ($r^2 = 0.13$). The second NMS axis can be thought of as a cottonwood-no vegetation axis. This axis was positively correlated with the relative abundance of cottonwood ($r^2 = 0.45$) and negatively correlated with the relative abundance of no vegetation ($r^2 = 0.66$), that is the portion of the stream bank that was free of large woody vegetation. The environmental variable with the highest correlation with the second axis was elevation ($r^2 = 0.12$). Although the correlation between cottonwood presence and the riparian zone and elevation was not quite significant ($r^2 = 0.14$, n = 25, p

= 0.06), cottonwood was more common at lower elevations and it appeared to be replaced by alder at higher elevations.

3.4.0. Discussion

For 25 streams on the Colorado Plateau, environmental variables explain a larger proportion of the variation in the insect community assemblage (density and genus-level richness) and riparian community composition than biological variables. Median substrate size was consistently a significant predictor of the insect community. Aquatic insect diversity tends to be positively related to the sediment size range at a site because more habitat niches are provided by a broad range of particle sizes (Vinson and Hawkins 1998). At the sites I sampled, sediment size variation was positively correlated to insect density ($r^2 = 0.42$, $n = 24$, $p < 0.01$) but not insect richness ($r^2 = 0.13$, $n = 24$, $p = 0.09$). Researchers have attributed the relationship between insect diversity and sediment size in part to invertebrate preference, such that some taxa show a preference for a particular substrate particle size (Minshall 1984). In addition, coarse substrates are more efficient than fine substrates at trapping particulate organic material, which aquatic invertebrates utilize as food (Minshall 1984). At the Colorado Plateau sites there was a significant positive correlation between median particle size and periphyton abundance ($r^2 = 0.38$, $n = 24$, $p < 0.01$) but not between particle size and in-stream leaf litter ($r^2 = 0.0$, $n = 21$, $p = 0.8$). Boyle and Strand (2003) examined the relationship between the biological community composition and substrate size class on the Colorado Plateau. They surveyed the macroinvertebrate communities of the free-flowing North and East Forks of the Virgin River and described the variation in the macroinvertebrate community

composition with Canonical Correspondence Analysis. They found that substrate size class was significantly ($p < 0.01$) correlated with the benthic community composition in both streams (Boyle and Strand 2003).

The number of days since the last flood was also a significant predictor of insect richness and abundance. The Colorado Plateau is a hydrologically dynamic, semi-arid environment. Hydrologic disturbances are known to cause insect mortality and reduce biomass in streams (Lake 2000). Aquatic communities in desert streams are not highly resistant to flood disturbances (Grimm and Fisher 1989); however, desert insect taxa are highly resilient. A flash flood in Sycamore Creek removed 98% of the in-stream biomass, but the biological community recovered within 2-3 weeks (Fisher *et al.* 1982). Previous research on the Colorado Plateau suggests that the insects in this ecoregion are also resilient to flood events. Baron *et al.* (1998) did not find an effect of flooding on invertebrate species richness in intermittent stream pools on the Colorado Plateau. However, a large proportion of the insects that they encountered in the rock pools that they sampled were predatory adult insects, which are able to exit the water during flooding and recolonize the stream by flight. Several aquatic Hemiptera and Coleoptera from the Sonoran Desert are known to have evolved specialized behavioral adaptations to avoid flood disturbances by exiting the stream (Lytle 2002; Lytle and White *In Press*).

3.4.1. Colorado Plateau Stream Types Based on Riparian Vegetation

Based on the NMS ordination of the riparian composition for 25 streams, I identified three stream types on the Colorado Plateau: mountain, valley, and canyon streams (Figure 3.6). Mountain streams had a higher proportion of alder than the other

two stream types. Other researchers suggest that alder is significantly more abundant at higher elevations (Patten 1998), but elevation was not significantly correlated with alder at these sites ($r^2 = 0.05$, n = 25, p =0.28). Although I did not quantify box elder abundance, it appeared to be common at mountain streams as well. The majority of the mountain streams that I sampled on the Colorado Plateau occurred in the northeast portion of the Plateau near the Rocky Mountains (Figure 3.2). They tended to be slightly wider than canyon and valley streams, although this may be driven by the wide San Miguel River. Mountain streams tended to have coarser substrates. Pool-riffle and step pool channel morphology (Montgomery and Buffington 1997) was common at high gradient mountain stream sites. The step-pool channels at some of the highest gradient sites (i.e. Right Fork of Mill Creek, Birch Creek) contained a considerable amount of large woody debris. In general, mountain stream habitats on the Colorado Plateau provide high quality benthic habitat, as evidenced by significantly higher insect genus-level richness at these sites (ANOVA: F = 4.78, d.f. = 2, 20, p = 0.02).

Streams in the inter-mountain West tend to have an open canopy dominated by *Populus* species (Patten 1998). On the Colorado Plateau this is especially true in valley streams, which have significantly more cottonwood than mountain or canyon streams (ANOVA: F = 13.4, d.f. = 2, 20, p < 0.001). Recruitment of cottonwood seedlings and saplings was common at valley sites, which tended to meander more than mountain or canyon streams (A. Moline, *pers. obs.*). Cottonwood establishment at these sites is probably successful because of the seasonal floods that provide the clean alluvial material required for seedling establishment (Mahoney and Rood 1998). Cottonwood and willow establishment at non-perennial sites tends to be episodic in response to large flood events

(McBride and Strahan 1984; Scott *et al.* 1997). Valley streams tended to be at lower elevations than mountain and canyon streams and they also tended to be lower gradient systems.

Approximately one quarter of the streams that I sampled were confined by canyon walls. These streams do not have "erodible margins" and, therefore, often do not accumulate the sediment necessary for riparian vegetation establishment (Scott *et al.* 1996; Patten 1998). Willow was significantly more abundant at canyon streams than at mountain or valley steams (ANOVA: $F = 10.3$, d.f. = 2, 20, $p < 0.001$). Most of the willow at these sites was sandbar willow, and canyon streams did tend to have finer substrates than the other stream types. At low gradient sites (e.g., Hackberry Canyon), canyon streams meandered over alluvial fill and frequently had dune-ripple morphology (Montgomery and Buffington 1997). At high gradient sites (e.g., Oak Creek) bedrock substrate was more common and the streams tended towards pool-riffle morphology.

Interestingly, there was no significant difference in the abundance of non-native vegetation (saltcedar or Russian olive) across the three stream types. There was, however, a trend towards a higher abundance of both species on valley streams. Land managers on the Colorado Plateau are concerned about saltcedar and Russian olive invasion (Tuhy *et al.* 2002), especially because these species are believed to have negative consequences for native biota (Ellis 1995; Gazda *et al.* 2002; Kennedy *et al.* 2005). There is also concern that saltcedar invasion could convert perennial streams to non-perennial systems due to groundwater declines, which can result from the high rates of evapotranspiration that occur when dense stands of saltcedar invade arid riparian zones (Stromberg 1998). Saltcedar was present at almost all of the sties that I sampled (23/25)

but it is not currently abundant at free-flowing streams on the Plateau; saltcedar invasion proceeded more quickly on regulated rivers than free-flowing streams (Grams and Schmidt 2002; Birken and Cooper 2006). Russian olive was present at less than half as many sites as saltcedar, but Russian olive invasion has proceeded more slowly than saltcedar invasion on the Colorado Plateau (Christensen 1963; Katz and Shafroth 2003). Where Russian olive does occur on the Plateau, it appears to be concentrated under a cottonwood canopy, approximately one stream width away from the wetted channel (A. Moline, *pers. obs.*). Future research on the effect of saltcedar and Russian olive on Colorado Plateau riparian communities should focus on valley streams, which appear to be the most susceptible to riparian invasion.

Environmental variables, such as median particle size and the number of days since the last flood, are good predictors of the insect community at the 25 streams that I examined on the Colorado Plateau. The separation of Colorado Plateau streams into three groups (mountain, valley, and canyon streams) based on riparian vegetation also lends some insight into the benthic community. At the 25 sites that I sampled, valley streams had significantly higher insect richness (ANOVA: $F = 4.5$, d.f. = 2, 22, $p = 0.02$) and periphyton abundance (ANOVA: $F = 3.9$, d.f. = 2, 22, $p = 0.04$) than mountain or canyon streams. These riparian groups have different vegetation composition (Figure 3.6), but the relative abundances of riparian tree species were not significant predictors of aquatic insect density or richness (Table 3.4). These results suggest that the stream community at these 25 sites is more strongly influenced by the abiotic environment than by biological interactions; this is probably due, in part, to the frequent floods that remove

benthic organic material and disrupt the stream community (Fisher *et al.* 1982, Schade and Fisher 1997).

3.5.0 Literature Cited

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Table 3.1. Environmental habitat variables for 25 Colorado Plateau streams. All streams are located in southern Utah except the San Miguel River, which is in southwestern Colorado.

	Site Name	Sample Date	UTM Easting	UTM Northing	Elev. (m)	Watershed Area (km^2)	Channel Width (m)	Dominant Substrate	d_{50} (cm)	Gradient (m/km)
1	Calf Creek	10/26/04	463,660	4,183,376	1630	25.3	2.2	Bedrock	40	1.28
2	Cottonwood Wash #1	11/18/04	419,575	4,124,544	1464	102.7	2.6	Fine	0.2	0.91
3	Cottonwood Wash #2	11/18/04	418,775	4,122,805	1436	286.3	3.9	Fine	0.2	0.62
4	Courthouse Wash	10/11/05	621,686	4,278,441	1248	365.4	-	Fine	0.2	0.57
5	Coyote Gulch	11/2/05	490,181	4,142,349	1292	279.2	1.5	Fine	0.2	0.81
6	Deer Creek	11/3/05	467,269	4,188,595	1765	51.5	2.9	Bedrock	5.3	1.88
7	East Fork Virgin R	11/16/04	325,153	4,114,362	1192	832.4	5.7	Coarse	3.4	1.36
8	Escalante River	10/27/04	462,822	4,181,010	1589	1173.4	4.7	Coarse	1.6	1.83
9	Hackberry Canyon	11/19/04	418,868	4,123,925	1457	167.2	3.8	Fine	0.2	0.91
10	Hall's Creek	10/24/04	509,722	4,165,050	1250	290.3	1.1	Fine[2]	-	1.70
11	Birch Creek	10/28/04	325,430	4,123,167	1307	9.8	1.5	Coarse	2.6	9.46
12	Indian Creek #1	10/4/04	630,242	4,205,245	1880	95.7	2.7	Coarse	1.8	1.72
13	Indian Creek #2	10/3/04	620,485	4,223,281	1500	670.1	3.7	Fine	0.2	0.72
14	Kanab Creek	11/15/04	363,397	4,112,184	1585	365.2	7.3	Fine	0.2	0.81
15	La Verkin Creek	10/18/05	306,913	4,141,835	1512	117.7	2.3	Fine	0.2	1.87
16	Left Fork North Cr.	10/20/05	315,281	4,128,853	1439	92.7	5.1	Bedrock	13	4.09
17	Mill Creek - Right Fork	10/7/04	630,094	4,269,161	1311	164.2	4.8	Coarse	6.5	1.19
18	Mill Creek - Left Fork	11/21/04	630,246	4,269,468	1308	70.5	3.5	Coarse	4.2	1.57
19	Negro Bill Canyon	10/8/04	627,862	4,274,274	1214	54.7	2.8	Coarse	5.3	2.59
20	N. Cottonwood Creek	10/6/04	623,806	4,209,870	1683	7.4	1.5	Fine	0.9	2.86
21	Oak Creek	10/6/05	487,848	4,214,943	1796	128.2	5.1	Fine	0.8	1.29
22	Pleasant Creek	10/9/04	484,069	4,225,727	1806	182.1	2.1	Coarse	1.9	1.76
23	San Miguel River	11/14/04	704,559	4,241,911	1580	3188.3	13.1	Coarse	5.2	0.88
24	Sulfur Creek	10/6/05	473,289	4,239,328	1795	115.3	5.5	Coarse	1.7	1.48
25	Trachyte Creek	10/8/05	537,113	4,201,074	1438	171.7	4.4	Coarse	3	1.20

1. Discharge estimated from GIS data and equation from Vogel (1999).
2. Pebble counts were not conducted at this site.

Table 3.1. cont.

	Site Name	Sample Date	NHD Description	Days Since Last Flood	Stream Temp (C)	Air Temp (C)	Periphyton (g AFDM)	In-stream Leaf Litter (g)
1	Calf Creek	10/26/04	Perennial	2	10	19	0.219	1.46
2	Cottonwood Wash #1	11/18/04	Perennial	2	11	20	0.011	2.31
3	Cottonwood Wash #2	11/18/04	Intermittent	2	5	14	0.007	0.31
4	Courthouse Wash	10/11/05	Intermittent	3	12	20	0.020	-
5	Coyote Gulch	11/2/05	Perennial	2	14	22	0.010	-
6	Deer Creek	11/3/05	Intermittent	2	7	16	0.024	-
7	East Fork Virgin R	11/16/04	Perennial	2	8	10	0.005	1.35
8	Escalante River	10/27/04	Perennial	2	8	10	0.033	4.95
9	Hackberry Canyon	11/19/04	Intermittent	2	4	11	0.003	0.98
10	Hall's Creek	10/24/04	Perennial	1	11	20	0.003	0.08
11	Birch Creek	10/28/04	Intermittent	0	5	10	0.012	8.40
12	Indian Creek #1	10/4/04	Perennial	1	9	26	0.011	4.30
13	Indian Creek #2	10/3/04	Intermittent	1	18	34	0.004	0.22
14	Kanab Creek	11/15/04	Perennial	2	8	14	0.015	1.20
15	La Verkin Creek	10/18/05	Perennial	0	11	15.5	0.038	0.44
16	Left Fork North Cr.	10/20/05	Perennial	1	13	22	0.011	0.03
17	Mill Creek - Right Fork	10/7/04	Perennial	3	16	24	0.022	1.68
18	Mill Creek - Left Fork	11/21/04	Perennial	2	6	9	0.012	2.05
19	Negro Bill Canyon	10/8/04	Perennial	3	11	20	0.015	1.73
20	N. Cottonwood Creek	10/6/04	Intermittent	2	9	24	0.018	1.06
21	Oak Creek	10/6/05	Perennial	2	-	26	0.012	3.20
22	Pleasant Creek	10/9/04	Perennial	1	7.5	24	0.008	0.46
23	San Miguel River	11/14/04	Perennial	2	4.5	8	0.124	-
24	Sulfur Creek	10/6/05	Perennial	2	4	15	0.016	0.10
25	Trachyte Creek	10/8/05	Intermittent	2	14	24	0.010	0.20

Table 3.2. Riparian composition: Proportion of sample points along the 250-m stream reach where *Populus, Salix, Elaeagnus, Tamarix,* and other vegetation occurred at 25 streams on the Colorado Plateau. No vegetation indicates that no riparian trees were present; this often occurred due to slickrock canyon walls. All streams are located in southern Utah except the San Miguel River, which is in southwestern Colorado.

	Site	*Cottonwood*	*Willow*	*Saltcedar*	*Russian olive*	Other veg.	No veg.
1	Calf Creek	0.0%	87.3%	1.2%	8.2%	29.6%	8.0%
2	Cottonwood Wash #1	54.4%	11.7%	11.5%	0.0%	0.5%	0.0%
3	Cottonwood Wash #2	52.3%	49.4%	20.3%	0.0%	26.4%	29.7%
4	Courthouse Wash	73.3%	59.4%	15.3%	0.0%	4.0%	9.9%
5	Coyote Gulch	71.4%	83.8%	1.5%	0.6%	55.6%	12.4%
6	Deer Creek	2.6%	38.8%	0.0%	0.0%	17.2%	51.1%
7	East Fork Virgin R	60.2%	85.5%	1.5%	0.0%	35.5%	0.0%
8	Escalante River	48.6%	35.9%	40.6%	83.9%	22.2%	3.5%
9	Hackberry Canyon	11.3%	0.0%	1.9%	0.0%	14.1%	62.2%
10	Hall's Creek	55.0%	7.1%	14.3%	0.0%	5.2%	37.7%
11	Birch Creek	38.4%	15.5%	5.4%	0.0%	29.5%	0.6%
12	Indian Creek #1	35.1%	56.7%	0.9%	0.0%	55.6%	2.6%
13	Indian Creek #2	58.0%	38.5%	54.5%	0.0%	8.0%	1.5%
14	Kanab Creek	14.0%	99.4%	2.3%	33.7%	53.0%	0.6%
15	La Verkin Creek	44.0%	23.2%	0.0%	0.0%	11.9%	40.2%
16	Left Fork North Cr.	90.0%	72.8%	2.3%	0.0%	37.8%	1.7%
17	Mill Creek - Right Fork	1.2%	52.7%	0.5%	16.6%	64.1%	32.4%
18	Mill Creek - Left Fork	4.3%	63.4%	5.3%	19.6%	88.1%	6.5%
19	Negro Bill Canyon	47.4%	82.6%	27.7%	0.0%	19.2%	0.0%
20	N. Cottonwood Creek	0.6%	54.5%	30.1%	1.2%	91.8%	1.8%
21	Oak Creek	11.6%	16.7%	41.9%	0.0%	7.5%	41.7%
22	Pleasant Creek	66.7%	69.7%	19.5%	0.0%	4.4%	20.7%
23	San Miguel River	0.0%	74.8%	10.9%	7.5%	85.7%	11.2%
24	Sulfur Creek	10.8%	0.0%	3.9%	5.9%	0.0%	79.4%
25	Trachyte Creek	30.4%	21.4%	18.8%	0.0%	3.2%	41.3%
	AVERAGE	**35.3%**	**48.0%**	**13.3%**	**7.1%**	**30.8%**	**19.9%**

Table 3.3. Invertebrate community metrics for 25 Colorado Plateau streams. Nearly all insects (99.9%) were identified to family and approximately half (51%) were identified to genus. These specimens came from 41 insect families and 48 insect genera (taxonomy listed in Appendix A). Five hess samples were collected at most stream sites (N=5). Density = number of invertebrates / m^2. Streams with a high portion of the insect taxa that are Ephemera, Plecoptera, Trichoptera (%EPT) tend to fall into the "mountain stream" category. Streams with a high portion Odonata, Coleoptera, Hemiptera (%OCH) tend to be "valley" or "canyon" streams. See Figure 3.1 for sample locations.

	Site	N	Density	%EPT	%OCH	Richness
1	Calf Creek	5	588.47	0.31	0.02	13
2	Cottonwood Wash #1	5	0.00	0.00	0.00	0
3	Cottonwood Wash #2	5	0.31	0.00	0.00	0
4	Courthouse Wash	5	19.95	0.38	0.00	3
5	Coyote Gulch	5	3.62	0.44	0.09	3
6	Deer Creek	5	259.48	0.79	0.00	7
7	East Fork Virgin R	1	29.52	0.52	0.00	4
8	Escalante River	5	45.50	0.86	0.02	7
9	Hackberry Canyon	5	0.22	0.00	0.00	0
10	Hall's Creek	5	0.51	0.73	0.00	0
11	Birch Creek	5	25.13	0.64	0.18	13
12	Indian Creek #1	5	16.74	0.86	0.00	10
13	Indian Creek #2	5	78.99	0.14	0.00	2
14	Kanab Creek	5	1.25	0.53	0.18	2
15	La Verkin Creek	3	44.54	0.47	0.00	4
16	Left Fork North Cr.	5	436.51	0.92	0.01	9
17	Mill Creek - Right Fork	5	29.04	0.33	0.13	5
18	Mill Creek - Left Fork	5	162.26	0.77	0.05	14
19	Negro Bill Canyon	5	12.98	0.49	0.00	4
20	N. Cottonwood Creek	5	15.88	0.67	0.10	4
21	Oak Creek	5	12.67	0.96	0.00	3
22	Pleasant Creek	5	8.00	0.60	0.00	12
23	San Miguel River	5	152.63	0.44	0.36	16
24	Sulfur Creek	5	24.28	0.73	0.00	3
25	Trachyte Creek	5	76.86	0.97	0.02	3
	AVERAGE		81.81	0.57	0.05	5.64

Table 3.4. Summary of multiple linear regression models that predict insect density (natural log transformed) and genus-level richness (square root transformed) from abiotic environmental variables. Linear regression models that predicted density and richness from biological variables such as periphyton biomass, riparian composition, and in-stream leaf litter were not significant ($p > 0.05$).

Insect Density, $R^2_{adj.} = 0.50$, $n = 24$, $p < 0.01$	**Coefficient**	**p-value**
Intercept	1.28	0.26
Median particle size	1.55	< 0.05
Days since last flood	-0.59	0.07
Watershed area	0.26	0.19

Genus Richness, $R^2_{adj.} = 0.51$, $n = 24$, $p < 0.01$	**Coefficient**	**p-value**
Intercept	2.04	< 0.01
Median particle size	1.03	< 0.01
Days since last flood	-0.50	< 0.05

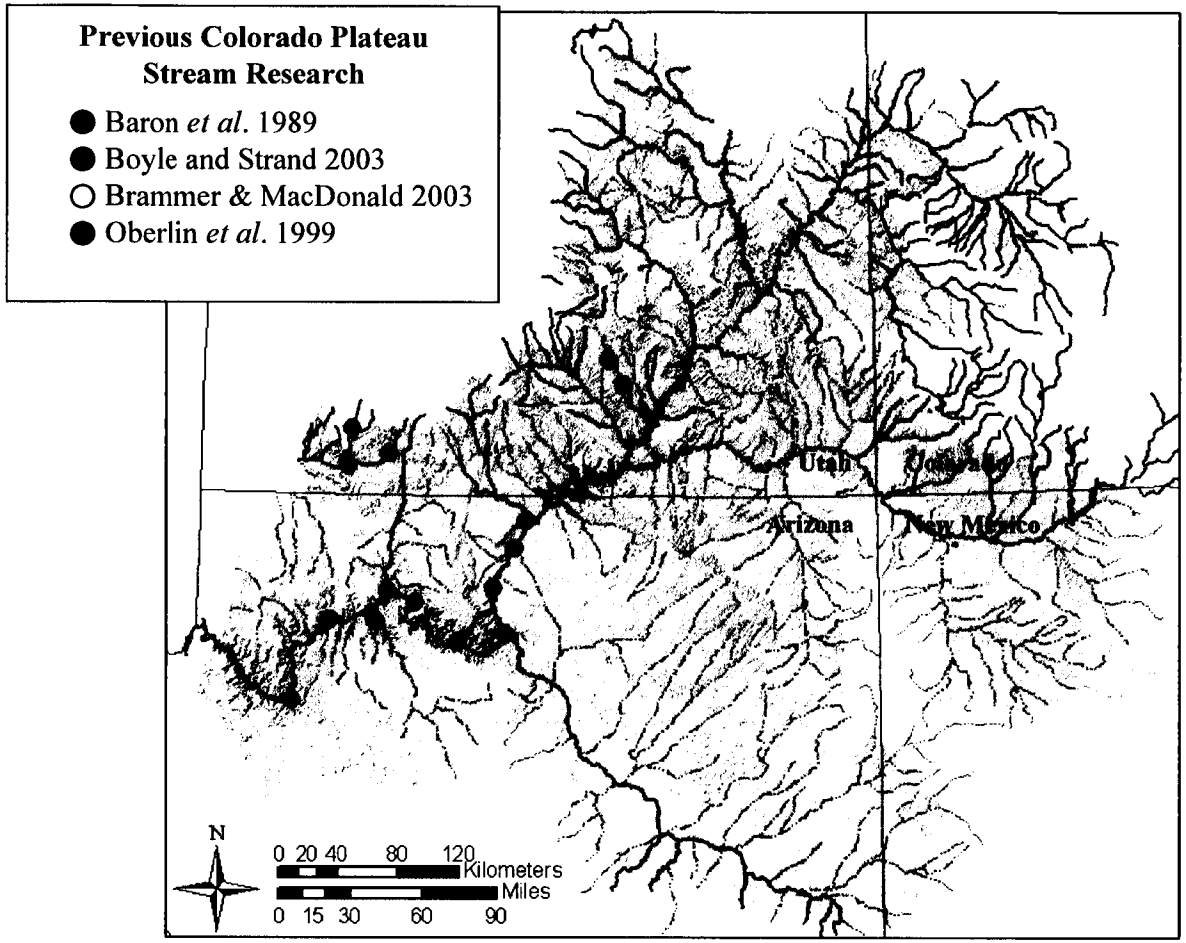

Figure 3.1. Location of peer-reviewed published stream ecology research on the Colorado Plateau.

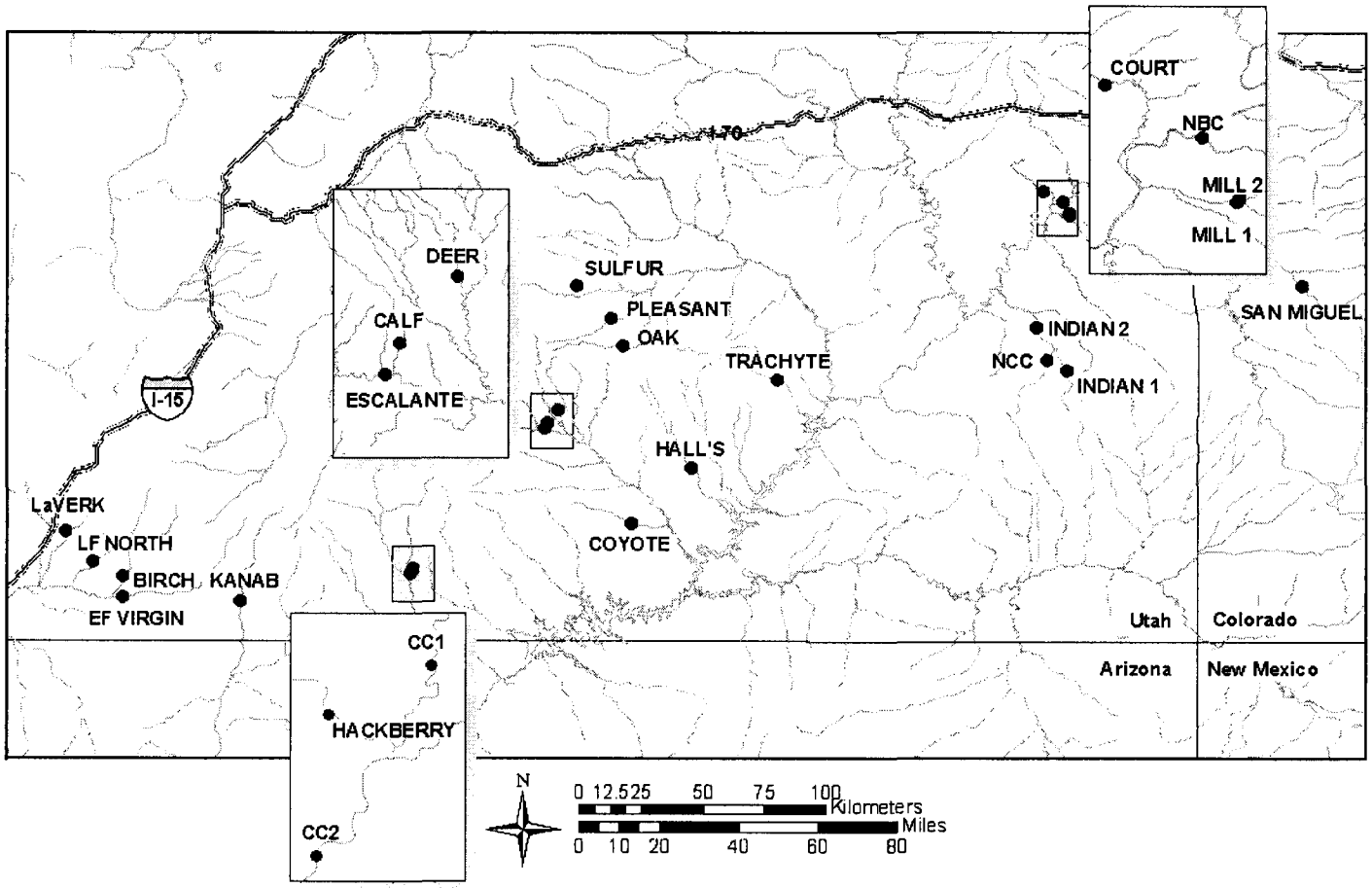

Figure 3.2. Map of twenty-five sample locations on the Colorado Plateau. All sites are in southern Utah except the San Miguel River, which is in southwestern Colorado.

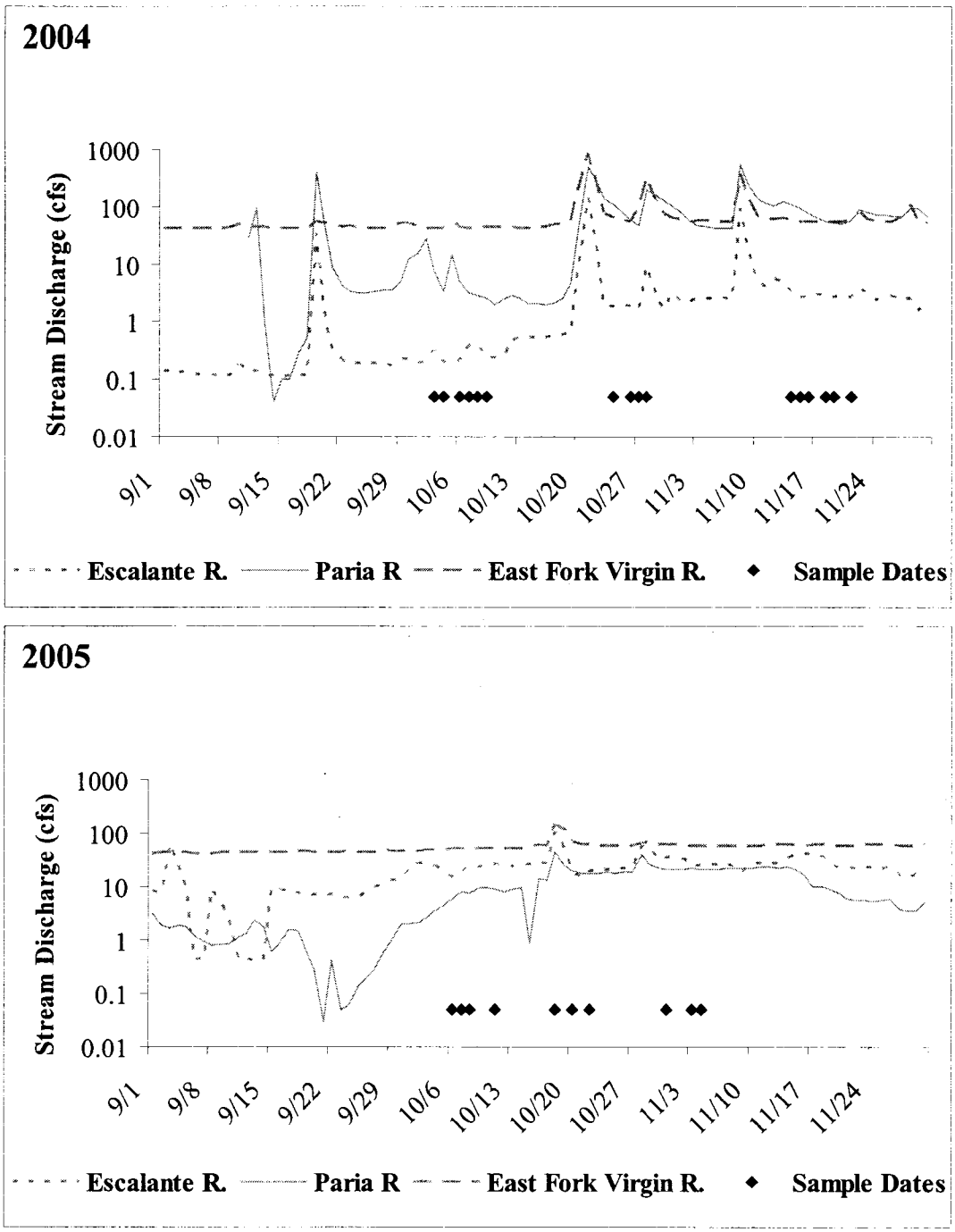

Figure 3.3. Daily streamflow measurements from three USGS gauging stations on the Colorado Plateau during study period in 2004 (top) and 2005 (bottom).

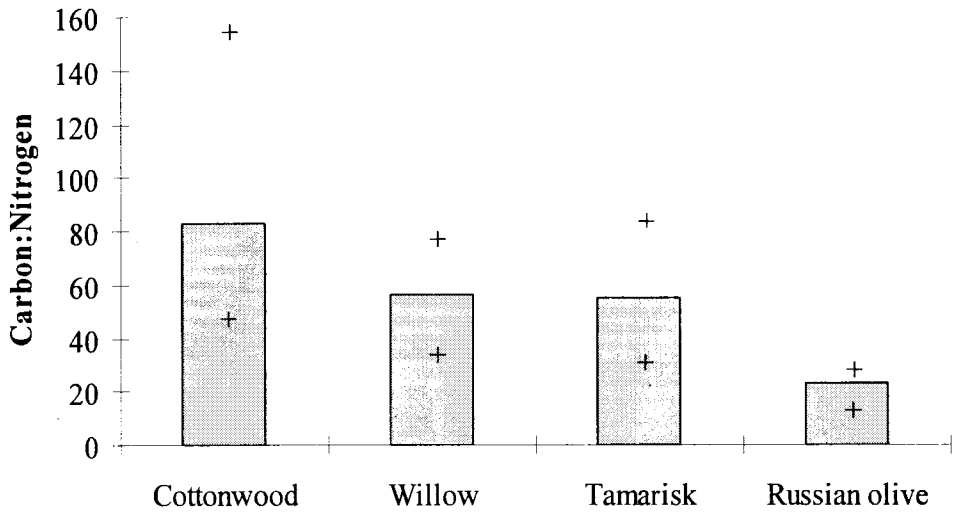

Figure 3.4. Carbon to nitrogen ratios of field collected leaf litter from riparian zones of the Colorado Plateau. Plus signs (+) indicates the minimum and maximum values.

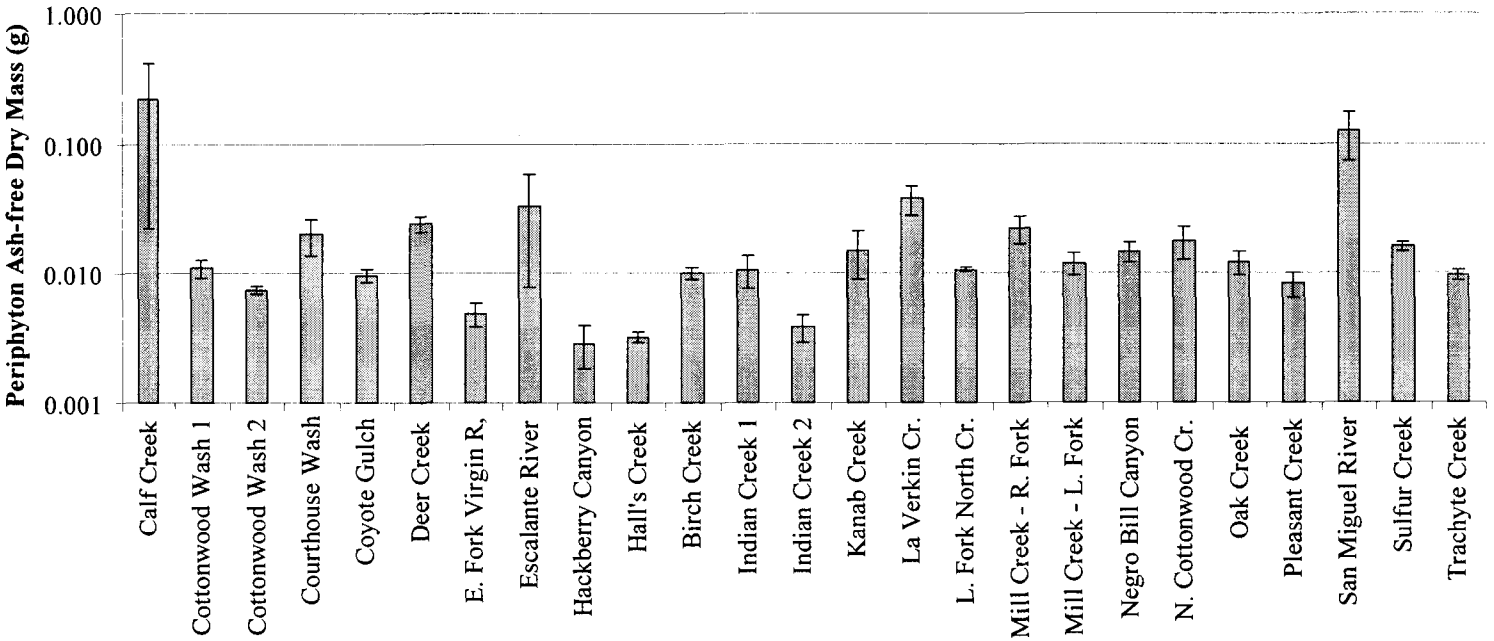

Figure 3.5. Average periphyton ash-free dry mass (n = 5) at 25 stream sites on the Colorado Plateau. Error bars are standard errors.

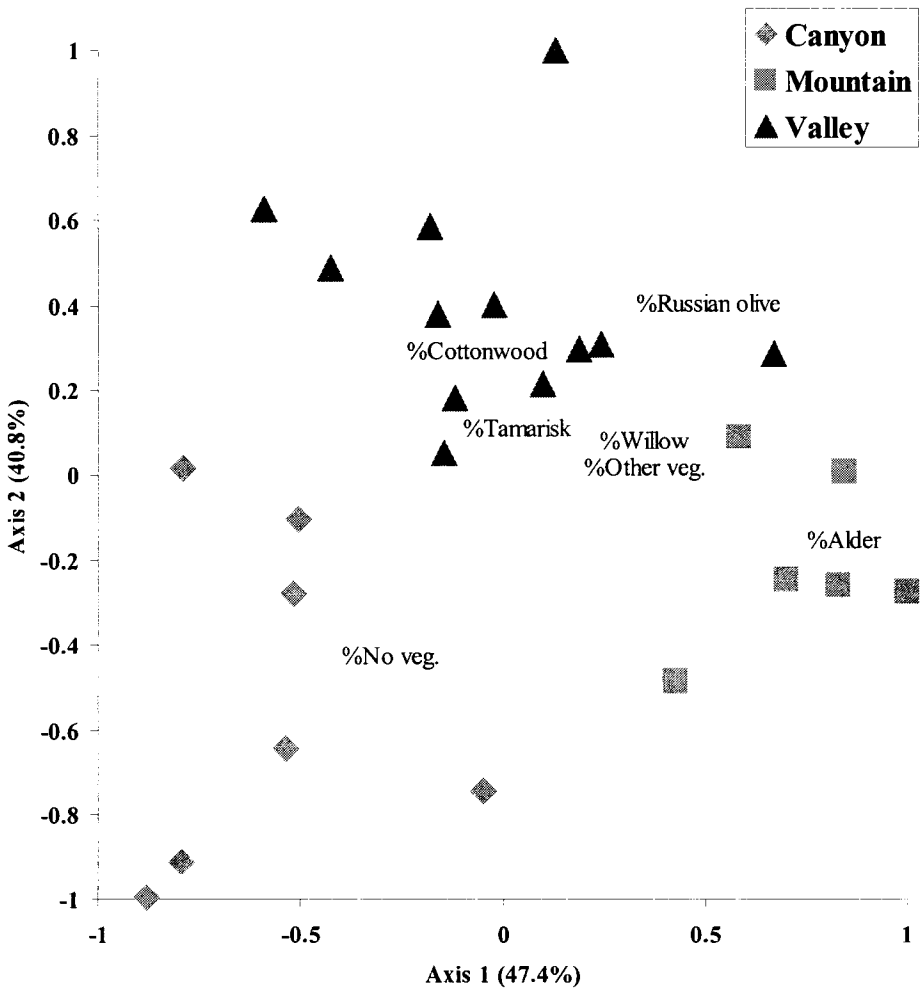

Figure 3.6. Results from non-metric multidimensional scaling analysis of riparian composition at 25 sites on the Colorado Plateau. Points are sites plotted in riparian composition space. Percent riparian vegetation indicates the centroid of the species in multivariate space. Canyon sites have a large portion of the riparian zone occupied by canyon walls and, therefore, a large portion of the riparian zone is without riparian vegetation. Mountain streams have a higher proportion (> 4%) of alder along the stream margins than valley or canyon streams. Valley streams are not tightly confined by canyons, although some are in canyon bottoms.

CHAPTER 4

A HYDROLOGIC CLASSIFICATION ON THE COLORADO PLATEAU

Chapter 4

Abstract

The Colorado Plateau of Utah, Arizona, Colorado and New Mexico is remote and one of the least studied regions in the United States from the perspective of stream ecology. The harsh hydrology of this arid region probably limits the distribution and abundance of aquatic biota as flooding and droughts eliminate sensitive taxa. Despite the harshness, a diversity of flow regimes on the Colorado Plateau range from snowmelt-driven perennial streams to ephemeral washes that flood after monsoon rains. The stream diversity in the region makes it well suited to test hypotheses of the habitat template concept. However, the stream hydrology of the Colorado Plateau has not been characterized in an ecologically-meaningful way, so researchers have not been able to examine the relationship between hydrologic variability and stream biota in this region.

I developed a conceptual model of unregulated streams on the Colorado Plateau that groups headwater streams through mid-sized rivers into hydrologic classes based on two ecologically-relevant flow axes: flow permanence (perennial vs. non-perennial) and flood regime (snowmelt- and rain-driven). My goal was to assign all unregulated streams (gauged and ungauged) on the Colorado Plateau to this typology using daily streamflow data from gauged sites and GIS-derived watershed variables. I did this by first calculating hydrologic metrics that describe the frequency, duration, and timing of high and low flows at 139 unregulated USGS stream gauges. Then I used these hydrologic metrics as input to a cluster analysis in order to assign the gauged streams to hydrologic classes. A GIS database was developed to characterize watershed variables at all

Colorado Plateau stream reaches. Next, a classification and regression tree (CART) was constructed to link the hydrologic classes and GIS-derived watershed variables at the 139 gauged sites. Finally, the CART model was used to predict hydrologic classes at ungauged, unregulated streams from the GIS-derived predictor variables.

Colorado Plateau streams were classified into four stream classes (perennial-snowmelt, non-perennial-snowmelt, perennial-rain-driven, and non-perennial-rain-driven streams) based on ecologically-relevant hydrologic metrics. Stream segments were assigned to these four stream classes based on GIS-derived variables with approximately 85% accuracy, which was comparable to the accuracy of the Statistical Model (83% correct classification). Perennial streams tended to occur around the high elevation margins of the Plateau, whereas non-perennial streams were located in the center of the region. This ecologically-based stream classification system should provide a habitat template that allows researchers to examine the effect of stream hydrology on the aquatic biota of the Colorado Plateau.

4.1.0 Introduction

Stream communities respond to variation along multiple environmental gradients simultaneously, including benthic substrate (Minshall 1984), water temperature (Vannote and Sweeney 1980), oxygen availability (Hynes 1970; Allan 1995), and stream discharge (Lytle 2000); however, because of its influence on a wide array of physical processes that affect stream biota (Poff and Ward 1989), streamflow is often considered to be the primary driver of broad-scale variation in streams (Poff 1997; Hart and Finelli 1999). The effect of flow on a particular stream changes over time as discharge responds to groundwater supply, regional climate, and local precipitation events (Allan 1995). Stream channel morphology is controlled by the balance between sediment supply and sediment transport, which are governed by watershed geology and stream discharge (Montgomery and Buffington 1997). On a scale of years to decades, stream channels experience cut- and fill-cycles due to changes in regional climate and land use; these cycles scour stream channels down to bedrock and then fill it with alluvial material(Hereford *et al.* 2002). Stream geomorphology determines the availability of physical habitat to aquatic biota, such as gravel bars for fish spawning, cobbles for black fly attachment, and sand grains for the construction of caddisfly cases (Allan 1995). On a scale of minutes to days, stream channels experience flash floods that scour and redistribute allochthonous organic material and inorganic substrate (Resh *et al.* 1988).

Aquatic community assemblages are shaped by hydrologic disturbances and hydrologic variability over ecological and evolutionary time scales (Lytle and Poff 2004). Hydrologic disturbances reduce the abundance of stream organisms and affect invertebrate growth, reproduction, dispersal, and biotic interactions (Resh *et al.* 1988).

Both floods and droughts constitute disturbances in streams; however, considerably more is known about the effect of flood flows on benthic communities than is known about the effect of droughts (Power *et al.* 1988; Hart and Finelli 1999; Lake 2000). Floods that are large enough to move the bed substrate can substantially reduce the benthic biomass in streams (Grimm and Fisher 1989; Poff 1992; De'ath 2003). Floods directly reduce the abundance of aquatic organisms through mortality. They also indirectly reduce the abundance in the next generation because of the lost reproductive potential. In places where floods cause high mortality rates, natural selection will favor species that adapt to minimize mortality or can quickly recover from the disturbance (Lytle 2001). Floods sometimes allow the coexistence of species that would otherwise exclude one another through competition or predation (McAuliffe 1984; Power *et al.* 1988; Resh *et al.* 1988). In coastal California streams, for example, hydropsychid (*Hydropsyche oslari,* Banks) and black fly (*Simulium virgatum*, Coquillett) larvae compete for space on cobbles (Hemphill and Cooper 1983). Wintertime spates tumble the stream cobbles and reduce the number of hydropsychid caddisflies, which are competitively dominant. This allows black fly larvae to colonize the habitat. Black flies dominate during winters with high flow and hydropsychid larvae dominate during winters with low flow in an unstable equilibrium (Hemphill and Cooper 1983; Hemphill 1991).

Although disturbances due to drought are not as well documented as flood disturbances, they too have been shown to have impacts on the growth and abundance of lotic organisms (Larimore *et al.* 1959; Williams and Hynes 1977; Boulton 2003). For example, an experimental manipulation of streamflow showed that rainbow trout (*Oncorhynchus mykiss,* Walbaum) experienced lower growth in streams with low flow

than in streams with high flow because of the reduced supply of drifting invertebrates (Harvey *et al.* 2006). Fish also appear to have reduced reproductive success in low-flow years compared to high-flow years. Durham and Wilde (2006) found that prairie stream cyprinid fish had lower reproductive success in dry years when the streams were composed of isolated pools, than when the stream contained continuous flow. Aquatic invertebrate community assemblages appear to be more strongly affected by droughts than floods (Boulton *et al.* 1992). Repeated stream drying eliminates flow-dependent invertebrates (Williams 1996) and favors taxa that are able to rapidly colonize when flow resumes (Lake 2000). Intermittent streams frequently have invertebrate taxa with rapid life cycles, high adult vagility, and/or drought resistant stages (Williams 1996; Lake 2000).

The habitat template concept suggests that species that persist in a particular habitat must have traits that allow them to survive and reproduce in the environment (Southwood 1977). Species may colonize a habitat to which they are not adapted, but over time a species will be "filtered out" by either disturbance or competition. Therefore, in theory habitats may favor either r-selected or K-selected species, depending on the disturbance regime (Southwood 1977; Minshall 1988). Disturbances due to fluctuations in flow are a major environmental filter in stream habitats (Poff and Ward 1990; Townsend and Hildrew 1994). Hydrologic disturbances in streams (i.e., floods and stream drying) affect the distribution and abundance of aquatic organisms in ecological time (Resh *et al.* 1988; Lake 2000). Over evolutionary time, natural selection can shape the behavior and life history of stream organisms to minimize mortality due to seasonal hydrologic variability (Lytle and Poff 2004). Therefore, the biological community

present at a stream reach and at a particular time is the product of current and recent historical hydrologic conditions (Minshall 1988; Townsend and Hildrew 1994). Stream ecologists are interested in describing environmental variability in lotic ecosystems so they can make predictions about the structure and function of the biological community (Resh *et al.* 1988; Poff and Ward 1989; Poff 1996).

Arid landscapes provide an excellent environment in which to test the effect of hydrologic variation on biological communities because desert streams are generally more hydrologically variable than humid, temperate streams (Fisher 1986; Poff and Ward 1989). Flash floods can remove up to 98% of benthic biomass in Sonoran Desert streams (Fisher *et al.* 1982). Prolonged droughts can also substantially reduce stream biomass in arid systems (Stanley *et al.* 1994). Over time, stream organisms that inhabit arid environments have evolved behavioral adaptations that minimize mortality due to floods and droughts (Lytle 2002; Lytle and Poff 2004). Biota, such as the Sonoran topminnow, has evolved to minimize the effect of disturbance. Other desert stream biota have evolved to avoid disturbances altogether by escaping from the stream. For example, in southern Arizona, adult giant waterbugs (Hemiptera: Belostomatidae) escape flash flood mortality by exiting the stream when rain falls on the channel (Lytle and Smith 2004). The waterbugs wait out the storm on dry land and return to the stream when the flood subsides. Aquatic insects have evolved behaviors to escape droughts as well. *Graptocorixa serrulata*, Uhler (Hemiptera: Corixidae) escapes drying habitats in the Sonoran Desert by flying away from the pool when temperatures rise (Velasco and Millan 1998).

Life history adaptations among aquatic insects in arid environments include timing reproduction and dispersal to minimize mortality due to floods, desiccation resistant life stages, and bet-hedging strategies that produce genetically different offspring that can take advantage of multiple environmental states (Lytle and Poff 2004). The timing of insect emergence (Lytle 2002) is tied to the long-term average timing of disturbance events. Many aquatic insects in the Sonoran Desert reproduce continuously so a portion of the population is always in the aerial adult stage where it is invulnerable to hydrologic disturbance (Gray 1981b; Lytle 2003). This also facilitates stream recovery after disturbances because adult insects are available to repopulate the stream via oviposition (Fisher *et al.* 1982; Cushing 1997). The persistence of invertebrate populations in desert streams appears to be related to the ability of the populations to recover from flooding and drying (Stanley *et al.* 1994). Many stream invertebrates have rapid larval development to reduce the amount of time that the aquatic larval stage is susceptible to hydrologic disturbances (Gray 1981b). Other aquatic insects, such as capniid stoneflies in New Mexico, lay eggs that diapause during the dry season (Hynes 1976; Jacobi and Cary 1996). However, in the hydrologically variable streams of the Sonoran Desert egg diapause is rare (Gray 1981b). This is believed to be due to the extreme flood flows that can scour over a meter of alluvial material from the stream channel, which make it more likely for aquatic larvae to survive flood flows than for eggs to resist flushing (Gray 1981b).

Although arid ecosystems provide ideal environments for testing hypotheses about how stream biota respond to hydrologic variation, streamflow classification is challenging because hydrologic data are focused primarily on perennial, rather than

intermittent streams. To mitigate this problem, hydrologists have developed a number of statistical modeling techniques to predict streamflow at ungauged sites based on data from gauged locations (Thomas and Benson 1970; Vogel *et al.* 1999; Chiang *et al.* 2002a; Chiang *et al.* 2002b). Several successful streamflow models have been developed for groups of streams with relatively homogenous flow regimes. Stream groups have been identified in geographically contiguous areas with relatively uniform geology and climate (Thomas and Benson 1970; Thomas *et al.* 1997; Vogel *et al.* 1999). These region-specific models link streamflow at gauged sites to watershed area and can be used to predict flow metrics at ungauged sites. Stream groups have also been identified in geographically disparate areas with cluster analysis (Haines *et al.* 1988; Poff and Ward 1989; Poff 1996). Linear regression models (Sanborn and Bledsoe 2006) and discriminant analysis (Chiang *et al.* 2002a; Chiang *et al.* 2002b) have been used to link watershed variables with streamflow within these stream groups. Although there are some exceptions (Poff *et al.* 2006; Sanborn and Bledsoe 2006), many of these flow prediction models are problematic for community ecologists: (1) these models have large errors associated with them in arid environments (Ries III *et al.* 2004), (2) the models have been developed at spatial scales that are larger than scale of interest of most ecological studies (i.e. watershed-scale models do not fit reach-scale research), (3) the most popular models have been developed on an yearly time scale that is broader than the scale of interest for most ecological studies (Richter *et al.* 1996), and (4) typically, they have not focused on ecologically relevant hydrologic metrics (Poff and Ward 1989; Poff 1996). Existing models for the Colorado Plateau (Thomas *et al.* 1997; Vogel *et al.* 1999) are inadequate for ecological research for *all* four of the reasons just mentioned.

In this paper I describe a streamflow classification based on daily flow data that can be accurately predicted at ungauged stream reaches based on GIS-derived variables. This classification would enables description of ecologically-relevant fine scale, intra-annual variability in stream flow on the Colorado Plateau.

The semi-arid Colorado Plateau of Utah, Arizona, New Mexico, and Colorado is perhaps one of the least-studied regions of the USA from the perspective of stream ecology (Call and Baumann 2002), yet it is well suited to test habitat template theory because it contains diverse stream types in a relatively small area. The Plateau contains mountain and desert streams, which tend to have contrasting disturbance regimes (Poff and Ward 1989). Desert streams are warm, flashy, and prone to drying, whereas mountain streams are colder and have predictable snowmelt floods. A description of stream hydrology on the Colorado Plateau would allow ecologists to test habitat template theory with data on the distribution and abundance of aquatic invertebrate or fish fauna in different stream types (Poff and Ward 1990). In addition, an ecoregion-wide description and classification of stream habitats on the Colorado Plateau would enable researchers to compare Plateau streams across watersheds; previous stream research in the region has focused primarily at the reach- and watershed-scale (Baron *et al.* 1998; Brammer and MacDonald 2003). Hopefully, an ecologically-relevant characterization of Colorado Plateau stream hydrology will stimulate research interest in the region.

I had four objectives for this chapter: (1) to develop an ecologically-based conceptual model that describes how hydrologic variability affects Colorado Plateau stream communities, (2) to use this conceptual model to build an ecologically relevant, quantitative streamflow classification for free-flowing, gauged streams in the Colorado

Plateau ecoregion, (3) to compare the ecologically-based classification to an alternate classification that captures the statistically-important hydrologic variation in free-flowing streams on the Colorado Plateau, but does not take ecological factors into account and (4) to extend both streamflow classifications to ungauged streams on the Colorado Plateau.

4.1.1. Description of the Colorado Plateau Ecoregion

The Colorado Plateau ecoregion (Bailey 1976; Omernik 1987) encompasses a 210,000 km^2 (130,000 mi^2) area at the four corners of Utah, Arizona, New Mexico, and Colorado (Hereford *et al.* 2002). The Colorado Plateau is bounded on the east and north by the Rocky Mountains, and on the west and south by the Basin and Range Province (Morris and Stubben 1994). The Colorado River and its major tributaries, including the Green, San Juan, and Little Colorado Rivers, drain the region (Figure 4.1). Several authors have delineated the Colorado Plateau ecoregion boundary (Bailey 1976; Omernik 1987; Hereford *et al.* 2002; Tuhy *et al.* 2002). All authors agree that the southern boundary of the Plateau is located at the Mogollon Rim and that the Rocky Mountains form the western edge, but there is some disagreement about where the northern and western boundaries should be drawn. I based my research on the Nature Conservancy's Colorado Plateau ecoregion boundary (Tuhy *et al.* 2002), which is smaller and more conservative than the ecoregion outlined by Bailey (1976) but corresponds to the boundary used by the Hereford *et al.* (2002).

The Colorado Plateau is comprised of a high-standing block of thick sedimentary strata (Baars 1995); it has been described as an "elevated, northward-tipping saucer" (Rigby 1976). The geology of the Colorado Plateau is relatively undeformed compared

to the adjacent Rocky Mountains and the Basin and Range (Morris and Stubben 1994). However, the region is characterized by monoclines, which are folds, dips and terraces formed as sedimentary strata are folded over deep-seated faults (Morris and Stubben 1994). These monoclines, such as the Waterpocket Fold of Capitol Reef National Park, can be 15-320 km long and 50 to several hundred meters above the surrounding land surface. The nearly circular Plateau is ringed by volcanic mountain ranges including the Henry (3,536 m / 11,600 ft.), La Sal (3,871 m / 12,700 ft.), Navajo, Abajo (3,463 m / 11,360 ft.), and Ute Mountains (Morris and Stubben 1994). The mountain ranges are igneous laccoliths, which were formed when igneous intrusions domed up the overlying sedimentary rock (Morris and Stubben 1994).

The geologic history of the Colorado Plateau explains the observed combination of sedimentary and igneous formations. The sedimentary strata that make up the cohesive mass of the Colorado Plateau were deposited during the Mesozoic (245-66 m.y.a.) when the ocean repeatedly advanced and retreated from the region (Morris and Stubben 1994). The Mancos Shale, for example, was formed when organic material was deposited on the bottom of the sea (Morris and Stubben 1994). The sandstone groups, including the Wingate, Kayenta, Navajo, and Entrada Sandstones, were formed by eolian and fluvial deposits during dry periods. The sandstones, especially the Navajo Sandstone, are the major groundwater aquifers for the region (Weiss 1987; Weiss 1991). The monocline deformations on the Colorado Plateau occurred during the Cenozoic (66 m.y.a. – present) due, in part, to the Laramide Orogeny (Morris and Stubben 1994). The igneous laccoliths, which form the Plateau's mountains, were also formed at this time. The Colorado Plateau has uplifted more than two kilometers throughout the Cenozoic,

which has resulted in extensive erosion and deep canyons along most of the major rivers (e.g. Grand Canyon, Virgin River Narrows, Escalante Canyon, and Goosenecks of the San Juan).

Colorado Plateau stream channels range from deep, relatively narrow slickrock canyons to meandering streams in wide valleys. Channel morphology determines the availability of physical habitat to aquatic biota, such as gravel bars for fish spawning, cobbles for black fly attachment, and sand grains for the construction of caddisfly cases (Allan 1995). The geomorphology of the Colorado Plateau has been well studied (Hereford 1984; Webb 1985; Bull 1997; McFadden and McAuliffe 1997; Allred and Schmidt 1999; Hereford 2002; McAuliffe *et al.* 2006) and will be only briefly summarized here. Stream channels experience aggradation and degradation cycles during which sediment is deposited and eroded due to a disequilibrium among sediment supply, stream gradient, and stream discharge (Easterbrook 1999). On the Colorado Plateau, valley-fill alluvium was widely deposited from 1400-1880 due to a decrease in large floods during the Little Ice Age (Hereford 2002). This alluvial material goes by a variety of names in valleys across the Plateau (i.e., Naha formation in the Escalante River, the post-Bonito alluvium in Chaco Canyon, the upper mesquite terrace in Grand Canyon and settlement alluvium in Zion NP). Beginning in the late 1880s, Colorado Plateau streams began to experience a period of degradation that probably began in the winter of 1861-1862 when rain fell almost continuously for 40-45 days (Hereford 2002). This widespread degradation, which occurred from approximately 1880-1940, is attributed to climatic changes (i.e. global warming after the Little Ice Age, an increase in El Niño events) that were exacerbated by livestock introduction. Perennial streams on the

Plateau have been aggrading since approximately 1940 (Hereford 2002). The ephemeral streams of the Colorado Plateau experience more rapid aggradation-degradation cycles than perennial streams, as sediment accumulates and erodes in flash floods of varying magnitude (Bull 1997). Degradation of sediment in ephemeral channels can lead to headcutting, which leads to channel incision (Bull 1997). Based on my field experience on the Plateau, entrenched non-perennial washes and arroyos are common in the bottoms of broad valleys. Perennial streams in canyon and valley bottoms frequently have pool-riffle and dune-ripple channel morphology (Montgomery and Buffington 1997). Higher gradient step-pool channels are common in stream channels draining the mountains and high plateaus.

The precipitation history of the Colorado Plateau is known since approximately 1900 (Hereford *et al.* 2002). Intra-annual precipitation on the Colorado Plateau is seasonally bimodal (Peterson 1994). Winter precipitation (mid-October – mid-April) is caused primarily by frontal systems that originate in the Pacific Ocean (Hereford *et al.* 2002). Winter precipitation on the Colorado Plateau falls as rain at low elevations and snow on the high plateaus and mountains. Summer rainfall (mid-June – mid-October) is related to the Mexican monsoon, which derives its moisture from the Gulf of California and the Gulf of Mexico (Hereford *et al.* 2002; Webb *et al.* 2004). Due to its distance from the oceans, the northern portion of the Plateau receives less monsoon precipitation than the southern portion (Douglas *et al.* 1993). For example, Flagstaff, Arizona is located at the southern edge of the Plateau (elev. 2134 m) and receives 217 mm of rain during the monsoon, while Loa, Utah (elev. 2147 m) is near the northern edge of the ecoregion and it receives only 113 mm (Western Climate Center 2007). Summertime

monsoon rain events tend to be short-duration, high-intensity events that occur in geographically isolated areas. Warm season rain produces 50-90% of the large floods (Webb 1985) and is probably responsible for the majority of stream channel erosion on the Plateau (Hereford and Webb 1992). The region has experienced three multi-decadal precipitation regimes since that time (Hereford *et al.* 2002). The early part of the 20th century (1905–1941) was relatively wet compared to the long-term average (Figure 4.2). The middle part of the century (1942-1977) was dry and the latter portion of the century (1978–1998) was wetter than average (Hereford *et al.* 2002).

4.1.2. Conceptual Model of Streamflow on the Colorado Plateau

The headwaters of many streams in the Western USA are in the mountains and are driven by snowmelt hydrology (Poff and Ward 1989; Poff 1996). Other Western streams, primarily in the south, are not affected by snowmelt runoff but are subjected to high-intensity, short duration rain events that result in flash floods (Thomas *et al.* 1997). Hydrologic regime is likely a primary, if not major, driver in streams that drain arid landscapes, where both floods and desiccation may limit invertebrate abundance and distribution (Lake 2000). For example, flash floods in the Sonoran Desert can remove up to 98% of stream biomass (Fisher *et al.* 1982) and drying can cause widespread mortality within days of flow cessation (Stanley *et al.* 1994; Velasco and Millan 1998). On the Colorado Plateau, Oberlin *et al.* (1999) surveyed the macroinvertebrate fauna of ten perennial tributaries to the Grand Canyon and found that streams that originated inside the Grand Canyon, which were not subject to severe floods, had significantly more (2x)

invertebrate biomass than streams that originated outside the Grand Canyon and were subject to flood disturbance.

The conceptual model that I have developed for Colorado Plateau streams partitions flow regimes along two major axes: *flow permanence* and *flood regime* (Figure 4.3). Both floods and droughts constitute significant hydrologic disturbances for aquatic communities (Lake 2000). Aquatic ecologists agree that floods reduce the abundance of stream organisms (Allan 1995); however, there is evidence to suggest that benthic community assemblages are more strongly affected by droughts than floods (Boulton *et al.* 1992). I hypothesize that stream permanence acts as a strong environmental filter that eliminates flow-dependent invertebrate taxa, which make up the majority of aquatic taxa (Williams 1996), from non-perennial sites. I also hypothesize that taxa are further screened by the flood regime, which allows habitat specialists to exist in snowmelt streams but presumably limits the invertebrate community to disturbance-adapted generalists in rainfall-driven flashy streams.

Flow permanence, the persistence of aboveground stream flow, is an important component of hydrologic variability because by definition aquatic taxa need aquatic habitat (Boulton 2003). Research in other ecoregions indicates that many aquatic invertebrate taxa are flow dependent and cannot persist in non-perennial streams (Miller and Golladay 1996; Williams 1996). The process of stream drying constricts, fragments, and eventually eliminates the aquatic habitat (Stanley *et al.* 1997; Lake 2000; Dodds *et al.* 2004). Over evolutionary time, repeated stream drying favors invertebrate taxa with rapid life cycles, high adult vagility, and/or drought resistant stages (Williams 1996; Lake 2000). For example, the winter stoneflies that inhabit temporary streams in New Mexico

(i.e., *Capnia californica* (Claassen), *Mesocapnia arizonensis* (Baumann and Gaufin), *Taenionema jacobii* (Stanger and Baumann)) exhibit egg diapause followed by rapid larval development (Jacobi and Cary 1996). However, drought resistant stages, such as egg and larval diapause, are absent from Sonoran Desert streams presumably because they would not persist in the stream channel after flash floods (Gray 1981b). Comparisons of perennial and non-perennial streams have found that benthic invertebrate community richness and diversity are negatively correlated with stream intermittency (Feminella 1996; Fritz and Dodds 2005; Robson *et al.* 2005).

Stream permanence exists along a continuous gradient from perennial streams that do not dry, even during the longest droughts, to ephemeral channels that only contain water during and immediately after precipitation events. Groundwater maintains perennial baseflow in some arid streams of the Colorado Plateau (Allan 1995); therefore, the proximity to groundwater partially explains the variation in stream permanence observed on the Plateau. Some Colorado Plateau stream channels are perched on bedrock that is tens to hundreds of meters above the water table, while other streams are well connected to groundwater aquifers (Weiss 1987; Robson and Banta 1995). Perennial streams have surface flow along their entire length throughout the entire year. Perennial streams on the Plateau have well developed stream channels, abundant cottonwood and willow in the riparian zone, and are marked on most maps. Ephemeral streams are dry along their entire length throughout the year *except* during and immediately after a precipitation event. On the Colorado Plateau ephemeral channels are carved into bedrock, have limited riparian vegetation, and are not typically marked on maps. Intermittent streams, as drawn on a map, must exist somewhere between perennial and

the ephemeral, and I have found that the dashed blue lines on maps represent a range of stream conditions in the field (Figure 4.4). Streams may be spatially "intermittent" if they are discontinuous over their length (Uys and O'Keeffe 1997), which happens on the Colorado Plateau in low gradient alluvial channels (Schelz 2001), or they may be temporally "intermittent" if they are seasonally dry. Most of the stream segments on the Colorado Plateau are neither strictly perennial nor ephemeral; they are spatially or seasonally intermittent. For this research I was able to identify temporally intermittent streams, but the stream gauge network rarely places two stream gauges along a single stream segment so I was not able to identify spatially intermittent streams. As described in the methods, I defined "perennial" stream segments as those which contain a stream gauge that has recorded some flow for ≥90% of the months on record.

The predictability of the *flood regime* on the Colorado Plateau is related to watershed area, stream elevation (Thomas *et al.* 1997), and the bimodal precipitation regime (Webb *et al.* 2004). Rainfall-runoff equations for the ecoregion indicate that watershed area and elevation are the two best predictors of flood magnitude and frequency (Thomas *et al.* 1997). High elevation streams on the Colorado Plateau flood in annually predictable high flow pulses due to snowmelt runoff. The timing of snowmelt runoff is relatively predictable from year to year, although there appears to be a recent trend towards earlier snowmelt in the Colorado River basin (Dettinger 2005). Snowmelt accounts for approximately 70-80% of the total annual runoff in the western USA (Doesken and Judson 1996; Dettinger 2005). Warm season rain (June 15 – October 15) accounts for 50-90% of the large floods on the Colorado Plateau (Hereford and Webb 1992). The predictability of monsoon floods at a particular site is low because monsoon

storms tend to have a limited spatial extent due to limited convective moisture (Hereford and Webb 1992). During the monsoon season, it is not uncommon for one stream to experience a catastrophic flood while an adjacent channel has no measurable flow. Low elevation streams (less than 2,286 m / 7,500 ft.) are especially affected by monsoon rainfall because the intensity of summer convective thunderstorms dissipates at higher elevations (Thomas *et al.* 1997; Webb *et al.* 2004).

Over time stream biota have evolved life history strategies that minimize mortality due to flooding (Lytle 2002); these adaptations are tied to the long-term average timing of flood disturbances (Lytle and Poff 2004). The two types of flood regimes on the Colorado Plateau (i.e. snowmelt and rain) exert very different selective pressures on stream organisms. Snowmelt increases stream discharge relatively slowly over a period of days to weeks at approximately the same time each spring. Summer convective storms, however, increase stream discharge very rapidly over a period of minutes to hours. Therefore, Colorado Plateau streams across the flood regime axis should select for aquatic organisms with different life history strategies. Snowmelt-driven streams should favor aquatic organisms that are adapted to seasonally predictable, ramped disturbance whereas rain-driven sites should favor organisms that are adapted to less predictable pulse disturbances.

There are few data on the life histories of aquatic invertebrates on the Colorado Plateau. However, we can make inferences about the region from the better-studied Rocky Mountains and Sonoran Desert because the species pools overlap (Nelson 1994; Call and Baumann 2002). Aquatic insects in the Rocky Mountains appear to minimize mortality due to snowmelt runoff by timing reproduction and emergence to avoid spring

flood flows (Robinson *et al.* 1992). For example, *Baetis tricaudatus* ,Dodds reproduces almost continuously in Lost Creek, Idaho, but emergence and reproduction peak immediately before the May-June snowmelt (Robinson *et al.* 1992). In the Rio Calaveras in the Jemez Mountains of New Mexico, snowmelt floods substantially reduce algal biomass and invertebrate density, which recover through succession over the summer (Peterson *et al.* 2001). The temperature of snowmelt may be partially responsible for aquatic insect emergence in early summer after floods have passed. Snowmelt runoff in the Rocky Mountains often causes stream water to remain cool, which reduces larval growth rates and delays insect emergence (Gregory *et al.* 2000). Sonoran Desert aquatic insects have adapted to the harsh flood regime by timing reproduction to minimize flood mortality (Gray 1981b). Some aquatic insect taxa, especially those with development times longer than 10 days (Gray 1981b), have evolved so that the timing of emergence and/or reproduction minimizes mortality due to flooding (Lytle 2002). For example, 86% of *Phylloicus aeneus*, Hagen caddisflies in the Sonoran Desert emerge before the arrival date of the 100-year average flood (Lytle 2003). Insect taxa in the Sonoran Desert tend to have less synchronized life cycles than insects in other regions (Gray 1981b). One of the benefits of asynchronous reproduction is that some members of the population are in the airborne adult stage to repopulate the stream after hydrologic disturbance (Fisher *et al.* 1982). The asynchronous taxa tend to have rapid life cycles, which allow them to quickly recover from hydrologic disturbances (Gray 1981b).

In order to apply this conceptual model as a classification system of Colorado Plateau streams, I have divided each of the flow axes into two categories; I divided the flow permanence axis into "perennial" and "non-perennial" and divided the flood regime

axis into "snowmelt" and "rain". The full factorial of these two axes results in a four-member conceptual classification system (Figure 4.4). In practice, however, either flood regime *or* flow permanence could be a better descriptor of the variation in natural streams on the Colorado Plateau. Therefore, there are two hierarchical classification systems that could result from this conceptual model (Figure 4.5). In the first case, the flow permanence axis best describes the hydrologic persistence. In this system, the hierarchical stream classification will first divide stream sites into perennial and non-perennial classes and further divide them into perennial-snowmelt, perennial-rain, non-perennial-snowmelt, and non-perennial-rain classes. Alternately, if variation in Colorado Plateau stream hydrology is best described by flood regime, then the hierarchical stream classification will first divide stream sites into "snowmelt" and "rain" classes and further divide them into snowmelt-perennial, snowmelt-non-perennial, rain-perennial, and rain-non-perennial classes.

4.2.0. Methods

The spatial extent of this analysis was limited to the Colorado Plateau portion of the Colorado River basin; the Colorado River drains approximately 90% of the Colorado Plateau (Webb *et al.* 2004). The analysis included Colorado Plateau streams and their tributaries within 40 km. There are 456 (real-time and historic) USGS daily streamflow gauges that fall within this spatial extent (Table 4.1). The spatial distribution of USGS stream gauges across the landscape is not random; the gauges tend to be located on larger, perennial streams that are now mostly regulated and are more easily accessed by roads (Figure 4.6). In the interest of classifying natural streams, I limited my analysis to

unregulated stream gauge sites. Regulated streams were eliminated from the analysis if they had reservoirs on the main channel or on tributaries upstream of the USGS gauge, which I determined through an examination of gazetteer maps (DeLorme 2000b; DeLorme 2000c; DeLorme 2000a; DeLorme 2004b; DeLorme 2004a). I also examined the upstream storage volume to mean annual discharge ratio for each of the unregulated stream gauges based on a GIS database developed for the Colorado River basin (Theobald and Norman 2007). The flow classification was based on data from 139 *unregulated* stream gauge sites with at least 8 years of continuous flow data between 1905 and 2005.

4.2.1. Hydrologic Metric Generation, Standardization, and Selection Criteria

I used HIT (Hydrologic Indicator Tools Version 1.0, U.S. Geological Survey, Fort Collins, Colorado) and GeoTools software (Geomorphology Toolbox Version 4.1, Engineering Research Center, Colorado State University, Fort Collins, Colorado) to calculate hydrologic metrics based on the daily streamflow data. These programs calculate a suite of 172 hydrologic metrics that describe the magnitude, duration, frequency, and timing of high and low flows as well as flow reversals (Olden and Poff 2003). Metrics that describe flow magnitude, duration, frequency, and timing encompass all major aspects of natural flow regimes (Lytle and Poff 2004).

Prior to using the hydrologic metrics in statistical analyses, I adjusted them to reduce the variation due to stream size and deviations from normality. First, I reduced all hydrologic metrics to unitless values in order to facilitate cross-stream comparisons. This was usually done by dividing by the mean annual flow. Second, I examined normal

probability plots and histograms of hydrologic metrics that I considered for inclusion. Hydrologic metrics were transformed to improve normality, as needed, with square root and log transformations. Third, I standardized all hydrologic metrics in STATISTICA (StatSoft, Inc., Tulsa, OK, USA) by subtracting the mean and dividing by the standard deviation (see Appendix A for metric definitions, normalization and transformation details).

Because one of my major goals for this classification was to characterize stream permanence on the Colorado Plateau, I needed to use data from a large number of gauges, some of which have limited records of continuous daily streamflow data. Hydrologic metrics are known to be sensitive to the length of time series (i.e. number of days of continuous streamflow data) used to calculate the metrics (Olden and Poff 2003). For example, Gan *et al.* (1991) suggest that a minimum of 20 years of continuous data are necessary to ensure stable estimates of Colwell's stream predictability metric. Limiting my analysis to stream gauges with $\geq$ 20 years of data, would have resulted in 56 sites and eliminated almost all intermittent streams. In the interest of including as many gauges as possible, I estimated the minimum number of years of continuous flow data needed to generate robust estimates of the specific ecologically-relevant hydrologic metrics that I used in my analysis. I did this by comparing mean values of the hydrologic metrics that were calculated from time series data of different lengths. Specifically, I calculated the suite of hydrologic metrics at ten gauges across the Plateau that had $\geq$ 40 years of continuous flow data (Table 4.2). I calculated the hydrologic metrics at ten sites for 8 different time series: 48, 20, 10, 9, 8, 7, 6, and 5 years. Each of the time series began in 1957 to eliminate variation in the hydrologic metrics due to fluctuations in climate (i.e.,

48 years = 1957-2005, 20 years = 1957-1977). In order to determine the sensitivity of various hydrologic metrics to the length of the time series, I examined box plots of hydrologic metrics for the 8 treatments. I found that most hydrologic metrics showed approximately the same mean value regardless of the period of record used to calculate the metric; however, some metrics generated a substantially different mean value when they were calculated with fewer than 8 years of continuous flow data. Therefore, I limited my analysis to stream gauges that had $\geq$ 8 years of continuous flow data.

All hydrologic metrics used in this analysis had to pass the period-of-record (POR) sensitivity test, which I developed to ensure that the hydrologic metrics were robust to variations in the amount of flow data available. The POR-sensitivity test was a one-way ANOVA with the hydrologic metric as the dependent variable and POR (48, 20, 10, 9, 8) as the independent variable. The test was designed to determine whether estimates of a specific hydrologic metric were significantly different among different periods of record. The hydrologic metrics were calculated at the same ten stream gauges as were used for the box plots and only metrics that passed the POR-sensitivity test were used to build the stream classification systems.

Hydrologic metrics estimates are also susceptible to changes in climate. We know that the Colorado Plateau experienced three multi-decadal precipitation regimes from 1905-2000 (Hereford *et al.* 2002); therefore, I also screened the hydrologic metrics based on their vulnerability to differences in climate. I used the same 10 gauges that I used for the POR analysis, except for Chinle Creek which had insufficient data, for the climate-sensitivity analysis. I calculated the suite of hydrologic metrics at each of the nine sites for different 10-year periods, which span the 1942-1977 dry period and the

1978-1998 wet period (Hereford *et al.* 2002). For comparison, I also calculated the hydrologic metrics for the entire period of record at each site. The climate-sensitivity test was a one-way ANOVA with the hydrologic metric as the dependent variable and climatic period (1950-1960, 55-65, 60-70, 65-75, 70-80, 75-85, 80-90, 85-95, 90-00, 95-05, and entire record) as the independent variable. Again, I limited my analysis to hydrologic metrics that had a non-significant p-value in a one-way ANOVA for the climate-sensitivity test.

To summarize, I chose hydrologic metrics for the development of the stream classification system that described all major aspects of the flow regime (magnitude, duration, frequency, and timing), were biologically relevant, and could be easily compared across stream sites. I only included hydrologic metrics for this analysis that were not significantly affected by the length of the flow time series or climate regime, as determined by the POR-sensitivity and climate-sensitivity tests. I calculated the hydrologic metrics with all available data from 139 unregulated stream gauges on the Colorado Plateau.

4.2.2. Ecologically-based Stream Classification Model

For the ecologically-based stream classification model, called the Ecological Model from this point forward, I chose seven hydrologic metrics that I believe describe the ecologically relevant facets of flow regime. The ecologically-relevant metrics that I selected describe the frequency (F_L3) and duration of low flows (D_L20, D_L18), and the magnitude (M_H20), duration (D_H20), and timing (T_H1, T_H2) of high flows (hydrologic metric notation and definitions from Olden and Poff 2003; Table 4.3). One of the seven

hydrologic metrics (T_H2) failed the POR- and climate-sensitivity tests, so only six metrics were used as input to the cluster analysis.

These six hydrologic metrics were calculated for each of the 139 stream sites and the data were adjusted, transformed, and standardized as described above. I used the standardized data as input to an agglomerative hierarchical cluster analysis in STATISTICA. Agglomerative clustering methods are more commonly used by ecologists than divisive clustering methods, which cannot recover from the assignment of a case to an incorrect cluster in the first step (Legendre and Legendre 1998; Gotelli and Ellison 2004). I used hierarchical cluster analysis, rather than a non-hierarchical approach such as k-means clustering, because I had predicted that the stream classes would be nested within one another (Figure 4.5). The cluster analysis for the Ecological Model was conducted on the Euclidean distances with Ward's minimum variance method. Unlike the more familiar unweighted arithmetic average clustering (UPGMA), Ward's method minimizes the cluster variance based on the cluster centroid, not the arithmetic cluster average (Legendre and Legendre 1998). At each step, Ward's method splits the data into the two clusters that minimize the Sum of Squares (as in ANOVA) between the two cluster centroids (Legendre and Legendre 1998). I chose Ward's method because it formed trees that contained clusters that had relatively balanced sample sizes when the trees were pruned to the two-cluster and four-cluster level. Ward's method has been criticized for forming small terminal clusters (Legendre and Legendre 1998), but that was not a problem in my analysis. I identified a two-class and four-class Ecological model from the dendrogram that resulted from Ward's cluster analysis.

4.2.3. Statistically-based Stream Classification Model

For the statistically-based stream classification model, hereafter called the Statistical Model, I used principal components analysis (PCA) to select hydrologic metrics as input to the cluster analysis. I used STATISTICA to conduct PCA on the correlation matrix of 108 standardized hydrologic metrics. I used the correlation matrix, rather than the covariance matrix, because I was interested in examining the relationship among the hydrologic metrics (Olden and Poff 2003). In addition, the correlation matrix ensures that all hydrologic metrics contribute equally to the PCA (Olden and Poff 2003). The 108 hydrologic metrics described the magnitude, duration, frequency, and timing of high and low flows (but not average flows). I used PCA to identify hydrologic metrics that explain a large amount of the variation in the flow data among the 139 sites. PCA uses linear regression to assign coefficients to the independent variables, in this case hydrologic metrics, such that the resulting equation explains the maximum possible variance in the data (Legendre and Legendre 1998). The first PCA axis is the one that describes the most variation in the data, while the second axis describes the second most variation and is also uncorrelated with the first axis (Manly 1986). Hydrologic metrics that have high factor loadings in the same PCA axis are highly correlated with one another and the various PCA axes, by definition, are orthogonal or uncorrelated (Legendre and Legendre 1998). Therefore, selecting one hydrologic metric from each PCA axis ensures that the chosen metrics describe a large amount of variation in the data (Olden and Poff 2003).

I selected from the significant PCA axes hydrologic metrics that had high explanatory power, represented all aspects of the natural flow regime, and were not

sensitive to changes in climate or the period of record. Metrics were deemed to have high explanatory power if they received a high (absolute value) factor loading on a significant PCA axis. Among the highly loaded metrics in each PCA axis, I chose metrics that represented flow magnitude, timing, duration, and frequency. In addition, the hydrologic metrics that I selected had to pass the POR- and climate-sensitivity tests. As described above for the Ecological Model, I used the normalized, standardized data from the hydrologic metrics on significant PCA axes calculated at 139 stream sites as input to an agglomerative cluster analysis using Ward's method. I identified a two-class and four-class system from the resulting dendrogram.

In summary, the difference between the Ecological Model and the Statistical Model was the manner in which the hydrologic metrics used to develop the classification systems were selected (Figure 4.7). The metrics used in the Ecological Model were selected because they represent aspects of the flow regime that are presumed to be important to aquatic invertebrates. The metrics in the Statistical Model were selected because they describe a large amount of variation at 139 stream gauges.

4.2.4. GIS Development and Prediction of Stream Class at Ungauged Sites

A classification and regression tree model (CART) was developed to predict stream classes at ungauged sites from landscape variables. Classification and regression trees are built by splitting the data into successively smaller groups until the groups at terminal branches are as homogenous as possible (Gotelli and Ellison 2004). CART differs from other discriminant functions (i.e., discriminant function analysis) because each division is based on a single variable. Classification and regression tree models are

well suited to Colorado Plateau stream segments for several reasons (De'ath and Fabricus 2002). First, CART models can incorporate both categorical and continuous data, so disparate data types could be included in the model. Second, tree-classifiers are relatively easy to construct. Third, the trees that result from CART analysis can be interpreted in a way that gives insight into ecological processes because the univariate splits at each node can lend insight into ecologically-relevant phenomena (De'ath and Fabricus 2002). Fourth, no assumption of normality or independence in observations is needed, which is frequently a problem with spatially-distributed data.

Landscape variables were generated in a Geographic Information System (GIS) database that was developed for the entire Colorado River basin (Theobald and Norman 2007). I was interested in classifying streamflow at stream segments on the Colorado Plateau; therefore this database was developed at the segment scale (e.g. the channel between two stream confluences or outlet points) (Frissell *et al.* 1986). The landscape variables in this GIS database were generated using reach catchment areas (RCAs), which are non-overlapping polygons that capture the portion of a watershed that contributes overland flow to a given stream reach (segment) (Theobald 2005; Peterson *et al.* 2007). This allows the differentiation between local and accumulated factors. RCAs were generated using the FLoWs 1.1 tool *Create Cost RCAs*, which models surface flow based on a cost surface derived from the Topographic position Index (TPI) and the Topographic Index (TOPMODEL) algorithms (Theobald 2005). The RCAs were developed from a 30-m digital elevation model (USGS National Elevation Dataset) using the 1:100k USGS National Hydrography Dataset flowlines (USGS 2004). The RCA

approach allows landscape variables to be developed at a scale that is ecologically relevant.

The landscape variables that were generated from the GIS include monthly precipitation, potential evapotranspiration, contributing drainage area, and estimated annual stream discharge (Table 4.4). Precipitation data were derived from the PRISM dataset (Daly *et al.* 1994). PRISM is a 1-km grid that provides 30-year mean and coefficient of variation of monthly precipitation for 1977 to 1997. Potential evapotranspiration (PE) data (Willmott and Kenji 2001) were used to calculate the P:ET index (precipitatation: evapotranspiration index), which is the proportion of the year during which precipitation exceeds potential evapotranspiration in a given RCA. Mean annual discharge was estimated for each stream segment based on a regional regression equation (Vogel *et al.* 1999). All landscape variables were calculated for each RCA and attributed to the appropriate stream segments. GIS stream segments were related back to the USGS stream gauges by "snapping" the gauges to the GIS channel network (Peterson *et al.* 2007). To ensure correct placement, each of the 139 USGS stream gauges was inspected to ensure that it was on the correct stream segment. Several landscape variables, including discharge, precipitation, and the P:ET index, were accumulated over the entire contributing watershed (e.g. all RCAs for all segments upstream), which was done with an area weighted average (value = sum of value for upstream RCAs / value for local RCA). The landscape variables that were used in the statistical classification model were local mean monthly precipitation, accumulated mean monthly precipitation, the coefficient of variation for accumulated mean monthly precipitation, accumulated segment discharge, accumulated P:ET index, and contributing watershed area.

A classification and regression tree model (CART; De'ath and Fabricus 2002) was used in a two step process in order to predict class membership of ungauged stream segments for the two-class and four-class Ecological and Statistical Models. In the first step, the GIS-derived landscape variables were used as predictors to build a CART tree that discriminated among the stream classes (response variable) at 139 gauged streams. In the second step, the CART tree that resulted from the first step was used to assign ungauged segments to classes based on the GIS-derived landscape variables. The CART tree was developed with the "tree" function in S-plus (2006). Although 10-fold cross-validation was used to determine the optimal tree size, the CART tree was not pruned because the unpruned trees made more accurate class predictions at the known sites. Each stream segment on the Colorado Plateau was assigned to the appropriate class based on the landscape variables with a Python script that read the CART tree into SQL (Structured Query Language), which was executed in ArcGIS 9.1 (ESRI 2006).

4.2.5. Accuracy of Stream Class Predictions at Ungauged Sites

I assessed the stability and accuracy of the stream classification systems and segment-scale stream class predictions in three ways. First, I tested the relative stability of the four trees that resulted from Ward's cluster analysis. Second, I tested the accuracy of the CART model in correctly assigning gauged streams to stream classes. Third, I tested the accuracy of the segment scale stream class predictions at ungauged sites by comparing to stream gauges with less than 8 years of data.

The goal of classification is to group similar objects into identifiable and interpretable classes that can be distinguished from neighboring classes (Gotelli and

Ellison 2004). All classification systems take continuous variation and cluster it into discrete groups; inevitably, some objects are closer to the center of the group than others are. This causes some objects, e.g. the ones in the center of the group, to have high fidelity to a class and other objects to be more mobile. I wanted to understand what portion of the stream gauges in a particular class was "mobile" in order to assess the relative stability of the classification systems. Ideally, I would like to have built classification systems from the gauge data with very tight clusters so the CART model could more readily classify ungauged streams into the classes. I assessed the relative stability of the four classification systems with Discriminant Function Analysis (DFA). I used the standardized hydrologic metrics as predictor variables and the stream classes as response variables. Discriminant Analysis constructs linear combinations of the predictor variables (hydrologic metrics) – as in PCA – that maximize the variation among groups (stream classes) (Gotelli and Ellison 2004). It is important to note that because I used the hydrologic metrics to *develop* the classes amongst which I was discriminating, this is not a true *test* of the classification strength but rather an indicator of the relative stability of the stream classes (P. Chapman, Colorado State University Statistical Consulting Center, *pers. comm.*). In any event, the probability of correct classification by DFA gives an indication of how tight the clusters that generated the stream classes are because "mobile" streams will likely be misclassified by DFA. I used the Discriminant Analysis function in STATISTICA to conduct this analysis.

I used two methods to elucidate the accuracy of the stream class predictions produced by of the CART model. First, I looked at the misclassification rate for the original (139) stream gauges used to build the CART tree from the GIS-derived

landscape variables. There are two metrics that are useful for assessing misclassification. The overall misclassification rate indicates what proportion of sites was correctly classified. Confusion matrices compare the number of gauges observed in a stream class based on the CART prediction with the number expected based on the original classification. Confusion matrices reveal the relative accuracy of the different classes within a classification system (Gotelli and Ellison 2004). Second, I compared the stream classification predicted by the landscape data to the stream classification predicted by hydrologic metrics at 59 gauged streams on the Colorado Plateau (see Appendix B for training and validation stream gauge data). Although I determined that these 59 sites had insufficient data (less than 8 years of continuous daily streamflow data) to be included in the training data for stream classification, they can give some insight into the accuracy of the simpler (two-class) classification systems. I ran a CART model in STATISTICA on the training data (e.g. 139 stream gauges) in order to predict the stream class from the original (untransformed) hydrologic metrics. I found that the CART trees for the two-class Ecological and Statistical Models consisted of one or two hydrologic metrics. I passed these hydrologic metrics through the POR-sensitivity test at 10 sites (Table 4.2) with 7 POR treatments (20, 10, 9, 8, 7, 6, 5 years). If the hydrologic metrics passed the POR-sensitivity test, I used the CART tree to predict the stream class at the 59 validation sites from the hydrologic metrics calculated at these sites. I used the misclassification rate and confusion matrices to assess the accuracy of stream classification by the GIS-based CART model at the validation sites.

4.3.0. Results

The site selection process revealed that 51% of the 456 current and historical stream gauges on the Colorado Plateau are on regulated rivers. Seven percent of the current and historical USGS gauges on the Colorado Plateau are located on the main stem Colorado River and its major tributaries, the Green, San Juan, and Little Colorado River. My selection criteria resulted in daily streamflow data from 139 gauges on 98 streams being used in the analysis (Table 4.1). The watershed area of gauges used to build the classification systems ranged from 5.7 – 18,752 km^2 (mean 1,211); the Period of Record ranged from 8 - 87 years (mean 25).

4.3.1. Ecologically- and Statistically-based Stream Classification Systems

The conceptual model of Colorado Plateau streams (Figure 4.4) was developed from field knowledge, expert opinion, and the literature and was not derived from streamflow data; however, the results of the cluster analysis on ecologically-relevant hydrologic metrics support the conceptual model. The Ecological Model was developed from three hydrologic metrics that describe the magnitude and timing of floods and three metrics that describe stream drying. The two-class Ecological Model divided Colorado Plateau streams along the flow permanence axis, which means that this axis explained more variation in the data at 139 unregulated sites than the flood regime axis (Figure 4.5a). The first group in the 2-class Ecological Model contained sites that were dry for an average of 0.9% of the months on record (D_L20). The second group contained mostly non-perennial sites that were dry an average of 15% of the months on record. Therefore, this system consists of a *perennial* and a *non-perennial* stream class (Table 4.7). On

average, the perennial streams were at a higher elevation (2063 m) and had smaller watersheds (1092 km^2) than the non-perennial streams (elevation: 1804m; watershed: 1262 km^2).

The four-class Ecological Model further divided the two-class system into classes based on flood regime. Both the perennial and non-perennial classes were divided into two groups that differed in the timing of peak flows (Table 4.8). The annual daily peak flow in the upper Colorado River basin occurs in May or June (Julian date = 121-181) and is always snowmelt dominated (Fassnacht 2006). Annual daily peak flow in the lower Colorado River basin occurs in any month except May or June and is only 50% snowmelt dominated (Fassnacht 2006). I designated the four classes in the Ecological Model as snowmelt or rain groups according to the Julian date of peak flow (T_H1). Both the perennial and non-perennial groups from the two-class system split into *snowmelt* and *rain* groups in the four-class system. Thus, the four groups that resulted from the four-class Ecological Model were perennial-snowmelt, perennial-rain, non-perennial-snowmelt, and non-perennial-rain (Figure 4.8, 4.9). On average, snowmelt-dominated streams were at higher elevations than rain-dominated streams (Table 4.7).

The results of the principal components analysis provide a description of the major components of flow variability in gauged streams on the Colorado Plateau. The PCA analysis of the hydrologic metrics at 139 sites resulted in 6 significant factors based on the broken stick method (Jackson 1993; Legendre and Legendre 1998). These six factors combined explained 71% of the variance across all sites (Table 4.5). The first PCA axis explains 29% of the variance in the data and describes the variation in

baseflow. The first PCA axis has hydrologic metrics with high factor loadings that describe the duration and frequency of low pulses (F_L3).

Five of the six hydrologic metrics that I used in the Statistical Model were the most highly loaded metric on their PCA axis (Table 4.9). In one case I did not use the most highly loaded metric because it failed the POR- and climate-sensitivity tests. The top two most highly loaded metrics on the 2nd PCA axis failed the sensitivity tests, so I used the third metric (D_H20). The six hydrologic metrics represent most major aspects of the natural flow regime (magnitude, frequency, duration, and timing). Two metrics represent the magnitude of low flows (M_L3 and D_L11) and one represents the frequency of low flow pulses (F_L3). Three hydrologic metrics that represent flow duration were used in the analysis. Two metrics describe low flow (D_L15 and D_L16) and one describes high flow (D_H20). Flow duration metrics received high factor loadings on many of the six significant PCA axes; 45% of the ten most highly loaded metrics on significant axes were duration metrics. No high or low flow timing metrics that passed the POR- and climate-sensitivity tests received high loadings (top 10) in the PCA. Therefore, no timing metrics were used in the Statistical Model.

The cluster analysis on hydrologic metrics selected by the Statistical Model produced trees that were based on variation in the magnitude and duration of high and low flows, which may be more difficult to interpret ecologically because, based on my experience on the Colorado Plateau, these stream are probably difficult to differentiate in the field (Figure 4.10). The two-class Statistical Model divided Colorado Plateau streams according to the variation in the frequency and magnitude of low flows. The two classes were larger streams (m.a.f. = 0.4 - 2042 c.f.s.) with *stable baseflow* (SB) and smaller

streams (m.a.f. = 0.9 - 938 c.f.s.) with *variable baseflow* (VB) (Table 4.9). The stable baseflow class contained sites that were mostly perennial, e.g. they were dry for an average of 0.9% of the months on record, whereas the variable baseflow contained more non-perennial sites, which were dry an average of 8% of the months on record.

The four-class Statistical Model divided the *stable baseflow* and *variable baseflow* classes differently (Table 4.11). These classes may be easiest to understand by looking at the sample hydrographs, which are for the stream gauge closest to each cluster centroid (Figure 4.11). The stable baseflow class was divided into a *snowmelt* class and a *snowmelt + rain* class. The snowmelt class, on average, had flows that peaked on May 26 and lasted 36 days. The snow + rain class had flows that peaked on June 4 and lasted 12 days. The variable baseflow class was divided into a *snowmelt + rain* class and a *rain* class. The snowmelt + rain class contained fewer perennial sites than the rain class; the snowmelt + rain and rain classes were dry for an average of 2% and 28% of the months on record, respectively. The four classes that resulted from the Statistical Model were stable baseflow-snowmelt, stable baseflow-snowmelt + rain, variable baseflow-snowmelt + rain, and variable baseflow-rain.

4.3.2. Accuracy of Stream Class Predictions at the Segment-scale

The cluster analysis for the Statistical Model produced stream classes that were, on average, slightly more stable than the classes in the Ecological Model (Table 4.11). Discriminant Function Analysis (DFA) revealed that hydrologic metrics were able to correctly predict class membership of 99% of gauged streams for the two-class Statistical Model compared to 97% correct classification of gauged streams for the two-class

Ecological Model. Overall, membership in the four-class Statistical Model was predicted with 95% accuracy by the hydrologic metrics compared to 93% accuracy for the four-class Ecological Model.

The CART models based on the GIS-variables did slightly better predicting class membership at gauged sites for the Ecological Models than for the Statistical Models (Figures 4.13, 4.14, 4.15, 4.16). The accuracy of stream class predictions was higher for both two-class systems than the 4-class systems; the 2-class Ecological Model had 93% accuracy (Figure 4.17) compared to 83% accuracy in the 4-class model (Figure 4.18). The Ecological Model was better at predicting perennial sites than non-perennial sites and perennial-snowmelt sites were especially well predicted. For the Statistical Model, the classification accuracy was approximately equal at stable baseflow and variable baseflow sites. Because two separate CART models were constructed to predict the 2-class and 4-class systems, there is some discrepancy between the class assignments for a particular stream. For example, Indian Creek near Moab, UT was predicted to be non-perennial by the two-class Ecological Model but perennial-snowmelt by the four-class system. There is disagreement at approximately 10% of the 139 gauged sites between the two-class and four-class systems; specifically, the Ecological Model showed 10.9% disagreement and the Statistical Model had 8.7% disagreement.

The four CART models used different GIS-derived variables to predict stream class at ungauged stream segments. All four trees included the contributing watershed area (accsqrkm) and estimated streamflow (acccms); however, the local and accumulated precipitation metrics that were used by the trees to discriminate among stream classes differed considerably. Average monthly precipitation metrics (local and accumulated)

for March, April, and May were common in the predictive CART models. This probably indicates the importance of late winter snowfall in streamflow regimes. The coefficient of variation of precipitation (acccv) in August and October was also included in several of the CART models, which highlights the variability of late-summer monsoon rainfall on the Plateau. I compared the mean annual flow, contributing watershed area, and site elevation of correctly- and incorrectly-classified stream gauges for the four models. There were no statistical differences in these three metrics for correct and incorrect classifications in the 2-class Ecological Model. However, sites that were correctly classified by the 2-class Statistical Model had a smaller mean annual flow than incorrectly classified sites (t-test; $t = 2.32$, d.f = 136, $p = 0.02$) but there were no differences in watershed area or site elevation. There were no statistical differences in mean annual flow or watershed area for the 4-class Ecological Model, but correctly classified sites tended to be at higher elevations than incorrectly classified sites (t-test; $t = 2.66$, d.f. = 136, $p < 0.01$). There were no statistical differences in these three metrics for correct and incorrect classifications in the 4-class Statistical Model.

The CART models that predicted stream class from untransformed hydrologic metrics at 139 training sites produced small trees: the tree for the Statistical Model had two nodes and the Ecological Model had one node. D_L11 and D_H20 were strong classifiers of streams with variable and stable baseflow for the Statistical model; however, neither of these metrics passed the POR-sensitivity test so I could not use these metrics to accurately classify the 59 validation sites, which had fewer than 8 years of streamflow data. For the Ecological Model, the duration of low flows (D_L20) was a strong classifier of perennial and non-perennial streams. The CART model suggested

that sites that were dry for less than 0.76% of the months on record were perennial. The POR-sensitivity test suggested that D_L20 did not differ significantly across PORs of varying length (ANOVA: F = 0.96, d.f. = 6, p = 0.45), therefore, I was able to classify the validation sites into perennial and non-perennial based on the CART tree. A comparison of the stream classification predicted by the landscape variables and the hydrologic metrics at the 59 validation sites revealed that segment-scale model had an overall accuracy of 58%. The model did a slightly better job of predicting non-perennial streams than perennial streams at ungauged sites.

4.4.0. Discussion

4.4.1. Accuracy of the Statistical and Ecological Models

Overall, the Colorado Plateau stream classification systems based on the Statistical and Ecological Models had approximately the same accuracy (Tables 4.11, 4.12). The slightly greater accuracy of the Ecological Model is probably due to the differential correlation strength between the hydrologic metrics and the watershed variables used to predict class membership by each of the CART models. There were 294 pairwise correlations between hydrologic metrics and GIS-derived watershed variables; 76% of these correlations were significant for the Ecological Model while only 47% were significant for the Statistical Model. Despite the large difference in the number of significantly correlated variables, both models correctly predicted class membership at 92-93% of the sites for the two class systems and 83-85% for the four class systems. Therefore, the difference in accuracy of stream class predictions at the gauged stream sites was very slight.

One of the difficulties of this research is evaluating the accuracy of the Colorado Plateau stream class predictions at *ungauged* sites. Because daily streamflow data for free-flowing streams on the Plateau are scarce, we chose to use all of the available stream gauges to build the classification systems. This method should give us the most robust classification system possible based on hydrologic metrics as well as the best prediction of stream classes at ungauged sites based on GIS-derived watershed variables. However, it also eliminates the possibility of validating the stream classification systems with high quality independent hydrologic data. The hydrologic metrics used to create the Ecological Model are insensitive to variations in the period of record (Table 4.3). Therefore, gauges with fewer than 8 years of data could be used to validate the stream class predication at ungauged sites for this model. When the accuracy of stream class predictions was compared at these sites, the Ecological Model correctly classified streams into the correct class (perennial vs. non-perennial) 58% of the time. It is likely that the Statistical Model performed approximately as well because the accuracy of the two models was almost equal for the training data.

The Colorado Plateau stream classification systems based on the Statistical and Ecological Models contain three systematic errors that are reflected in the stream classification maps (Figures 4.17, 4.18). First, the stream class predictions are probably more accurate and reliable in areas with higher gauge density, such as the high mountains on the western edge of the Plateau (Figures 4.19, 4.20). The Colorado Plateau has been underrepresented by previous streamflow classification studies because it lacks abundant, high-quality stream gauges (Poff and Ward 1989; Poff 1996). The CART model is more accurate in areas of high gauge density because it was trained on the typography and

climate of the gauges in these areas. The stream classification maps are probably not as reliable in areas with low gauge density, such as the Four Corners region, because stream class predictions at these sites are extrapolations outside of the topography and climate upon which the model was trained. Extrapolations outside the range of the training data inevitably have greater uncertainty associated with them (Gotelli and Ellison 2004). Second, this streamflow classification was developed for free-flowing headwaters streams to mid-sized rivers, therefore, the stream class predictions at large rivers (i.e., San Juan River) are likely problematic. Additionally, most of these large rivers are regulated and, therefore, their altered flow regimes would not fit into this classification. Third, the streamflow predictions probably underestimate perennial streams in areas that receive considerable groundwater input. This is partially due to the coarse resolution of the geology data that were available to incorporate into the GIS database and CART model. For example, the model accurately predicted the perennial streams in the Virgin River basin, which is an area rich in Navajo Sandstone (Weiss 1987). The model was probably able to make accurate predictions in this region due to the high density gauge data. However, the Navajo Sandstone also contributes groundwater to stream segments in the lower Escalante River Canyon (i.e., Coyote Gulch), but it appears that the Ecological Model was not able to accurately predict the perennial streams in that region.

4.4.2. Ecological Application of the Statistical and Ecological Models

From an ecological perspective, the two streamflow classification systems address two similar sources of hydrologic variation: fluctuations in baseflow and the timing and predictability of flooding. The Statistical Model divides streams into two classes based

on baseflow variability, with one class containing lower elevation streams that frequently dry and the other, smaller, class containing higher elevation streams that rarely dry. These two stream classes are similar to the non-perennial and perennial classes of the Ecological Model. All classification systems take continuous variation and cluster it into discrete groups and some objects inevitably are closer to the center of the group than others. The difference between the two classification systems is really in where the center of the group is located along the continuous gradient of stream permanence. The variable streamflow class of the statistically-based model can be thought of as the non-perennial class of the ecologically-based model that has been shifted slightly to include more streams that do not dry. The two classes also separate streams into groups based on the timing and frequency of flood flows; in both cases the floods originate from snowmelt or rainfall.

The Ecological Model may be more useful to ecologists than the Statistical Model because more comparative research has been done on perennial and non-perennial streams than on stable and variable baseflow streams. Many lotic taxa require flowing water for respiration, food acquisition, and the maintenance of high quality benthic habitat. Flowing water delivers oxygen to the gills (and other respiratory structures) of aquatic organisms. Stream insects have behavioral adaptations to improve oxygen diffusion in slow flowing or standing water (i.e. stoneflies do "push ups", some mayfly taxa flutter their gills, caddisflies undulate their bodies inside their cases to improve water flow) but these behaviors have energetic costs (Allan 1995). Filter feeding insects and drift feeding fish require a steady supply of drifting detritus and invertebrates (Allan 1978; Hart and Finelli 1999); the cessation or reduction of streamflow in non-perennial

streams can limit the growth of these taxa (Harvey *et al.* 2006). Several species of aquatic organisms require clean, inorganic substrates for burrowing (Minshall 1984) and spawning (Tetzlaff *et al.* 2005). Flow reduction or cessation may increase fine sediment deposition and can lead to the decline of rheophilic taxa (Albano 2006). The reliance of many stream organisms on streamflow suggests that while variation in baseflow is important, the cessation of streamflow in riffle habitats has a disproportionate effect on stream biota (Feminella 1996; Stanley *et al.* 1997; Fritz and Dodds 2005; Robson *et al.* 2005; Bunn *et al.* 2006). This suggests that distinction between perennial and non-perennial streams may be more useful to ecologists than the distinction between variable and stable baseflow streams.

In addition to its theoretical foundation, the Ecological Model probably has more utility for researchers and managers because it is more intuitive and more highly correlated with landscape variables; therefore, it should be more useful for management because the field identification of stream classes should be easier. Although temporally intermittent streams can be difficult to recognize at certain times of year, non-perennial streams can easily be identified when there is no water in the channel. In other regions, perennial streams have characteristic invertebrate fauna that can be used to classify streams in the field (Boulton and Lake 1992; Bogan and Lytle 2007). Perennial and non-perennial streams on the Colorado Plateau have characteristic riparian species (Scott *et al.* 2005). Perennial, free-flowing small streams on the Plateau frequently have multi-aged stands of cottonwood and/or willow due to ongoing recruitment (A. Moline, *pers. obs.*); whereas cottonwood and willow establishment at non-perennial sites tends to be episodic in response to large flood events (McBride and Strahan 1984). Non-perennial

streams on the Plateau have upland vegetation nearby but do not typically have a dense riparian canopy of cottonwood or willow (A. Moline, *pers. obs.*). Cottonwood and willow can survive at non-perennial sites by taking up groundwater (Snyder and Williams 2000; Friedman and Lee 2002), but they are not abundant at non-perennial sites on the Plateau. Any mention of riparian vegetation on the Colorado Plateau necessitates a brief discussion of tamarisk invasion. Tamarisk invasion on the Colorado Plateau appears to be occurring fastest on perennial regulated rivers (Grams and Schmidt 2002; Cooper *et al.* 2003; Birken and Cooper 2006); however, it is also present along non-perennial washes that are underlain by shallow groundwater (P. Evangelista, Natural Resource Ecology Laboratory, Colorado State University, *pers. com.*). It is possible that tamarisk invasion on the Colorado Plateau could convert perennial streams to non-perennial systems due to groundwater declines, which appear to result from the high rates of evapotranspiration that occur when dense stands of tamarisk invade arid riparian zones (Stromberg 1998). Perennial and non-perennial streams on the Colorado Plateau are probably easier to distinguish in the field than variable and stable baseflow sites because of these differences in cottonwood, willow, and tamarisk abundance.

4.4.3. Ecological Predications and Implications

The classification maps make spatially-explicit predictions of the habitat template of streams on the Colorado Plateau that could be tested with aquatic community data. Although a test of the classification is beyond the scope of this chapter, I will highlight some of the interesting findings that could provide the foundation for future research. The Ecological Model predicted that 75% of the stream length on the Colorado Plateau

are non-perennial. Given the abundance of non-perennial streams, permanent waterpockets and large rivers should be an important refuge for aquatic invertebrates (Baron *et al.* 1998; Lake 2000; Bunn *et al.* 2006). These refuges should serve as source populations to recolonize non-perennial streams after rain events or during snowmelt (Gray 1981a). The abundance of non-perennial streams in the interior of the Plateau suggests that the two maps should be blended wherever there is a large homogeneous expanse. For example, the Statistical Model predicts a mixture of stable-baseflow and variable-baseflow streams in northern Arizona, but the Ecological Model predicts only non-perennial streams (Figure 4.21, 4.22). This suggests that the statistically-based classification is picking up subtle physical and biological processes that are not detected by the ecologically-based classification. The spatial distribution of non-perennial streams around the Plateau should be tracked by the presence of desiccation resistant taxa.

The snowmelt-fed habitat (25% of perennial and non-perennial stream kilometers) is distributed around the edge of the Colorado Plateau, particularly in the San Juan Mountains to the east. Snowmelt-driven streams are also present on the Henry and La Sal Mountains as well as the Kaibab Plateau at the North Rim of the Grand Canyon. The sharp gradient between snowmelt- and rain-driven streams in mountainous areas of the Plateau should provide an excellent location to test whether snowmelt- and rain-adapted taxa track flow in years with varying temperature regimes. These locations would be ideally suited to a test of the template theory because snowmelt-adapted taxa, such as stoneflies that emerge prior to snowmelt runoff should be common at high elevation sites (Jacobi and Cary 1996) and flash flood adapted taxa, such as aquatic Hemiptera and some species of Trichoptera should be more common at lower elevations (Lytle and Smith

2004; Lytle and White *In Press*). These mountainous areas should also provide a location at which to monitor cool stenothermic taxa for responses to global climate change. Researchers in the Sonoran Desert have identified a similar hydrologic gradient in the seasonally intermittent streams of the Sky Islands, which are a series of mountain habitats in a desert landscape (Bogan 2006). In the Sky Islands, researchers have found evidence to suggest that two insect faunas co-exist in the hydrologically variable streams through "time sharing", such that montane temperate fauna colonize the seasonally intermittent streams during periods of high flow and aquatic neotropical hemipterans and coleopterans occupy the sites during periods of low flow (Bogan and Lytle 2007). Localized species extinctions of temperature-sensitive montane fauna have also been identified in the Sky Islands, presumably in response to local warming (Finn *et al.* In Press).

Harsh hydrologic regimes in arid environments exert a strong selective pressure on aquatic taxa; therefore, arid environments provide a unique habitat template in which to test mechanistic predictions about aquatic insect functional traits. Over evolutionary time, aquatic invertebrates must develop life history and/or behavioral adaptations in order to survive in these environments (Lytle 2001; Lytle and Poff 2004). I expect that insect taxa will have functional traits that allow them to exist amidst variation in flow permanence and flood predictability (Figure 4.23). Flow permanence probably exerts a stronger selective pressure on Colorado Plateau stream communities than the flood predictability axis because of high mortality due to drying, after all, these are *aquatic* biota (Boulton 2003). I expect non-perennial sites to have a higher proportion of desiccation resistant insects (Jacobi and Cary 1996) (Figure 4.23). As non-perennial

streams dry, flow ceases and disconnected remnant pools remain (Stanley *et al.* 1997); therefore, rheophilic taxa are probably less common in non-perennial streams. The water temperature increases and the dissolved oxygen level decreases as fragmented pool habitats bake in the sun. Changes in water temperature and oxygen availability cause insects with mobile adult stages to exit the water (Velasco and Millan 1998) or crawl upstream (Lytle *et al.* In Review). Therefore, insects that have the ability to exit the stream as juveniles or adults should be common in non-perennial streams (Williams 1996). Insects that are cold water obligates should also be rare in non-perennial streams because they cannot survive the changes in water temperature that accompany flow cessation (Velasco and Millan 1998).

The frequency and timing of floods in snowmelt streams are more predictable than floods in rain-driven streams. Much of what is known about the adaptations of aquatic insects to stream habitats is based on the timing of emergence (Lytle 2002; Harper and Peckarsky 2006) and amount of time required for larvae to develop (Richardson 1991; Bunn *et al.* 2006). The spatially and temporally heterogeneous nature of streamflow in rain-driven streams leads me to suggest that disturbance-adapted taxa will be more common in rain-driven than snowmelt streams. Therefore, I expect that insect drift is more common in rain-driven than snowmelt-fed streams. Drift can serve as a recolonization pathway in rain-driven streams that experience flash floods due to tributary inputs; these floods can severely disturb the stream channel downstream of the tributary but leave upstream reaches intact. Asynchronous emergence can also serve as a source of colonists to recently flooded streams (Gray 1981a); therefore, I expect that insects in rain-driven streams will commonly exhibit asynchronous life cycles.

Some insect functional traits will probably respond to variation in flow permanence and flood predictability. Adversity-adapted taxa with short life cycles and high mobility should dominate at these sites (Minshall 1988). Multivoltine taxa are common in frequently disturbed stream habitats (Gray 1981b). Insect life cycles with several generations per year are less likely to be locally extirpated by flooding because rapid larval development reduces the time that the population is susceptible to hydrologic disturbance (Lytle 2001). In the inevitable event that a stream experiences a catastrophic flood that removes a large portion of the aquatic insect biomass, taxa with strong female dispersal ability would have a selective advantage in streams that dry (flow permanence axis) and streams that flood frequently (flood predictability axis) because adults could repopulate denuded streams through oviposition (Gray 1981a; Cushing and Gaines 1989).

Any use of the classification maps as a means for choosing sites in which to test the habitat template should take into account the limitations of testing a single habitat variable and the inaccuracies inherent in the classification methods. The streamflow classification that I have presented here represents two components of a single environmental variable (streamflow); however, there are a multitude of gradients on the Colorado Plateau that affect stream communities. Several authors have suggested that hydrologic disturbances are *the* major environmental driver of stream communities (Resh *et al.* 1988; Poff and Ward 1990; Townsend and Hildrew 1994; Lake 2000); however, others have suggested that meaningful characterization of the stream habitat template must also include a description the stream-specific thermal regime and substrate-geomorphologic characteristics in addition to streamflow (Poff and Ward 1990). Finally, as with any exercise in statistical modeling, there are errors inherent in the process

including the uncertainty associated with extrapolating to areas with few stream gauges, flow regulation, and the presence of groundwater.

4.5.0 Literature Cited

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Table 4.1. Summary data for the 139 gauged stream sites on the Colorado Plateau used in the classification analysis.

	Period of Record (years)	Elevation (m)	Watershed Area km^2	(mi^2)	Mean daily flow (M_A1) ($m^3 s^{-1}$)	($ft^3 s^{-1}$)
Min.	8	590	5.7	2.2	0.011	0.4
25%	11	1,559	90.7	35.0	0.21	7.5
Mean	25	1,965	1,211.1	467.6	2.68	95.7
75%	33	2,353	1,023.1	395.0	2.11	75.4
Max.	87	3,385	18,751.6	7,240.0	57.19	2,042.3

Table 4.2. Sites included in the POR-sensitivity and climate-sensitivity analyses.
* Chinle Creek was not included in the climate sensitivity analysis because it did not have sufficient data.

	Start	End	POR (years)
09172500 SAN MIGUEL RIVER	1943	2005	62
09310000 GOOSEBERRY	1941	2003	62
09310500 FISH CREEK	1939	2005	66
09330500 MUDDY CREEK	1949	2005	56
09346000 NAVAJO RIVER	1935	1995	60
09365000 SAN JUAN RIVER	1931	2005	74
09365500 LA PLATA RIVER	1918	2005	87
09366500 LA PLATA RIVER	1921	2005	84
09379200 CHINLE CREEK *	1965	2005	40
09405500 NORTH FORK VIRGIN RIVER	1928	2005	77

Table 4.3. Hydrologic Metrics used as input to the Ecological Model. Metrics were chosen that were believed to maximize differences in biologically relevant aspects of the flow regime for the Colorado Plateau (e.g. flood timing and flow intermittency). Metrics were also chosen that were robust to changes in the length of the time series (POR) and robust to changes in decadal climate changes (climate). These p-values are for Main Effects ANOVA with site x climate and site x POR.

Metric	POR p-value	Climate p-value	Definition of original metric (units given are before adjustment)	Biological Justification
M_H20	0.76	0.49	Specific mean annual maximum flow. M_H20 is the mean of the annual maximum flows divided by the drainage area (ft^3/s per square mile – temporal).	Relative magnitude of high flows may separate snowmelt-driven streams from rain-driven streams
F_L3	0.46	0.51	Frequency of low pulse spells. Compute the average number of flow events with flows below a threshold equal to 5 percent of the mean flow value for the entire flow record. F_L3 is the average number of events (number of events/year – temporal).	Low flow frequency should separate perennial sites from non-perennial sites.
D_L18	0.57	0.47	Mean annual number of zero-flow days. Count the number of zero-flow days for the entire flow record (number of days/year – temporal).	Relative measure of intermittency; should separate perennial from intermittent streams.
D_L20	0.42	0.45	Number of zero-flow months. While computing the mean monthly flow values, count the number of months in which there was no flow over the entire flow record (percent – spatial).	Relative measure of intermittency.
D_H20	0.31	0.44	Average high flow duration. Compute the 75th percentile value for the entire flow record. Compute the average duration of flow events with flows above a threshold equal to the 75th percentile value for the median annual flows (days – temporal).	High flow duration should separate snowmelt-driven sites from flashy rain-driven sites.
T_H1	0.34	0.56	Julian date of annual maximum. Determine the Julian date that the maximum flow occurs for each year; calculated on a circular scale as in T_L1. (Julian day – spatial).	Timing of high flows affects invertebrate life history, growth, reproductive success.

Table 4.4. GIS-derived variables that were used in the CART model. Accumulated values sum the variable over the contributing watershed area for each stream gauge. 30 year mean for precipitation = 1967 to 1997

Variables	Definition
accsqrkm	Contributing drainage area in km^2 (accumulated).
acccms	Accumulated discharge (Vogel method) in m^3/s
accpptdef	Percent of the year that a reach receives precipitation above potential evapotranspiration (accumulated)
avgppt1-12	30-year mean **January-December** precipitation
avgppt14	30-year mean **annual** precipitation
accppt1-12	30-year mean **January-December** precipitation (accumulated).
accppt14	30-year mean **annual** precipitation (accumulated).
acccv1-12	Coefficient of variation of 30-year mean **January-December** precipitation (accumulated).
acccv14	Coefficient of variation of 30-year mean **annual** precipitation (accumulated).

Table 4.5. Principal components analysis output for ten most highly loaded hydrologic metrics (metric abbreviations are taken from Olden and Poff 2003) on the six significant axes according to the broken stick method (Jackson 1993). Metrics that were used as input to the Statistical Model and their respective factor loadings are marked in **bold** and are described in Table 4.4. Metric definitions are given in Appendix B.

	Axis 1		Axis 2		Axis 3		Axis 4		Axis 5		Axis 6	
Variance Explained	29%		13%		10%		8%		7%		4%	
1st Metric	**F_L3**	**-0.91**	D_H19	0.85	**D_L15**	**0.81**	**M_L3**	**-0.64**	**D_L11**	**0.62**	**D_L16**	**-0.65**
2nd Metric	M_L20	0.90	D_H18	0.84	M_H27	0.75	D_H6	-0.60	D_L12	0.61	F_H9	0.58
3rd Metric	D_H3	-0.83	**D_H20**	**0.75**	M_H24	0.75	D_H8	-0.60	D_L13	0.60	F_L1	0.47
4th Metric	F_H7	-0.82	F_H1	-0.74	D_H11	0.74	D_H7	-0.59	T_A1	0.55	F_H5	0.46
5th Metric	D_H2	-0.81	F_H8	-0.74	M_H25	0.74	D_H9	-0.57	D_L20	0.43	T_L2	0.42
6th Metric	M_L17	0.78	D_H15	0.72	M_H16	0.73	M_L4	-0.57	M_L16	0.43	D_L20	-0.41
7th Metric	D_L3	0.77	D_H5	0.70	D_H13	0.73	M_L2	-0.54	D_H4	0.43	M_H18	-0.38
8th Metric	D_L2	0.77	M_L5	0.67	D_H12	0.73	D_H10	-0.50	T_A2	0.42	F_H6	0.37
9th Metric	D_L4	0.77	M_H5	0.67	M_H17	0.71	M_L1	-0.50	D_H3	0.42	M_H14	0.34
10th Metric	D_H1	-0.77	F_H5	-0.67	M_H26	0.71	M_L12	-0.47	M_L14	0.42	M_H22	-0.34

Table 4.6. Hydrologic Metrics used for **Statistical Model** Hydrologic metrics were chosen that explained a high proportion of the variance as described by a principal components analysis. The first six PCA axes were significant according to the Broken Stick Method (Jackson 1993). The superscripts indicate the loading of the axis; the hydrologic metric with the highest loading was used except for on axis 2 (because the first two HMs were susceptible to variation in POR and climate). Metrics were also chosen that were robust to robust to changes in the length of the time series (POR) and changes in decadal climate changes (climate). These p-values are for main effects ANOVA with site x climate and site x POR. Abbreviated definitions are given for each of the hydrologic metrics.

Metric	PCA Axis	POR p-value	Climate p-value	Definition of original metric (units given are before adjustment)
F_L3	Axis 1^1	0.46	0.51	Frequency of low pulse spells. Compute the average number of flow events with flows below a threshold equal to 5 percent of the mean flow value for the entire flow record. F_L3 is the average number of events (number of events/year – temporal).
D_H20	Axis 2^3	0.32	0.44	Average high flow duration. Compute the 75th percentile value for the entire flow record. Compute the average duration of flow events with flows above a threshold equal to the 75th percentile value for the median annual flows (days – temporal).
D_L15	Axis 3^1	0.13	0.49	Low exceedence flows. Compute the 90 percent exceedence value for the entire flow record. DL14 is the exceedence value divided by the median for the entire record (dimensionless – spatial).
M_L3	Axis 4^1	0.31	0.32	Minimum flows for March averaged across all years. (cubic feet per second)
D_L11	Axis 5^1	0.32	0.99	Annual minimum daily flow divided by the median for the entire record. Compute the minimum daily flow for each year. DL11 is the mean of these values divided by the median for the entire record (dimensionless – temporal).
D_L16	Axis 6^1	0.13	0.16	Low flow pulse duration. Compute the average pulse duration for each year for flow events below a threshold equal to the 25th percentile value for the entire flow record. DL16 is the median of the yearly average durations (number of days – temporal).

Table 4.7. Mean values of hydrologic metrics that were used as input to the two-class Ecological Model.

	Class	n	Elev. (m)	Drain (km^2)	M.A.F. (cfs)	D_L18	D_L20	T_L1	Date	D_H20	T_H1	Date
Perennial	P	94	2063	1092	135.5	0.9	0.0	195	14-Jul	24.9	164	13-Jun
Non-Perennial	NP	45	1804	1262	12.4	113.7	15.2	247	4-Sep	12.7	196	15-Jul

Table 4.8. Mean values of hydrologic metrics that were used as input to the four-class Ecological Model.

	Class	n	Elev. (m)	Drain (km^2)	M.A.F. (cfs)	D_L18	D_L20	T_L1	Date	D_H20	T_H1	Date
Perennial - Snowmelt	PS	60	2289	657	130.6	0.7	0.0	204	23-Jul	32.5	140	20-May
Non-Perennial - Snowmelt	NPS	16	2180	163	5.7	69.0	10.4	267	24-Sep	25.0	125	4-May
Perennial – Rain	PR	34	1666	1862	144.3	1.1	0.0	178	27-Jun	11.5	206	25-Jul
Non-Perennial - Rain	NPR	29	1588	1890	16.1	138.4	17.8	235	23-Aug	5.9	235	23-Aug

Table 4.9. Mean values of hydrologic metrics that were used as input to the two-class Statistical Model

	Class	n	Elev. (m)	Drain (km^2)	M.A.F. (cfs)	D_L18	F_L3	D_L11	M_L3	D_H20	T_H1	Date
Variable Baseflow	VB	82	2274	1502	73.5	62.8	4.7	0.1	29.5	14.1	192	11-Jul
Stable Baseflow	SB	57	1774	642	127.5	0.9	0.4	0.4	31.3	31.0	148	28-May

Table 4.10. Mean values of hydrologic metrics that were used as input to the four-class Statistical Model

	Class	n	Elev. (m)	Drain (km^2)	M.A.F. (cfs)	D_L18	F_L3	D_L11	M_L3	D_H20	T_H1	Date
Stable Baseflow – Snowmelt	SB1	45	2385	699	151.7	1.2	0.5	0.4	33.4	35.9	146	26-May
Stable Baseflow – Snow & Rain	SB2	12	1854	426	36.5	0.0	0.0	0.5	23.6	12.3	155	4-Jun
Variable Baseflow – Snow & Rain	VB2	63	1821	1676	93.4	24.3	3.9	0.1	34.6	16.4	182	30-Jun
Variable Baseflow – Rain	VB1	19	1612	426	7.7	190.3	9.1	0.1	0.5	6.4	228	16-Aug

Table 4.11. Discriminant function analysis output (based on standardized hydrologic metrics) indicates the reliability of clusters in the a) two-class and b) four-class Ecological Model.

a)

	Class	n	Training Data % Correct
Perennial	P	94	98
Non-Perennial	NP	45	96
	Total		**97%**

b)

	Class	n	Training Data % Correct
Perennial – Snowmelt	PS	60	93
Perennial – Rain	NPS	16	88
Non-Perennial – Snowmelt	PR	34	88
Non-Perennial – Rain	NPR	29	100
	Total		**93%**

Table 4.12. Discriminant function analysis output (based on standardized hydrologic metrics) indicates the reliability of clusters in the a) two-class and b) four-class Statistical Model.

a)

	Class	n	Training Data % Correct
Variable Baseflow	VB	82	98
Stable Baseflow	SB	57	100
	Total		**99%**

b)

	Class	n	Training Data % Correct
Stable Baseflow – Snowmelt	SB1	45	99
Stable Baseflow – Snow & Rain	SB2	12	92
Variable Baseflow – Snow & Rain	VB2	63	97
Variable Baseflow – Rain	VB1	19	84
	Total		**95%**

Table 4.13. Significant correlations between hydrologic metrics used to build the stream classification systems and landscape variables used to predict stream class membership. These correlations are calculated at 139 gauged stream sites on the Colorado Plateau. Significant p-values are given (less than 0.05)

	Ecological Model Hydrologic Metrics				Metrics in Both Models		Statistical Model Hydrologic Metrics			
	M_H20	D_L20	D_L18	T_H1	F_L3	D_H20	D_L11	D_L15	D_L16	M_L3
accsqrkm	-0.204	-0.041	0.013	0.132	0.048	-0.173	-0.153	-0.039	-0.131	0.613
	0.021	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	p < 0.01
acccms	-0.001	-0.135	-0.152	-0.061	-0.190	0.024	0.034	-0.044	-0.099	0.732
	n.s.	n.s.	n.s.	n.s.	0.031	n.s.	n.s.	n.s.	n.s.	p < 0.01
accpptdef	0.586	-0.258	-0.341	-0.558	-0.441	0.733	0.444	-0.004	0.096	-0.004
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt1	0.597	-0.127	-0.200	-0.472	-0.329	0.490	0.389	0.002	0.154	-0.090
	p < 0.01	n.s.	0.023	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt2	0.594	-0.123	-0.197	-0.467	-0.334	0.431	0.388	-0.009	0.156	-0.095
	p < 0.01	n.s.	0.026	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt3	0.622	-0.155	-0.239	-0.480	-0.376	0.458	0.420	0.006	0.159	-0.106
	p < 0.01	n.s.	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt4	0.629	-0.166	-0.251	-0.445	-0.360	0.530	0.415	0.031	0.139	-0.102
	p < 0.01	n.s.	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt5	0.635	-0.208	-0.299	-0.457	-0.405	0.593	0.412	0.016	0.164	-0.131
	p < 0.01	0.018	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt6	0.664	-0.212	-0.307	-0.449	-0.409	0.643	0.423	0.008	0.180	-0.135
	p < 0.01	0.016	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	0.041	n.s.
avgppt7	0.583	-0.154	-0.213	-0.370	-0.293	0.479	0.370	0.038	0.089	-0.057
	p < 0.01	n.s.	0.015	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt8	0.584	-0.151	-0.216	-0.366	-0.314	0.433	0.397	0.035	0.059	-0.006
	p < 0.01	n.s.	0.014	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt9	0.655	-0.132	-0.219	-0.441	-0.337	0.545	0.392	0.045	0.125	-0.078
	p < 0.01	n.s.	0.013	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt10	0.608	-0.090	-0.179	-0.443	-0.305	0.508	0.323	0.010	0.119	-0.093
	p < 0.01	n.s.	0.043	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt11	0.647	-0.159	-0.227	-0.447	-0.346	0.503	0.379	0.002	0.132	-0.071
	p < 0.01	n.s.	0.010	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt12	0.611	-0.135	-0.203	-0.433	-0.317	0.488	0.370	0.007	0.152	-0.096
	p < 0.01	n.s.	0.021	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
avgppt14	0.660	-0.159	-0.241	-0.471	-0.366	0.534	0.417	0.016	0.144	-0.092
	p < 0.01	n.s.	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt1	0.591	-0.219	-0.292	-0.544	-0.413	0.597	0.392	-0.016	0.077	-0.032
	p < 0.01	0.013	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt2	0.609	-0.222	-0.298	-0.553	-0.443	0.556	0.419	-0.017	0.089	-0.029
	p < 0.01	0.012	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt3	0.645	-0.259	-0.347	-0.531	-0.481	0.563	0.441	-0.010	0.081	-0.018
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt4	0.657	-0.271	-0.365	-0.498	-0.486	0.635	0.463	0.018	0.090	-0.016
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt5	0.612	-0.314	-0.406	-0.519	-0.505	0.677	0.445	-0.006	0.092	-0.038
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt6	0.598	-0.310	-0.398	-0.521	-0.491	0.729	0.439	-0.006	0.101	-0.028
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt7	0.482	-0.223	-0.259	-0.378	-0.308	0.485	0.316	0.012	-0.018	0.033
	p < 0.01	0.011	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt8	0.483	-0.211	-0.250	-0.359	-0.320	0.421	0.334	-0.004	-0.036	0.064
	p < 0.01	0.017	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt9	0.623	-0.226	-0.303	-0.476	-0.412	0.569	0.368	-0.002	0.055	0.000
	p < 0.01	0.010	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt10	0.608	-0.201	-0.282	-0.487	-0.395	0.559	0.353	-0.006	0.065	-0.036
	p < 0.01	0.023	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt11	0.661	-0.259	-0.325	-0.484	-0.446	0.594	0.418	0.002	0.070	-0.004
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt12	0.625	-0.238	-0.309	-0.509	-0.423	0.605	0.401	-0.006	0.080	-0.009
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
accppt14	0.642	-0.259	-0.337	-0.522	-0.455	0.613	0.427	-0.004	0.066	-0.010
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	n.s.
acccv1	-0.438	0.222	0.338	0.346	0.438	-0.591	-0.307	0.019	-0.180	-0.158
	p < 0.01	0.012	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	0.042	n.s.
acccv2	-0.423	0.162	0.227	0.387	0.319	-0.631	-0.340	-0.083	-0.105	-0.257
	p < 0.01	n.s.	0.010	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	p < 0.01
acccv3	-0.484	0.197	0.319	0.426	0.436	-0.593	-0.365	-0.009	-0.182	-0.243
	p < 0.01	0.025	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	0.039	p < 0.01
acccv4	-0.495	0.257	0.384	0.465	0.538	-0.612	-0.400	0.026	-0.152	-0.238
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	p < 0.01
acccv5	-0.390	0.327	0.454	0.458	0.622	-0.518	-0.453	0.099	-0.102	-0.295
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	p < 0.01
acccv6	-0.390	0.327	0.454	0.458	0.622	-0.518	-0.453	0.099	-0.102	-0.295

	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	p < 0.01
acccv7	**-0.277**	**0.215**	**0.247**	0.158	**0.285**	**-0.323**	**-0.198**	0.013	0.064	**-0.464**
	p < 0.01	0.015	p < 0.01	n.s.	p < 0.01	p < 0.01	0.024	n.s.	n.s.	p < 0.01
acccv8	**-0.308**	**0.243**	**0.282**	**0.255**	**0.354**	**-0.390**	**-0.375**	0.001	0.110	**-0.606**
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	p < 0.01
acccv9	**-0.234**	0.107	0.130	0.098	**0.181**	**-0.275**	**-0.173**	-0.013	0.041	**-0.536**
	p < 0.01	n.s.	n.s.	n.s.	0.040	p < 0.01	0.050	n.s.	n.s.	p < 0.01
acccv10	**-0.376**	**0.249**	**0.417**	**0.462**	**0.528**	**-0.495**	**-0.409**	0.134	-0.158	**-0.274**
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	p < 0.01
acccv11	**-0.427**	0.155	**0.266**	**0.345**	**0.366**	**-0.519**	**-0.265**	0.021	-0.154	**-0.349**
	p < 0.01	n.s.	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	p < 0.01
acccv12	**-0.293**	**0.181**	**0.277**	**0.270**	**0.326**	**-0.426**	**-0.276**	0.031	-0.126	**-0.405**
	p < 0.01	0.040	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	p < 0.01
acccv14	**-0.474**	**0.298**	**0.405**	**0.404**	**0.497**	**-0.641**	**-0.395**	0.036	-0.122	**-0.196**
	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	p < 0.01	n.s.	n.s.	0.026
% Significant	0.98	0.62	0.93	0.90	0.98	0.95	0.95	0.00	0.07	0.33

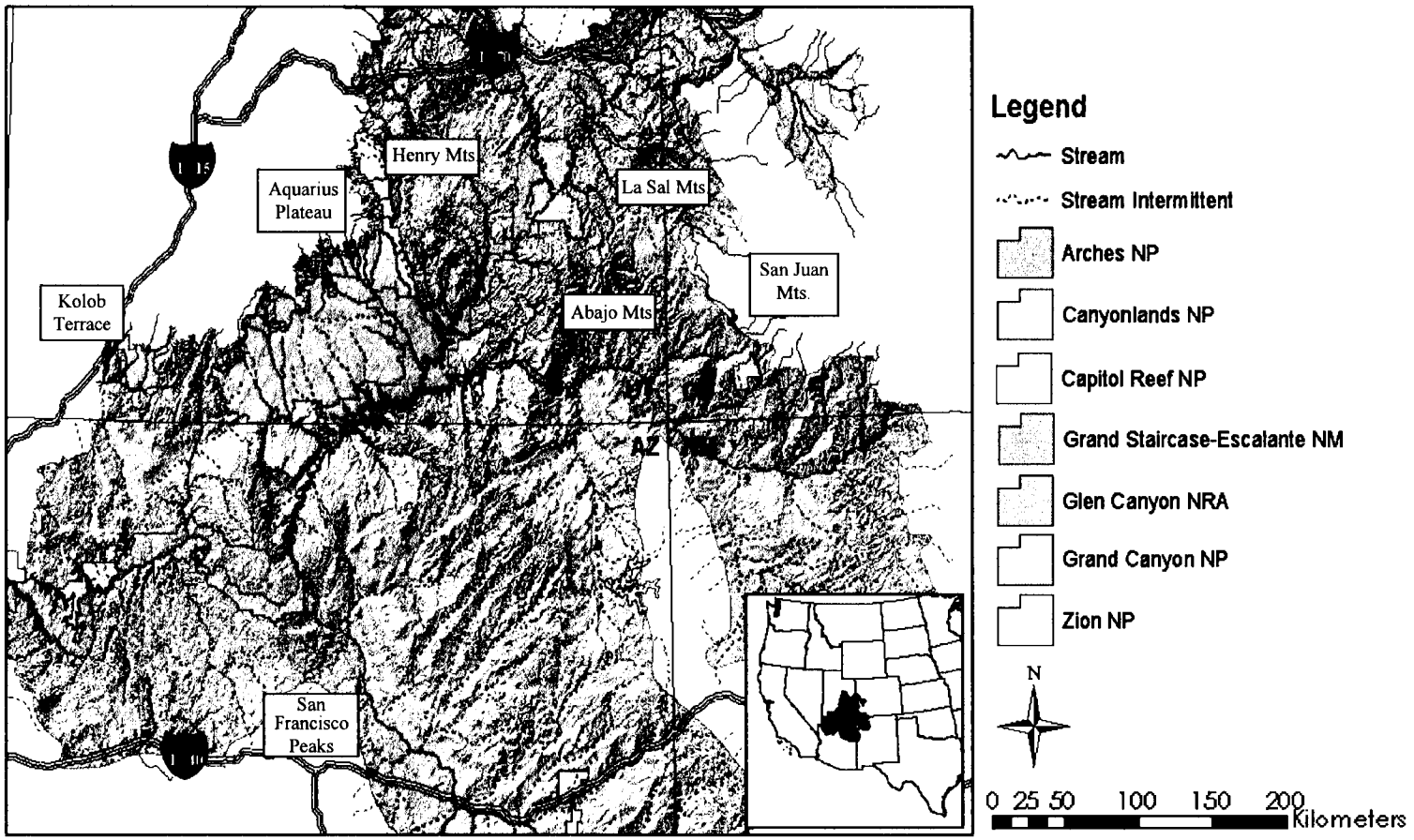

Figure 4.1. Map National Parks on the Colorado Plateau with major mountain ranges and plateaus. Many snowmelt-driven streams originate in the Henry, La Sal, Abajo, and San Juan Mountains.

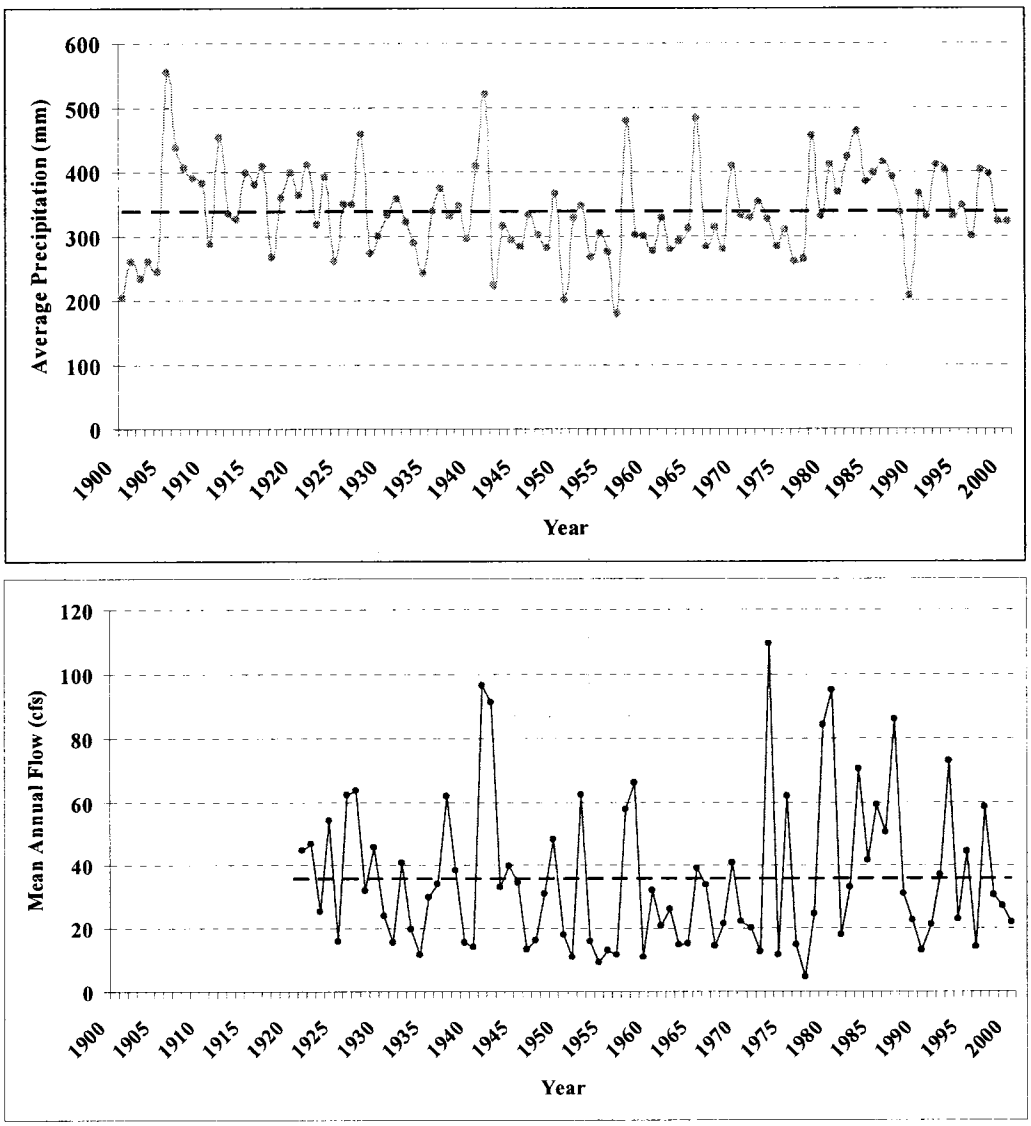

Figure 4.2. top) Average precipitation on the Colorado Plateau from 1990-2000 (n = 97 weather stations). The dark dashed line shows the mean annual precipitation for the century (338.4 mm). The century began with a relatively wet period. The middle of the century was drier. The century ended wetter than average (data from Hereford *et al.* 2002). **bottom)** Average streamflow at La Plata River on the Colorado-New Mexico state line (USGS #09366500) from 1921-2000. This gauge has the longest continuous period of record of the gauges included in this analysis.

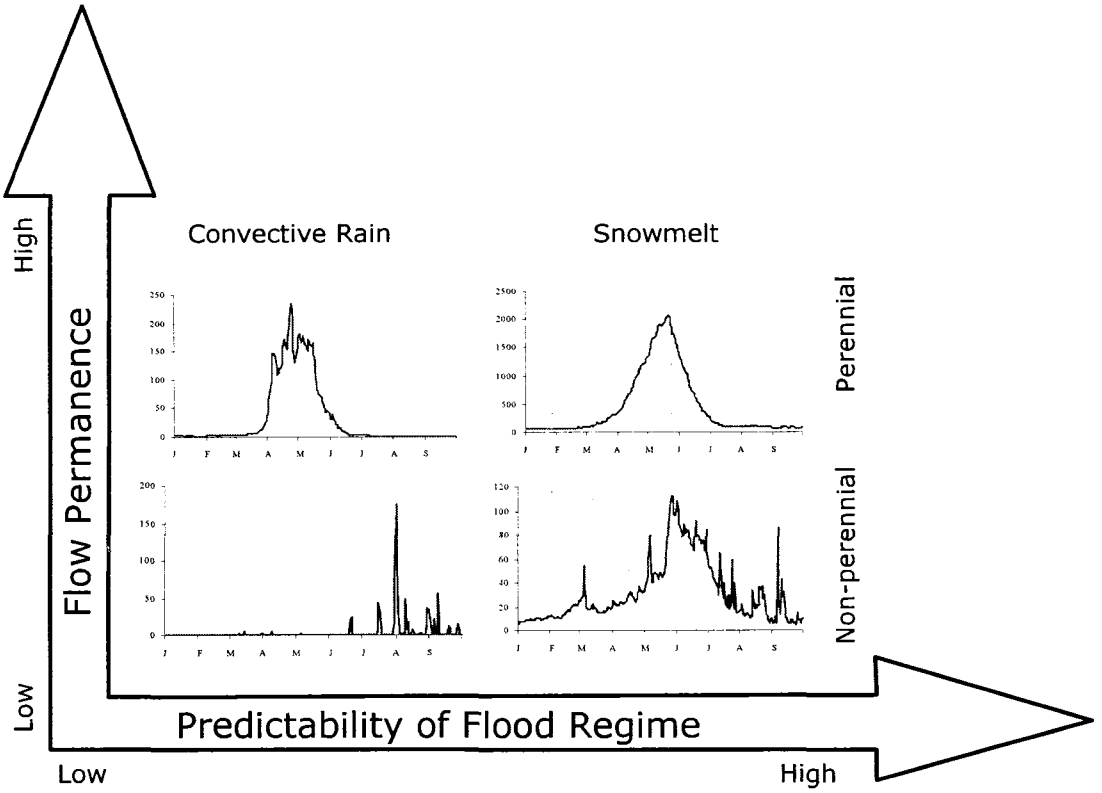

Figure 4.3. Conceptual model of hydrologic drivers of invertebrate communities the Colorado Plateau stream community. The inset hydrographs are an example of what the flow regime looks like. Flow regimes on the Plateau exist along a continuum from perennial streams to streams that flow only during snowmelt or after rain events. The two major sources of floods are snowmelt and summer convective rain events. Snowmelt tends to occur at higher elevations, whereas summer convective storms occur mostly below 2,286 m / 7,500 ft. (Thomas *et al.*, 1997). These stream classes correspond to classes suggested by Poff (1996) as follows: snowmelt-perennial stream = snowmelt, summer convective-perennial = perennial flashy, snowmelt-non-perennial = none, summer convective-non-perennial = harsh intermittent.

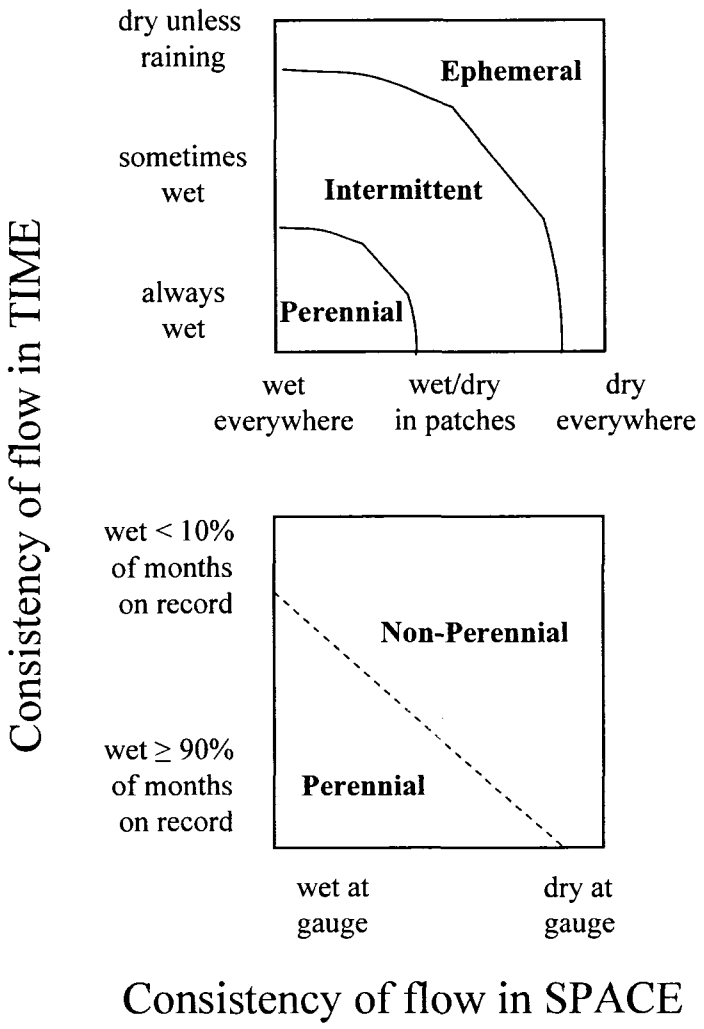

Figure 4.4. Streamflow permanence on the Colorado Plateau exists on a gradient from perennial to ephemeral at the segment scale in both space and time. Top) Perennial streams have surface flow along their entire length throughout the entire year. Ephemeral streams are dry along their entire length throughout the year *except* during and immediately after a precipitation event. Intermittent streams may be either spatially intermittent (e.g. dry channel with perennial pools) or temporally intermittent (e.g. wet in winter and dry in summer). Bottom) For this classification, non-perennial stream segments are those that contain a stream gauge that has registered zero flow ≥ 10% of the months on record. The ability to analyze spatial heterogeneity along a stream's length is limited by the number of stream gauges on that stream. Therefore, in general, spatially intermittent streams cannot be accurately represented.

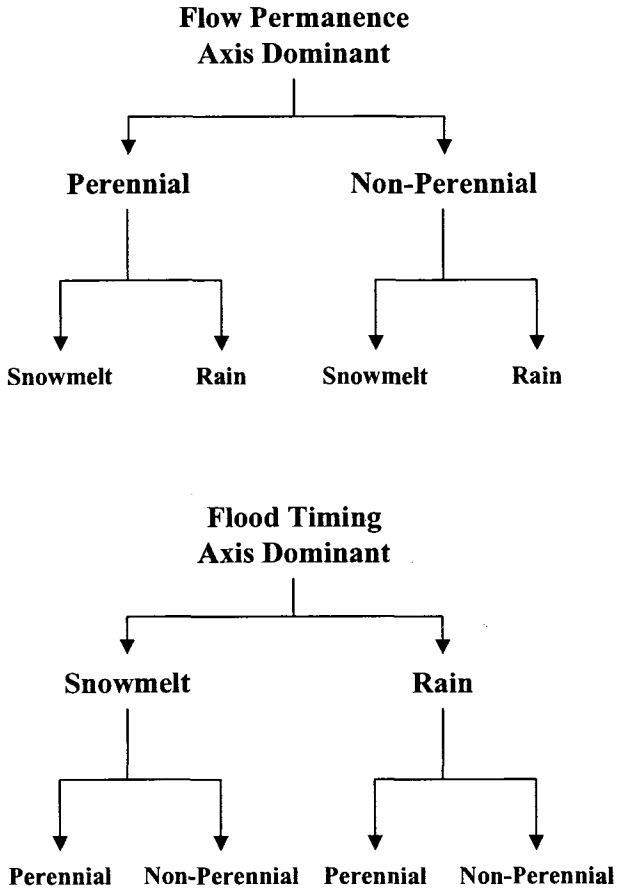

Figure 4.5. Alternate hierarchical stream classification systems predicted by the conceptual model of Colorado Plateau stream hydrology. Top) If variation in Colorado Plateau stream hydrology is best described by flow permanence, then the hierarchical stream classification will first divide stream sites into "perennial" and "non-perennial" classes and further divide them into perennial-snowmelt, perennial-rain, non-perennial-snowmelt, and non-perennial-rain classes. Bottom) Conversely, if variation in Colorado Plateau stream hydrology is best described by flood regime, then the hierarchical stream classification will first divide stream sites into "snowmelt" and "rain" classes and further divide them into snowmelt-perennial, snowmelt-non-perennial, rain-perennial, and rain-non-perennial classes.

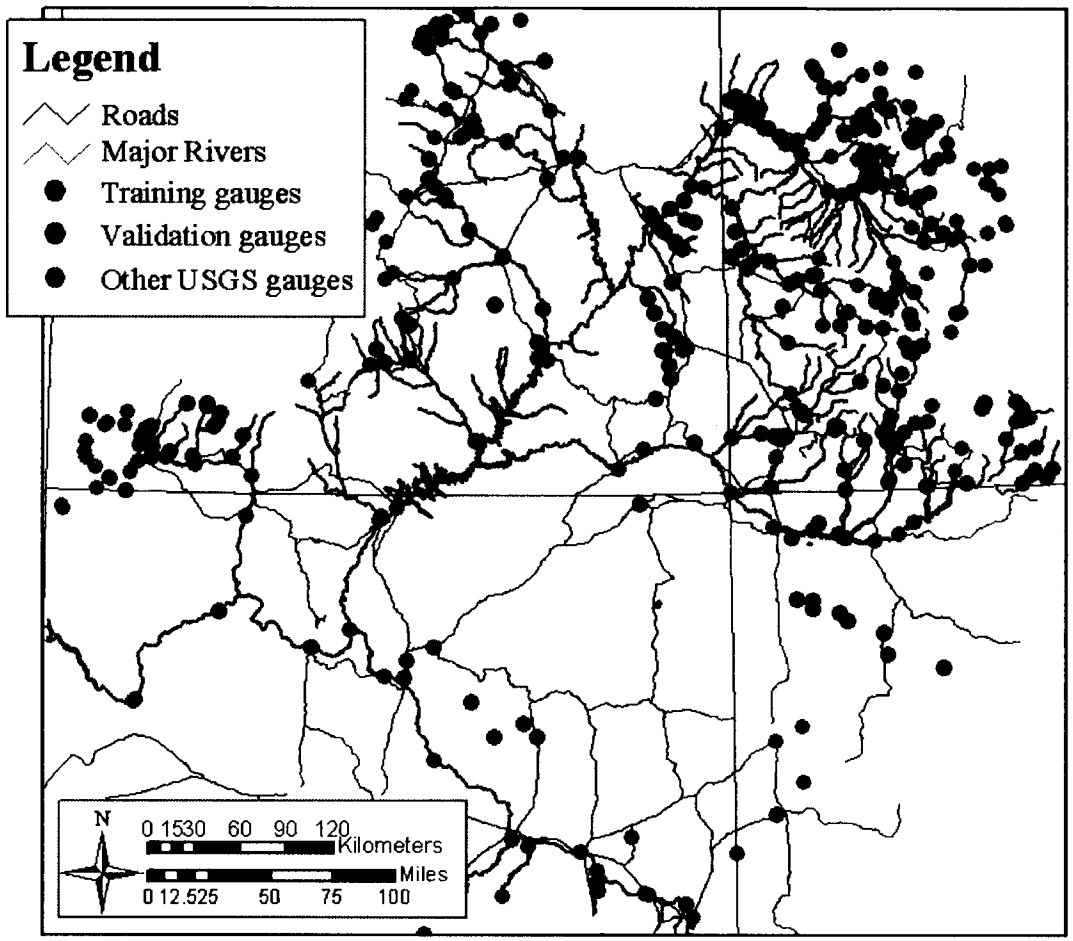

Figure 4.6. Map of USGS gauging stations on the Colorado Plateau. Stream gauges are not distributed evenly across the landscape, but rather are biased towards large, regulated rivers and roads.

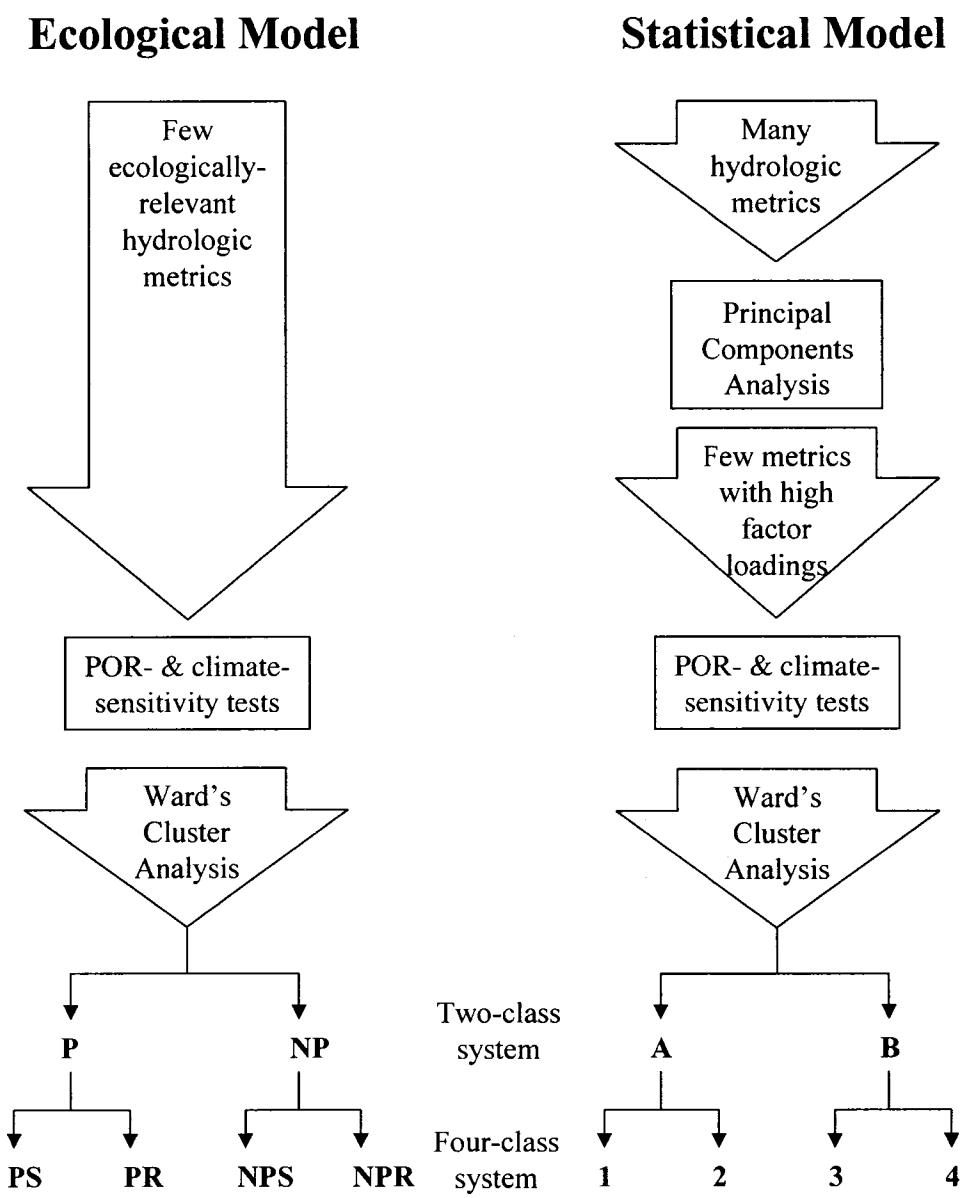

Figure 4.7. Comparison of the Ecological and Statistical approaches used to derive streamflow classification systems. The Ecological Model starts with 7 hydrologic metrics that represent a priori biologically-relevant aspects of flow permanence and flood regime. The 6 metrics that passed the POR- and climate-sensitivity tests are used as input to the cluster analysis. The Statistical Model starts with 112 hydrologic metrics that represent all aspects of the flow regime. Principal components analysis reduces this to 6 hydrologic metrics that are used as input to the cluster analysis.

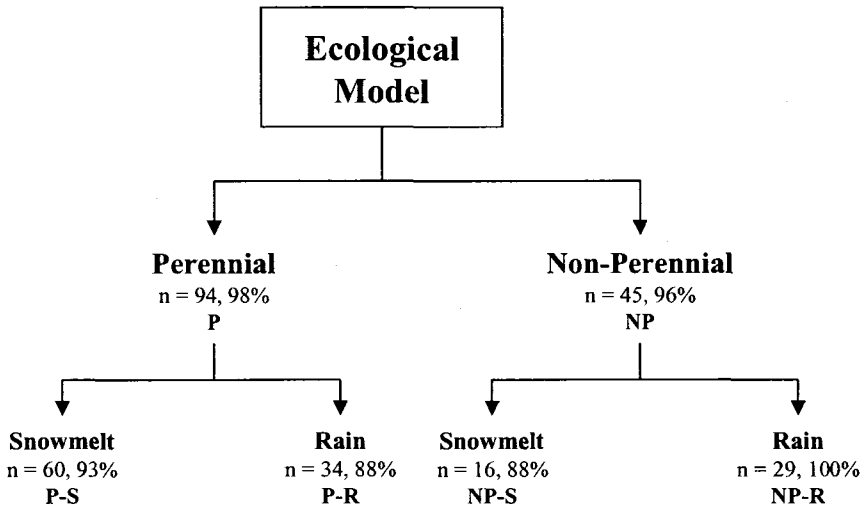

Figure 4.8. Dendrogram of the classification system based on the Ecological Model. The sample sizes and relative stability of the classes are given at each node. Relative stability is based on the ability of the hydrologic metrics to discriminate among the stream classes in a Discriminant Function Analysis. See text for details.

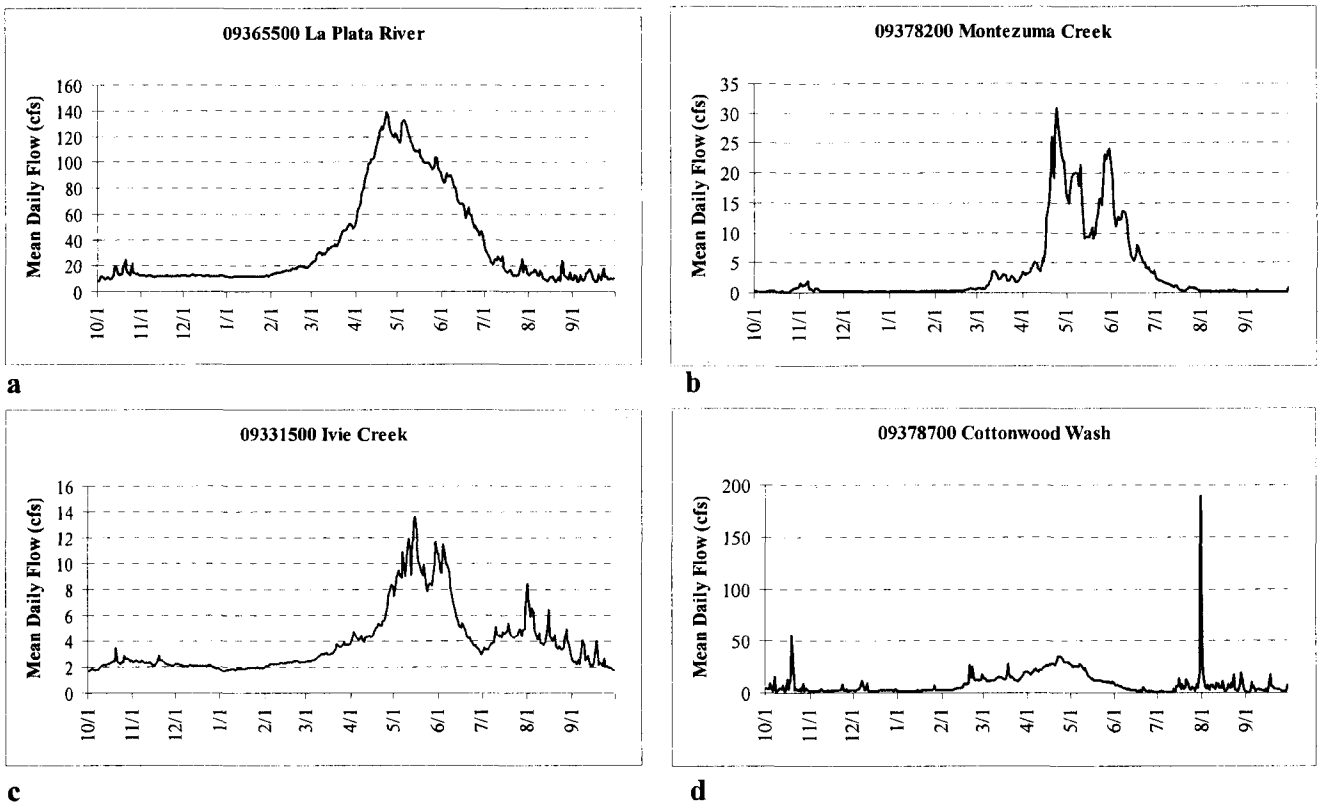

Figure 4.9. Sample hydrographs for each class in the Ecological Model. These hydrographs were chosen because they were the closest to the centroid of the cluster. **a)** Perennial-Snowmelt stream: La Plata River, **b)** Non-Perennial-Snowmelt stream: Montezuma Creek, **c)** Perennial-Rain stream: Ivie Creek, **d)** Non-Perennial-Rain stream: Cottonwood Wash

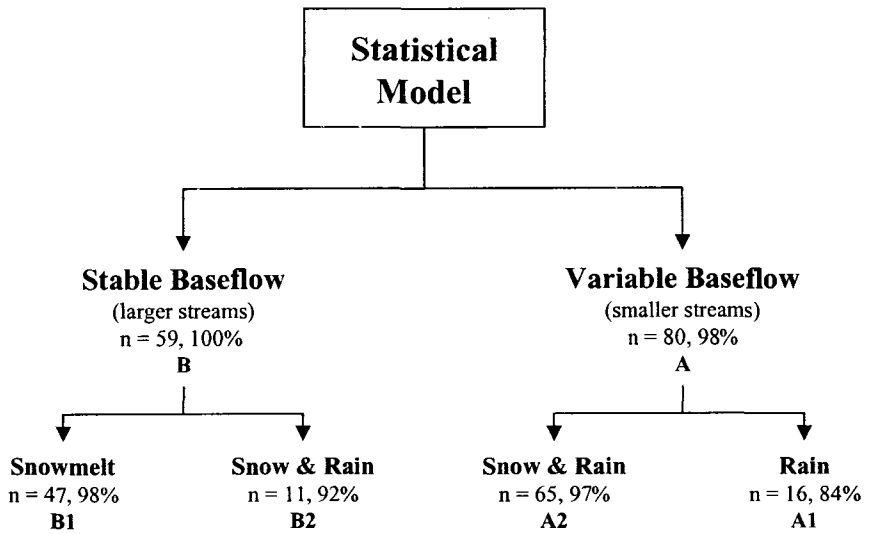

Figure 4.10. Dendrogram of the classification system based on the Statistical Model. The sample sizes and relative stability of the classes are given at each node. Relative stability is based on the ability of the hydrologic metrics to discriminate among the stream classes in a Discriminant Function Analysis. See text for details.

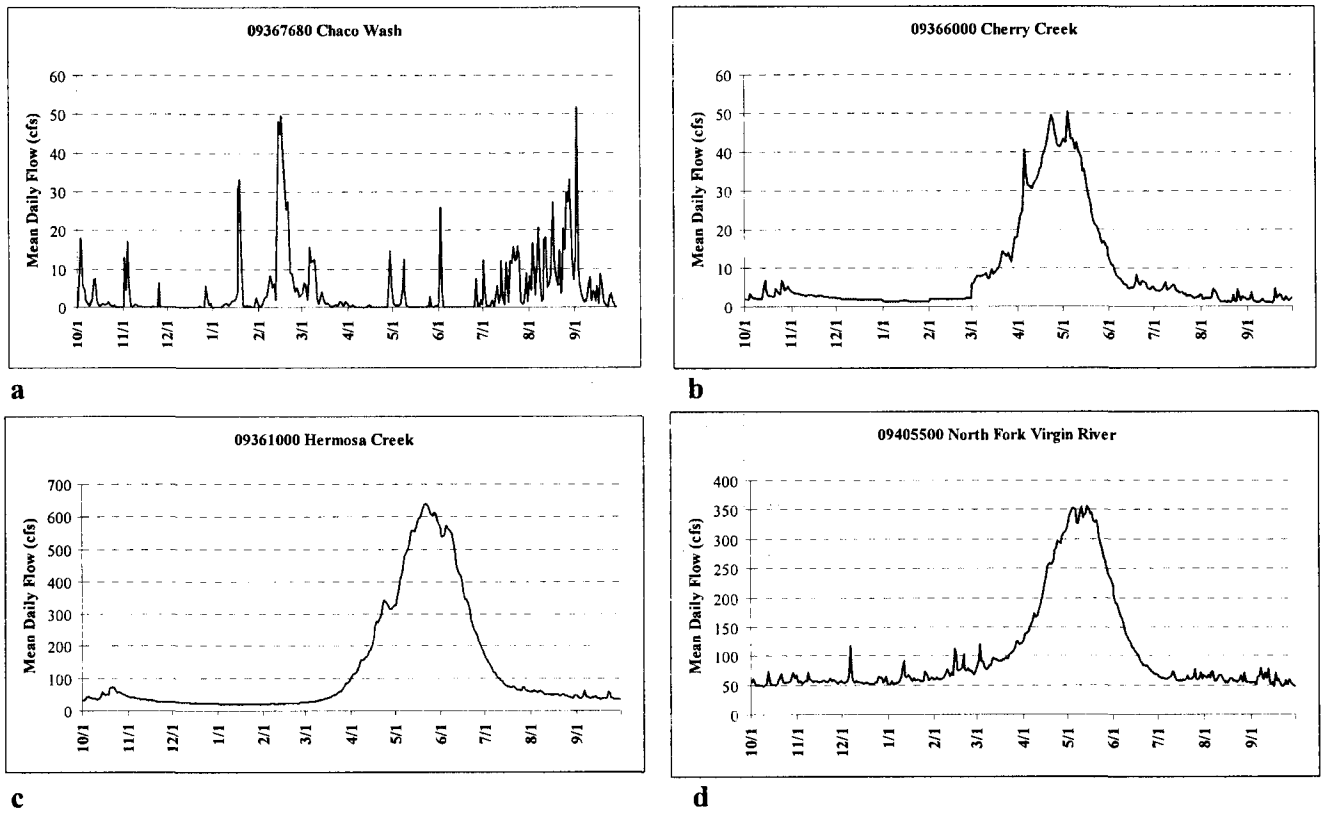

Figure 4.11. Sample hydrographs for each class in the Statistical Model. These hydrographs were chosen because they were the stream gauge closest to the cluster centroid . a) Variable Baseflow – Rain: Chaco Wash, b) Variable Baseflow – Snow & Rain: Cherry Creek, c) Stable Baseflow – Snowmelt: Hermosa Creek, d) Stable Baseflow – Snow & Rain: North Fork of the Virgin River

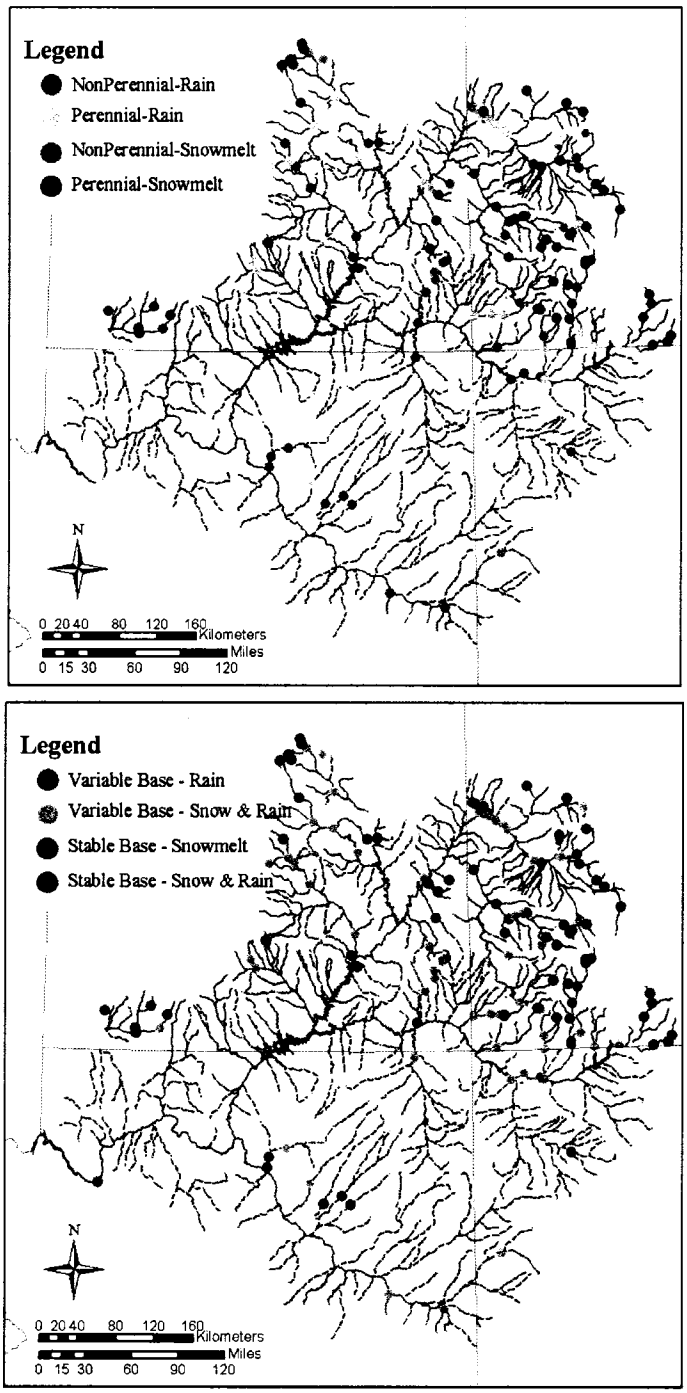

Figure 4.12. Top) Ecological Classification of 139 stream gauges on the Colorado Plateau. Bottom) Statistical classification of 139 stream gauges on the Colorado Plateau.

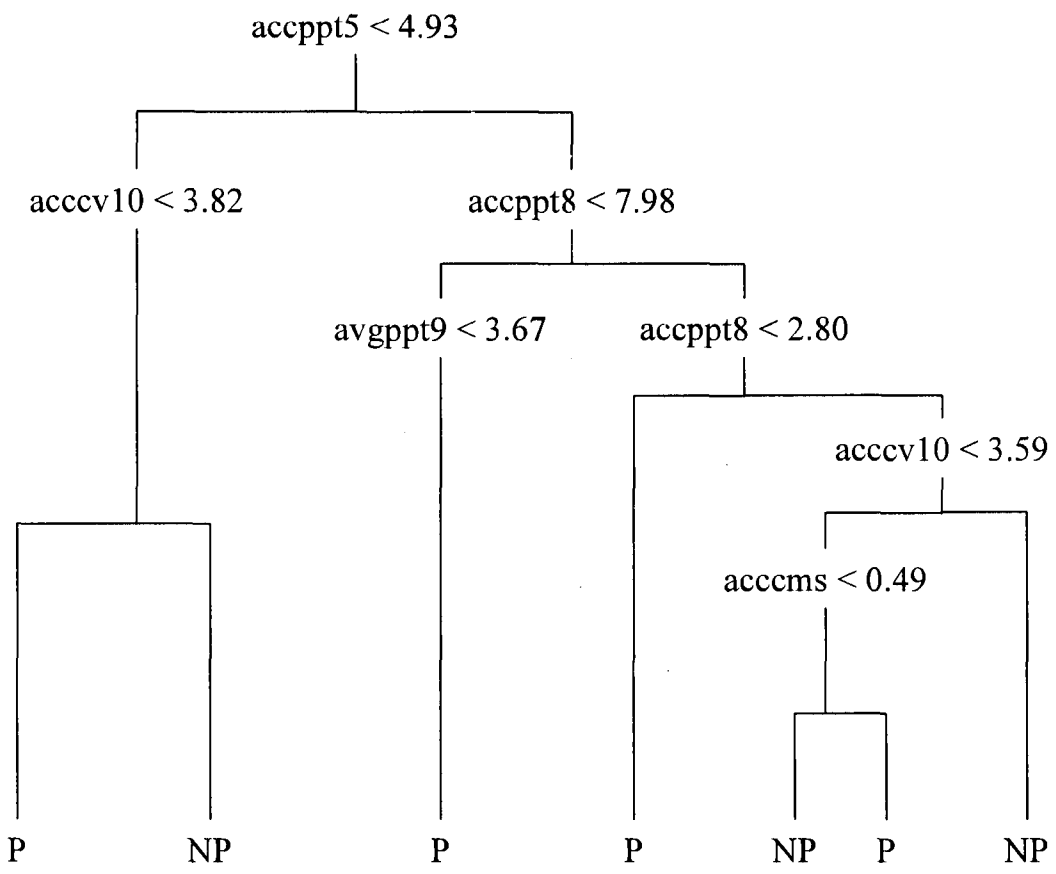

Figure 4.13. Classification and Regression Tree (CART) for the two-class Ecological Model, which divides stream gauges into perennial (P) and non-perennial (NP) groups. Variable definitions given in Table 4.4.

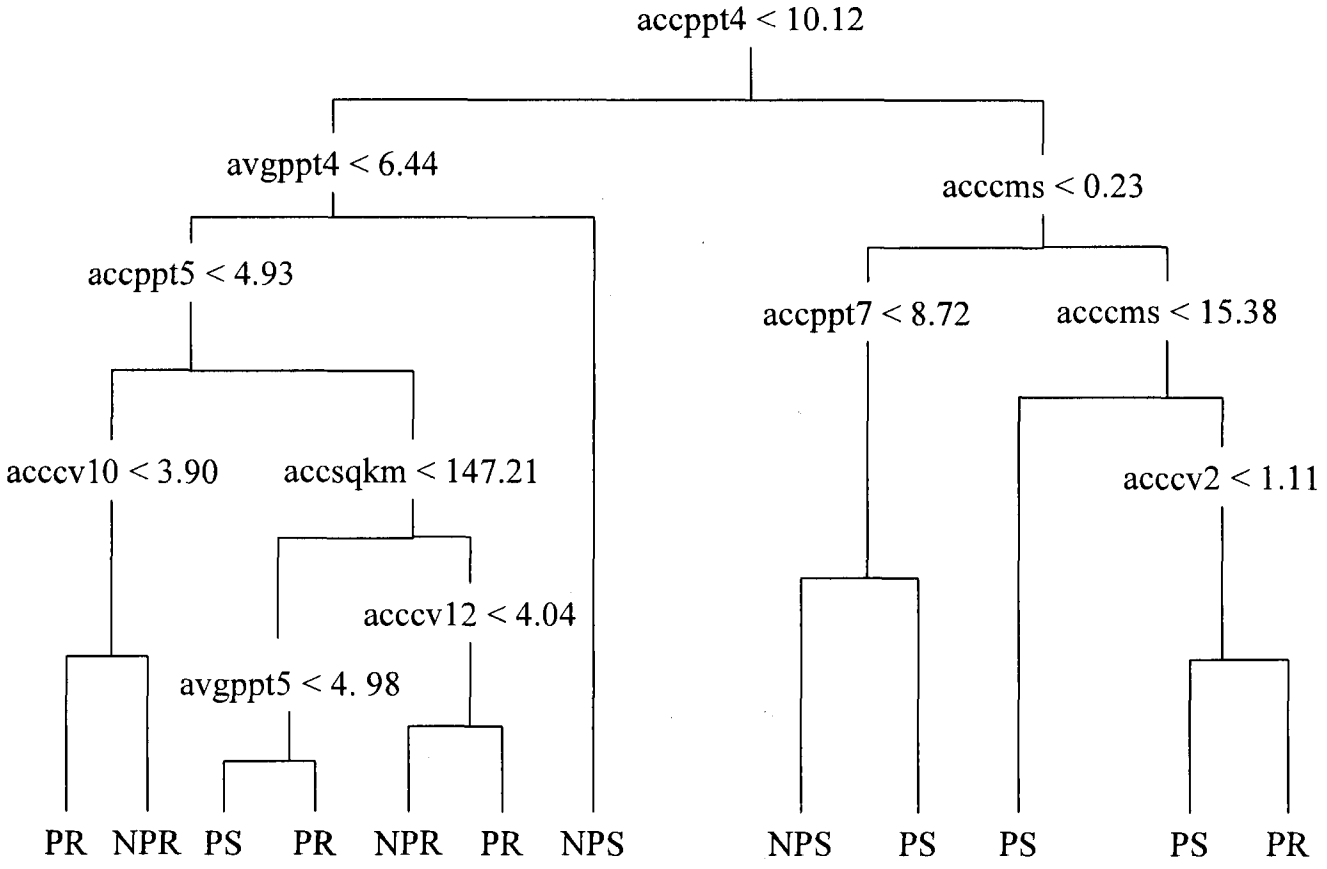

Figure 4.14. Classification and Regression Tree (CART) for the two-class Ecological Model, which divides stream gauges into perennial-rain-driven (PR), perennial-snowmelt (PS), non-perennial-rain-driven (NPR), and non-perennial-snowmelt (NPS) groups. Variable definitions given in Table 4.4.

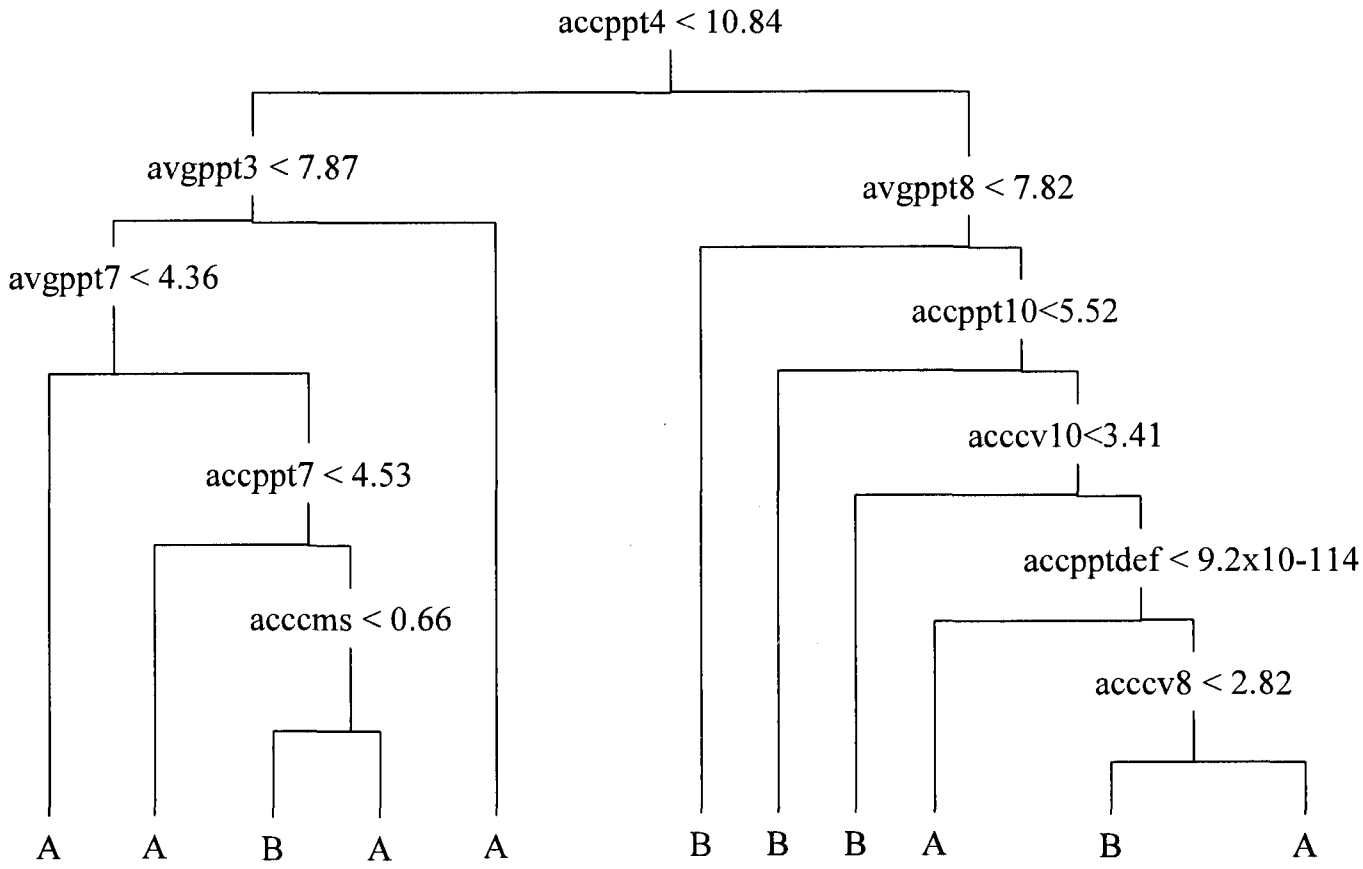

Figure 4.15. Classification and Regression Tree (CART) for the two-class Statistical Model, which divides stream gauges into variable baseflow (VB) and stable baseflow (SB) groups. Variable definitions given in Table 4.4.

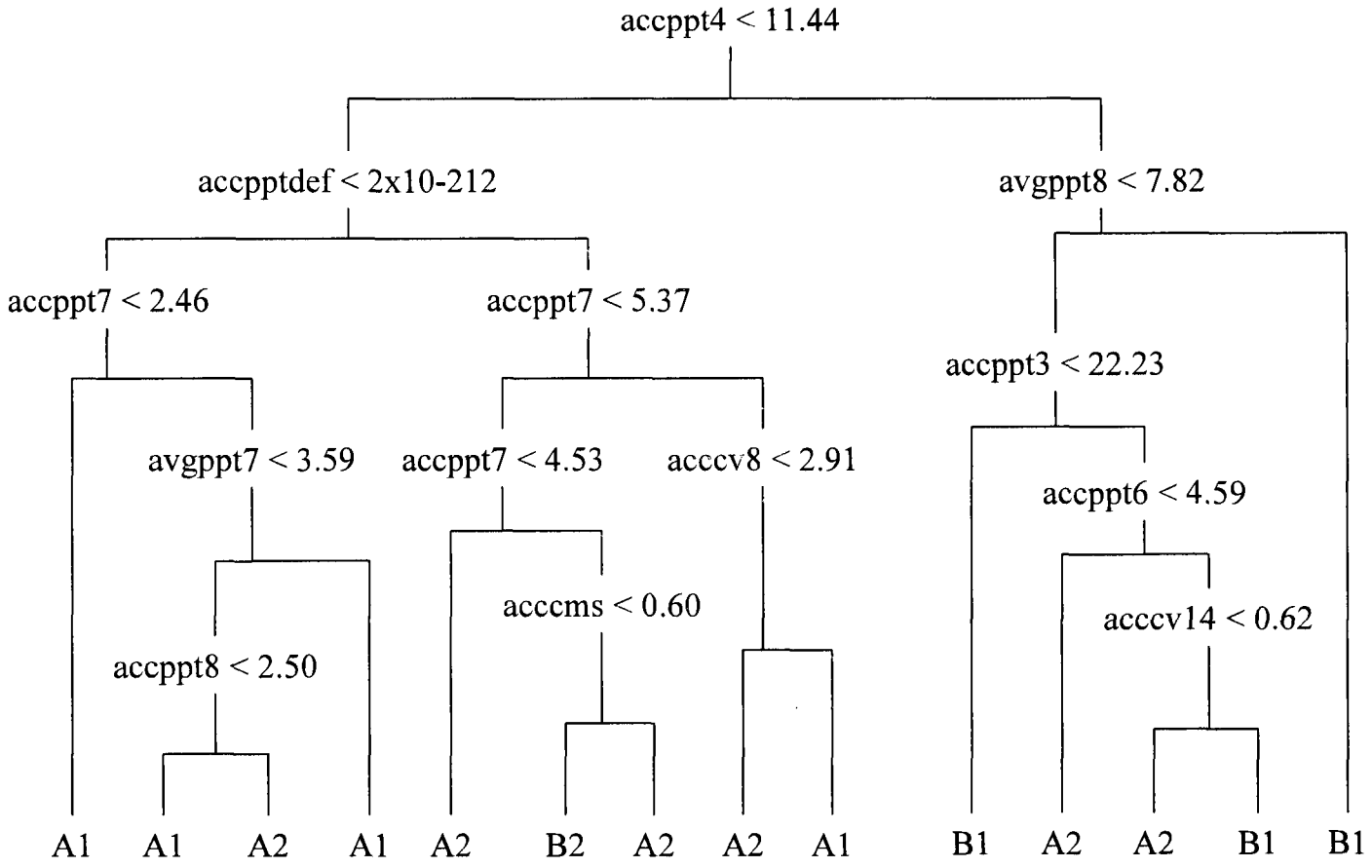

Figure 4.16. Classification and Regression Tree (CART) for the four-class Statistical Model, which which divides stream gauges into variable baseflow-rain-driven (VBR), variable baseflow-snowmelt + rain-driven (VBSR), stable baseflow-snowmelt + rain-driven (SBSR) and stable baseflow-snowmelt (SBS) groups. Variable definitions given in Table 4.4.

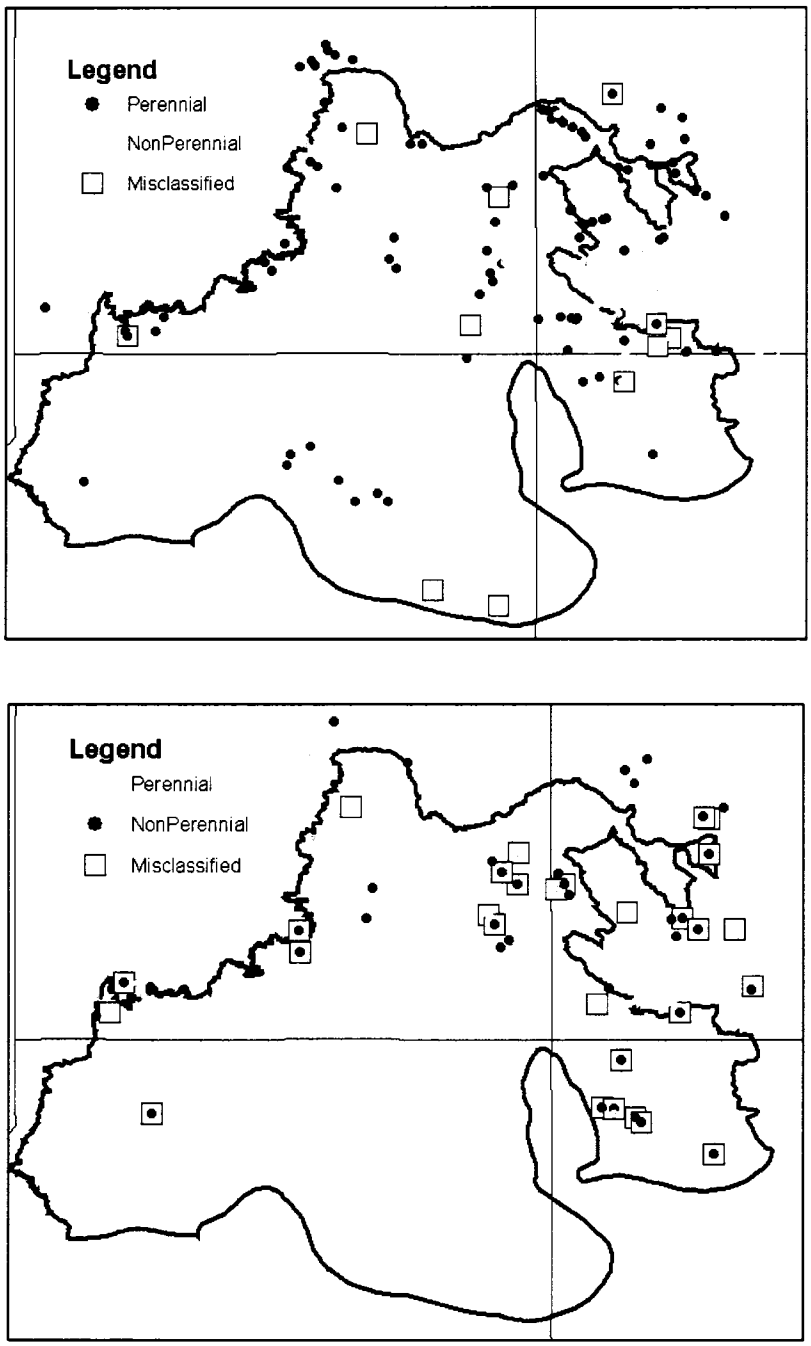

Figure 4.17. Classification of USGS stream gauge locations for the 2-class Ecological Model. This classification was done with a classification and regression tree using GIS-derived landscape variables. Top) training data (n = 139). Bottom) validation data (n = 59)

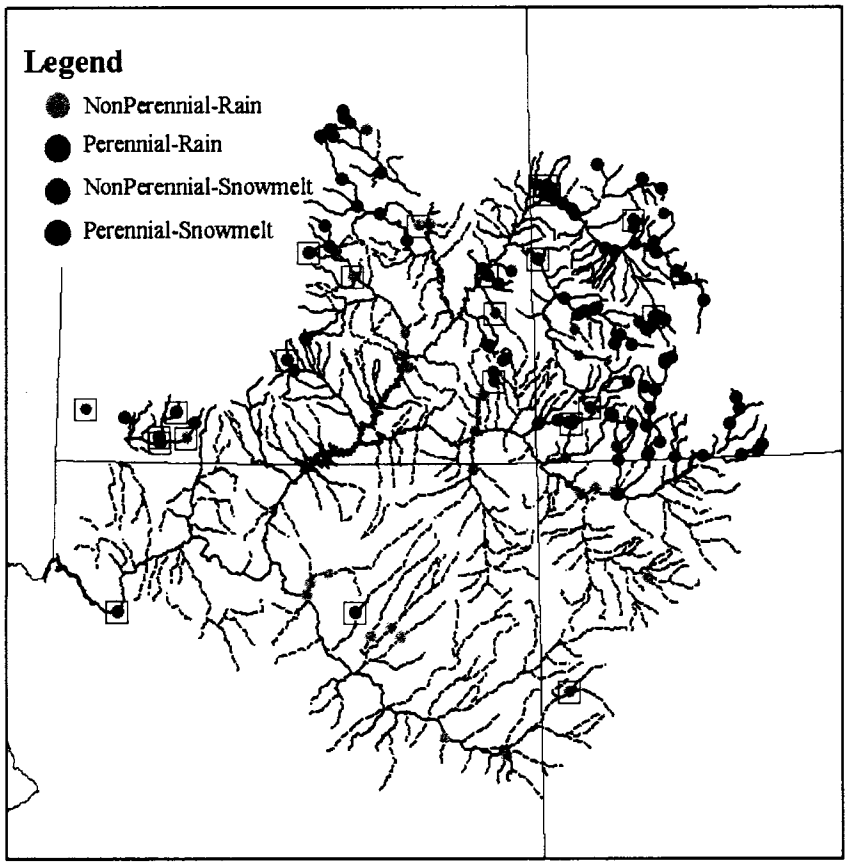

Figure 4.18. Classification of USGS stream gauge locations for the 4-class Ecological Model. This classification was done with a classification and regression tree using GIS-derived landscape variables.

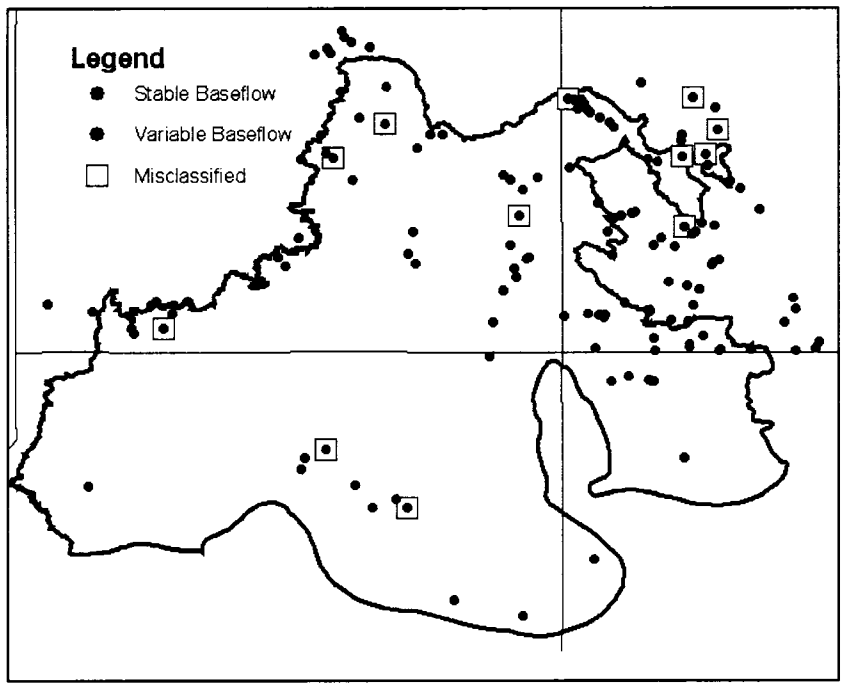

Figure 4.19. Classification of USGS stream gauge locations for the 2-class Statistical Model. This classification was done with a classification and regression tree using GIS-derived landscape variables. Top) training data (n = 139)

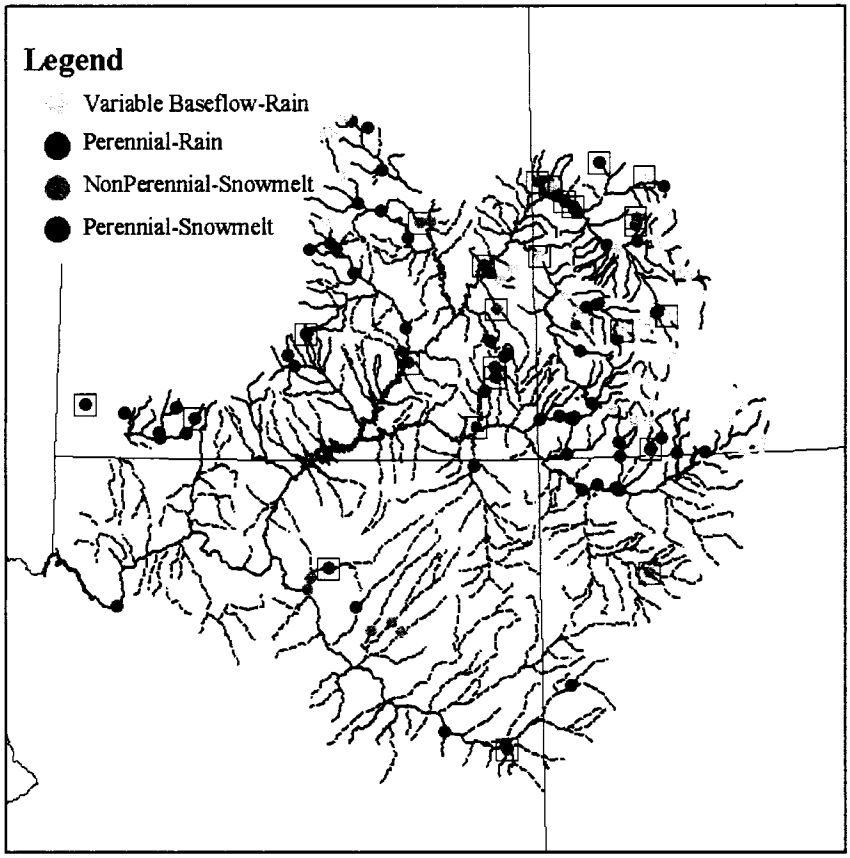

Figure 4.20. Classification of USGS stream gauge locations for the 4-class Statistical Model. This classification was done with a classification and regression tree using GIS-derived landscape variables.

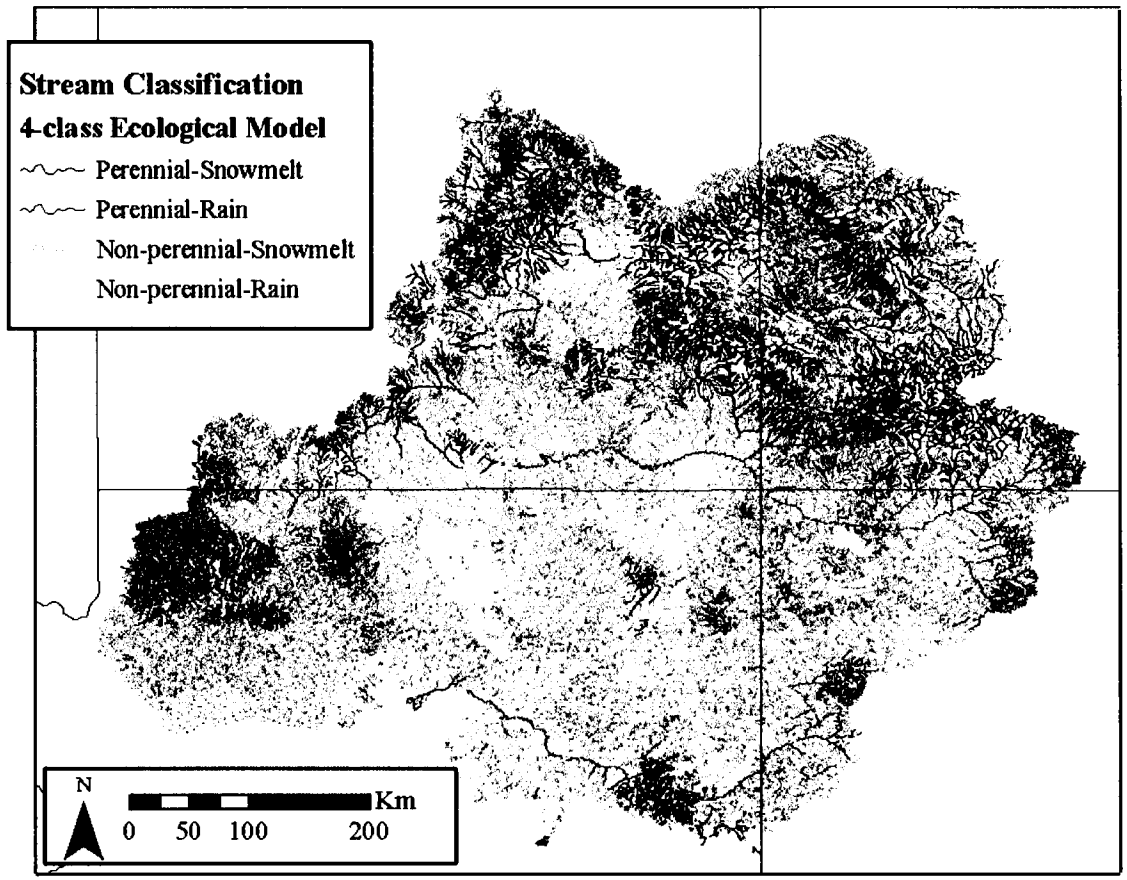

Figure 4.21. Classification of all stream segments on the Colorado Plateau into the 4-class Ecological Model. This classification was done with a classification and regression tree using GIS-derived landscape variables.

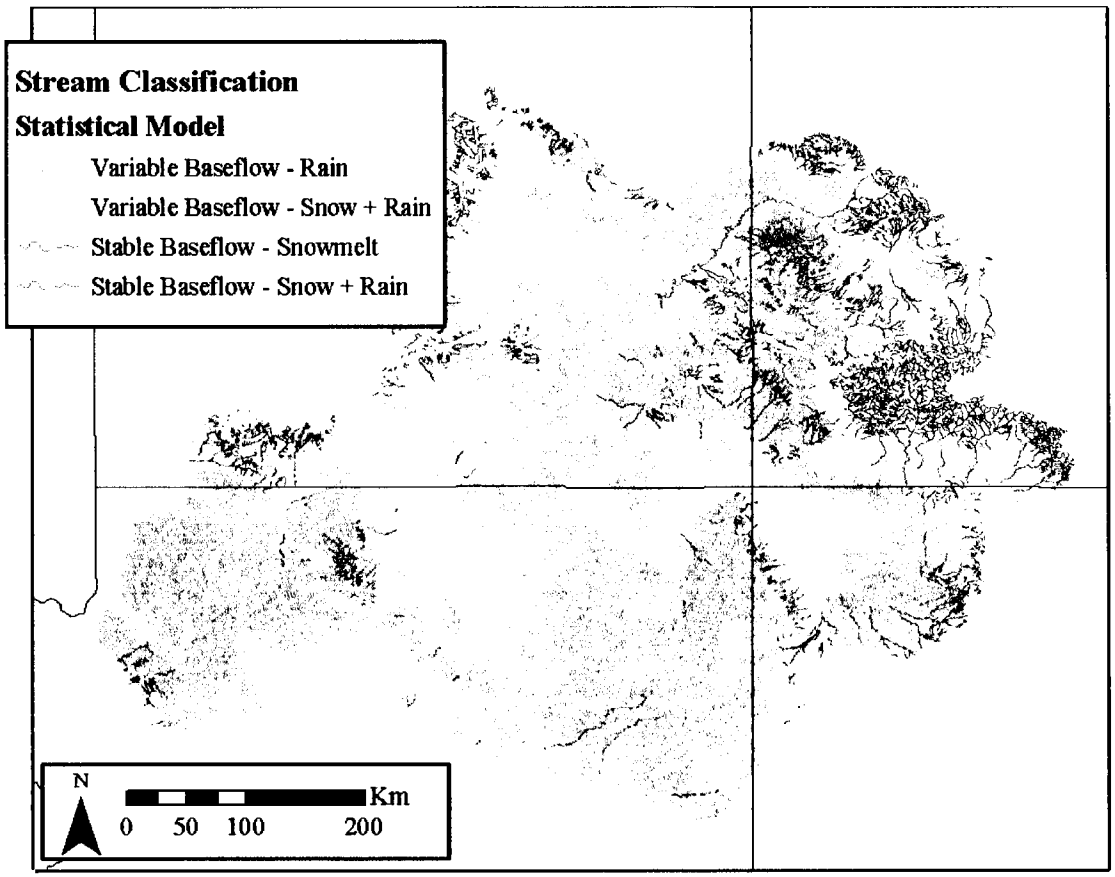

Figure 4.22. Classification of all stream segments on the Colorado Plateau into the 4-class Statistical Model. This classification was done with a classification and regression tree using GIS-derived landscape variables.

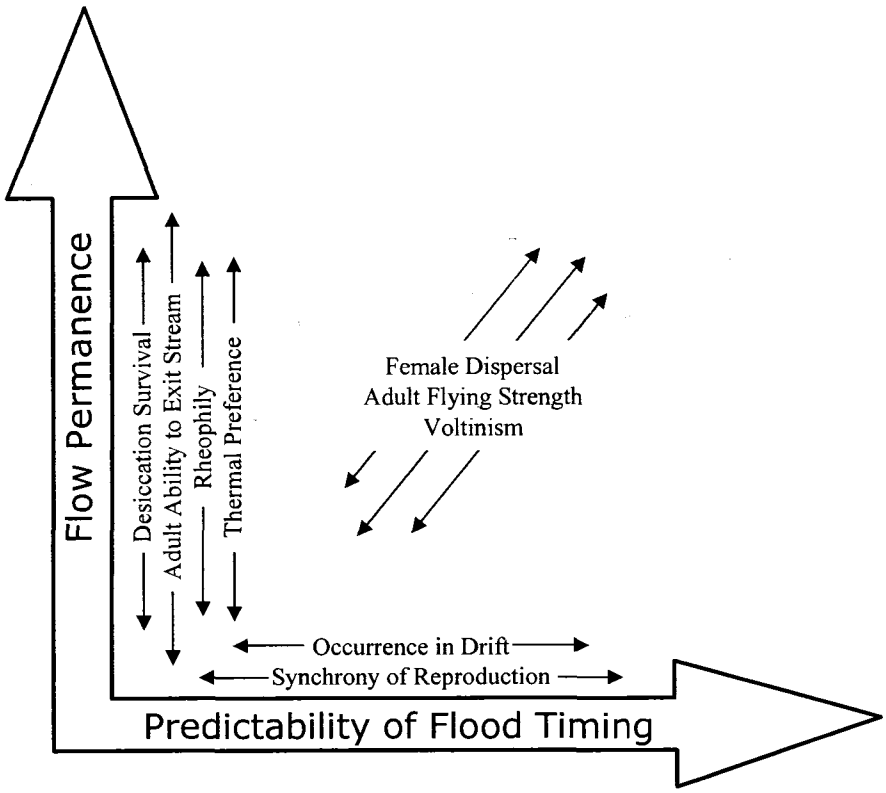

Figure 4.23. Invertebrate traits that are believed to confer a survival advantage to invertebrates in streams across two gradients of hydrologic variability on the Colorado Plateau.

CHAPTER 5

A TEST OF HABITAT TEMPLATE THEORY ON THE COLORADO PLATEAU: DOES A STREAMFLOW TYPOLOGY PREDICT INSECT COMMUNITIES?

Chapter 5

Abstract

Habitat template theory suggests that organisms either respond to environmental variation through evolutionary adaptation or through environmental filters. Therefore, if we can accurately characterize ecological habitats, we can predict the distribution and abundance of organisms on the landscape. In this chapter, I address habitat template theory by testing the hypothesis that hydrologic disturbances, including floods and droughts, are the major drivers of stream insect communities on the Colorado Plateau. I use family-level community metrics and 6 evolutionarily labile functional traits (drift, female dispersal, rheophily, thermal preference, size, and voltinism) to test differences in the insect community assemblages at perennial-snowmelt, perennial-rain, non-perennial-snowmelt, and non-perennial-rain streams.

Disturbance-adapted insect taxa were common at all Colorado Plateau stream sites. Multivariate measures of community similarity failed to detect a difference among the four stream types; this was probably due to the abundance of generalist taxa at all sites. However, I detected significant differences in family richness, %EPT, and % Diptera among groups. These differences in the community assemblage were driven by snowmelt-adapted taxa at higher elevation sites. I was able to predict snowmelt stream types from insect functional traits with 61% accuracy. Snowmelt streams contained taxa that were rare in the drift, semi- or univoltine, and medium/large size. The limited mobility of snowmelt-adapted taxa suggests that unique populations may exist at high elevation sites on the Plateau.

5.1.0. Introduction

Community ecologists are interested in predicting species distribution and abundance. Given the diversity of species and heterogeneity of habitats, this task is so daunting that some ecologists have suggested that community-scale research should be abandoned (Lawton 1999). Southwood (1988) proposed that community ecology would benefit from a habitat template approach. This theory put forward that "habitat provides the templet on which evolution forges characteristic life-history strategies..." (Southwood 1988). According to the habitat template, species that persist in a particular habitat have functional traits that allow them to survive and reproduce in the habitat, whereas those species that lack adaptive traits are removed from that habitat either by disturbance or competition (Southwood 1977; Southwood 1988). Southwood suggested that the habitat template could become the "periodic table of ecology" and if we could accurately describe habitats in an ecologically relevant way, we would be able to predict the species that occur in them.

Ecologically-meaningful habitat characterization must occur at spatial and temporal scales that are relevant to the organisms of interest (Southwood 1988). Several authors have proposed axes along which the environment should be quantified in order to provide the most ecologically-relevant habitat template (Figure 5.1). Southwood (1977) first suggested habitat stability and resource availability axes. Greenslade (1983) amended these two axes to include a third axis that he called "biotic unpredictability". He also put forward the idea that resource availability could be viewed as "habitat adversity". Hildrew and Townsend (1987) proposed a habitat template for streams that separated habitat variability into axes of productivity and disturbance frequency.

Southwood (1988) reconciled these systems into a cohesive habitat template theory based on disturbance and productivity. Townsend and Hildrew (1994) described a three step process for testing the habitat template concept in streams. The first step is to identify where the habitat of interest occurs within the habitat template.

Poff and Ward (1990) suggest that a characterization of the stream habitat template must minimally include a description of daily historical streamflow variability, the stream-specific thermal regime, and substrate-geomorphologic characteristics. Other researchers have supported the importance of stream hydrology, temperature, and substrate to aquatic organisms (Vinson and Hawkins 1998). Several authors have proposed that hydrologic disturbances are a major environmental driver of stream communities (Resh *et al.* 1988; Poff and Ward 1990; Townsend and Hildrew 1994; Lake 2000). Therefore, the majority of work characterizing the stream habitat template has focused on hydrologic variability (Poff and Ward 1989; Poff 1996; Sanz and del Jalon 2005; Poff *et al.* 2006b). Townsend and Hildrew (1994) indicate that the spatial and temporal heterogeneity of the stream habitat must be described in order to accurately describe the environmental that aquatic organisms experience. Temporal heterogeneity is defined as the frequency and magnitude of excursions away from some long-term average in the physiochemical habitat (Poff 1992; Townsend and Hildrew 1994). Organisms can adapt to the long-term average stream condition over evolutionary time scales; therefore, deviation from the long-term average in ecological time constitutes a habitat disturbance and can cause widespread mortality (Southwood 1977; Southwood 1988). Spatial heterogeneity has been defined as variation in habitat adversity, (Greenslade 1983), productivity (Hildrew and Townsend 1987), or the spatial scale of

disturbance (Poff and Ward 1990). Several authors indicate that the spatial and temporal scales (or grain) at which the environment is described are important factors to consider in tests of the habitat template (Townsend 1989; Poff 1997; Vinson and Hawkins 1998; Doledec *et al.* 2000). Townsend and Hildrew (1994) make several general predictions about how aquatic communities should respond to the axes of spatial and temporal heterogeneity. For example, "K-selected" species should dominate at areas of low temporal heterogeneity, "r-selected" species should prevail in areas of high temporal heterogeneity, and community richness should be highest at intermediate sites because there will be a blend of "r-selected" and "K-selected" taxa (Pringle *et al.* 1988; Townsend *et al.* 1997 but see Resh *et al.* 1994). Here the r-K continuum is used as shorthand for a suite of traits that are commonly found in frequently disturbed habitats ("r-selected" taxa) or stable systems ("K-selected" taxa); this notation should not be interpreted to mean that these are r- and K-species as defined by MacArthur and Wilson (1967).

The second step is to predict the relationship between species traits and the habitat template. Adaptive functional traits arise when a species is exposed to environmental stress over evolutionary time. Southwood (1988) suggests that adaptive traits arise when natural selection invests in one of five categories: 1) physiological adaptations to unfavorable physical conditions, 2) defense, 3) food harvesting and somatic development, 4) reproductive activities, 5) tactics for escape in space and time. Differential investment in these five categories results in a variety of adaptive traits among organisms. The r-K continuum (MacArthur and Wilson 1967) is a well-known example that describes specific functional trait groups that have arisen to meet environmental challenges. Although the r-K continuum was originally developed to address density-dependent

competition for resources, it translates well to the disturbance and productivity gradients suggested by the habitat template (Southwood 1988). K-selected species are characterized by long life cycles with low fecundity, superior competitive ability, and poor dispersal ability. K-selected taxa are favored by spatially homogeneous, temporally stable habitats (Ricklefs 1997). R-selected species, which have short life cycles, high fecundity, high dispersal ability, and generally poor competitive ability, are favored by spatially heterogeneous, frequently disturbed habitats (Ricklefs 1997). A species' adaptation to environmental stress is constrained by its evolutionary history, so not all trait combinations are possible in a particular species (Southwood 1988; Poff *et al.* 2006a).

Habitat template research in streams has focused on adaptations of lotic biota to hydrologic variability (Townsend 1989; Poff and Allan 1995; Peterson *et al.* 2001; Gjerlov *et al.* 2003; Beche *et al.* 2006; Bunn *et al.* 2006). Aquatic organisms have evolved a number of adaptations to natural flow regimes (Lytle and Poff 2004). Adaptive traits in streams confer resistance or resilience to disturbance (Townsend and Hildrew 1994). Aquatic insects that are resistant to disturbance may have desiccation resistant stages (Jacobi and Cary 1996) or behaviors that allow species to remain in place during flood events (Meffe and Minckley 1987). Traits that confer resilience may allow taxa to better take advantage of disturbance refugia, either through life history adaptations such as airborne adult stages (Gray 1981b; Stanley *et al.* 1994) or behavioral adaptations such as exiting the stream during floods (Velasco and Millan 1998; Lytle 2003; Lytle and Smith 2004). Resilience traits, such as rapid larval development, may allow a species to more quickly populate a denuded habitat after drying or flooding (Gray 1981a; Cushing

and Gaines 1989). Bonada *et al.* (2007) found that aquatic insects inhabitation intermittent streams in the Mediterranean had pool-like traits (i.e., aerial respiration, strong aerial dispersal), whereas insects in ephemeral streams possessed life-history adaptations to floods and droughts (i.e., drought resistant stages, cutaneous respiration, asexual or sexual reproduction). In order to formulate testable hypotheses, species trait predictions must be made *before* looking at the species that occur at the habitat in question (Townsend and Hildrew 1994).

The third step is to compare the traits predicted for a habitat with the traits that occur in the biotic community at that habitat (Townsend and Hildrew 1994). Explorations of trait-habitat relationships must be mechanistically-based in order to contribute to our understanding of the habitat template. Simple observations of taxa in differential habitats may contribute to our understanding of specific natural history and phenology that underlie adaptations to environmental stressors, but they do not move our predictive abilities forward. Researchers have explored the relationship between insect traits, such as maximum size, body form, mode of attachment to the substrate, feeding habits, reproduction, lifespan, and stream habitat variables, such as Froude number (ratio of hydraulic inertial forces to gravitational forces), substrate size, and benthic particulate organic matter, in streams (Richards *et al.* 1997; Lamouroux *et al.* 2004; Finn and Poff 2005; Bonada *et al.* 2007).

5.1.1. Colorado Plateau Stream Habitat Template

The semi-arid Colorado Plateau of Utah, Arizona, New Mexico, and Colorado is perhaps one of the least-studied regions of the USA from the perspective of stream

ecology (Call and Baumann 2002). The Colorado Plateau encompasses the high alpine peaks of the San Juan Mountains and the hot desert environment at the bottom of the Grand Canyon. Because of this broad variation in elevation and climate, the Colorado Plateau contains mountain and desert streams, which have contrasting disturbance regimes (Poff and Ward 1989). Desert streams are warm, flashy, and prone to drying (Fisher 1986), whereas mountain streams are colder and have predictable snowmelt floods (Finn and Poff 2005). The aquatic insect fauna of the Colorado Plateau is a mix of species characteristic of the Rocky Mountains to the east of the Plateau, the Great Basin/Sonoran Desert to the south, and widespread generalist taxa (Nelson 1994; B. Kondratieff, *pers. com.*). The Colorado Plateau is well suited to test habitat template theory because it contains diverse stream types *and* is host to aquatic insects from regions with distinctly different disturbance regimes within a relatively small area.

I created a streamflow typology to explain the Colorado Plateau hydrologic variation with two hydrologic axes: flow permanence and flood predictability (Figure 5.2). Along the flow permanence axis Colorado Plateau streams range from perennial to ephemeral. Perennial streams on the Colorado Plateau are maintained by groundwater inputs, especially from an aquifer in the Navajo Sandstone (Heilweil and Freethey 1992; Heilweil 2005). Groundwater underlies the entire Colorado Plateau; however, it only intersects surficial streams in some locations. Non-perennial streams may be dry bedrock channels or sandy stream channels that have perennial pools and/or subsurface flow but only intermittent surface flow. Because a large portion of the Colorado Plateau is unvegetated bedrock, ephemeral channels exist almost anywhere there is a depression in the rock and these depressions are filled when it rains.

The flood predictability axis captures the difference between snowmelt-driven streams and rain-driven streams. Spring floods in snowmelt streams peak slowly and predictably in May or June as the high elevation snow pack melts due to longer, warmer days (Doesken and Judson 1996). This predictable spring flood serves as a spawning and emergence cue to some aquatic biota (Lytle and Poff 2004). Summertime floods in Colorado Plateau streams occur quickly and much less predictably due to convective monsoon thunderstorms (Hereford and Webb 1992; Douglas *et al.* 1993). High-intensity, localized monsoon storms can cause catastrophic flooding in one watershed, while the adjacent watershed receives no measurable precipitation. Low elevation streams (less than 2,286 m / 7,500 ft.) are especially affected by monsoon rainfall because the intensity of summer convective thunderstorms dissipates at higher elevations (Thomas *et al.* 1997; Webb *et al.* 2004). In sum, the flood predictability axis describes the type of flood – ramped and seasonal for snowmelt floods versus flashy and sporadic for rain-driven floods (Figure 5.3). The flow permanence axis describes the probability of year-round surface flow, which is low in non-perennial and high in perennial streams.

The Colorado Plateau stream typology is really a two-dimensional representation of the single "habitat stability" axis suggested by other authors (Figure 5.1). The non-perennial-rain-driven streams on the Colorado Plateau exist at the unstable end of the spectrum; these are among the most hydrologically harsh streams in the USA (Figure 5.3; Poff and Ward 1989; Poff 1996). Perennial-snowmelt streams occur at the other end of the spectrum, as they are much more hydrologically gentle. This streamflow typology separates streams into discrete groups but there is a range of hydrologic regimes in the field. Even "perennial" streams have ceased to flow in hot, dry years (D. Worthington,

Biologist, Capitol Reef National Park, *pers. comm.*). If we extended the flow permanence and flood predictability axes to include stream types that are not observed on the Colorado Plateau, it would also encompass stable-groundwater streams, which very rarely flood (Poff and Ward 1989). As suggested by habitat template theory (Southwood 1977; Southwood 1988; Townsend and Hildrew 1994), r-selected or "weedy" taxa should be most common at the harsh end of the spectrum (non-perennial-rain sites) and "K-selected" traits should be more common in more benign habitats (perennial-snowmelt) (Figure 5.2b). K-selected species are typically defined as long-lived, strong competitors that are able to persist when an ecosystem is near its carrying capacity (Ricklefs 1997). K-selected taxa are rare in stream habitats because hydrologic disturbances frequently reset the invertebrate community, so it rarely reaches carrying capacity. Because all stream types on the Colorado Plateau are on the unstable end of the harsh-benign spectrum, r-selected traits should be more common than K-selected traits in all Colorado Plateau habitats.

5.1.2. Predictions of Colorado Plateau Insect Functional Traits

Following Townsend and Hildrew (1994), I made predictions about how invertebrate functional traits will respond to the two flow axes *before* looking at the distribution of insect traits among the taxa or Colorado Plateau streams (Table 5.1). I expect that the flow permanence axis would exert a stronger selective pressure on the insect community than the flood timing axis because, as Andrew Boulton (2003) so eloquently said, "it is axiomatic that unusually long dry periods (droughts) adversely affect aquatic biota". While many aquatic insect larvae can survive stream flooding by

moving to flow refugia, it is less likely that aquatic taxa can survive prolonged desiccation because fewer refugia exist (Stanley *et al.* 1994). I expect non-perennial sites to have a higher proportion of desiccation-resistant insects and fewer rheophilic taxa than at perennial sites. As non-perennial streams dry, the riffle habitats are the first to dewater (Stanley *et al.* 1997); therefore, rheophilic taxa are probably less common in non-perennial streams. Habitat contraction also increases the water temperature and drops the dissolved oxygen level in remnant pools (Stanley *et al.* 1997). These habitat changes cue insects with mobile adult stages, such as beetles, to exit the water (Velasco and Millan 1998) or crawl upstream (Lytle *et al.* 2007), I expect that insects that have the ability to exit the stream as adults will be common in non-perennial streams. In addition, I expect that cold stenothermic taxa are rare in non-perennial streams because they cannot survive the changes in water temperature that accompany flow cessation.

The frequency and timing of floods in snowmelt streams are more predictable than floods in rain-driven streams (see Chapter 4). Flash floods on the Colorado Plateau are most common at lower elevations due to small catchment basins and the dissipation of convective Monsoon thunderstorms at high elevations (Thomas *et al.* 1997). Monsoon thunderstorms tend to be limited in their geographic extent (Hereford and Webb 1992; Webb *et al.* 2004). This precipitation regime makes it possible for a stream to receive a catastrophic flood from a tributary stream while its headwaters remain at baseflow. The spatially and temporally heterogeneous nature of streamflow in rain-driven streams leads me to suggest that disturbance-adapted taxa will be more common in rain-driven streams. Therefore, I expect that insect drift is more common in rain-driven streams than snowmelt-fed streams. Drift can serve as a recolonization pathway in rain-driven streams

that experience flash floods, which can severely disturb the stream channel downstream of a tributary but leave upstream reaches intact. Asynchronous emergence can also serve as a source of colonists to recently flooded streams because some portion of the population is always in the airborne adult stage (Gray 1981a); therefore I expect that insects in rain-driven streams will commonly exhibit asynchronous life cycles.

I expect that voltinism and female dispersal ability vary along *both* axes because they are generalized adaptations to disturbance. Multivoltine taxa are common in frequently disturbed stream habitats (Gray 1981b; Richards *et al.* 1997; Robinson and Minshall 1998). Insect life cycles with several generations per year are less likely to be locally extirpated by flooding because rapid larval development reduces the time that the population is susceptible to hydrologic disturbance (Lytle 2001). Flashy desert streams have also tend to have a large number of small-bodied taxa (Gray 1981b; Scarsbrook and Townsend 1993). Size and voltinism are highly correlated in field-collected data, although they have different evolutionary origins (Poff *et al.* 2006a). When a stream experiences a catastrophic flood that removes a large portion of the aquatic insect biomass, taxa with strong female dispersal ability have a selective advantage in streams that dry (flow permanence axis) and streams that flood frequently (flood predictability axis) because adults from other undisturbed drainages could repopulate denuded streams through oviposition.

Mechanistic predictions about aquatic insect functional traits allow stream ecologists to link the biotic community and environmental drivers. Multivariate tests of these predictions tend to treat the functional traits as independent variables, even though the traits did not evolve independently (Poff *et al.* 2006a). As a means to mitigate this

problem, Poff *et al.* (2006a) suggest that tests of the relationship between environmental drivers and insect functional traits consider the evolutionary lability and statistical correlation of functional traits. Labile traits are those that have arisen and disappeared several times throughout the evolution of an insect family or genus; these traits are identified by examining the current insect phylogenies (Poff *et al.* 2006a). After making prediction about the nine insect functional traits just mentioned, I eliminated three traits (adult exiting ability, synchronization of emergence, and desiccation resistance) from the analysis because they were highly evolutionarily constrained (Table 5.1).

5.1.3. Major Questions

I examined the hypothesis that the functional traits of aquatic insect communities vary among the four classes of the streamflow typology that I developed for the Colorado Plateau. In order to test the stream community response to the flow typology, I examined six evolutionarily labile traits (Figure 5.4). I tested this hypothesis using community similarity metrics and by comparing the relative abundance of individuals in each trait state across the four stream types. I was also interested in which axis of the flow typology – flow permanence or flood predictability – better describes the aquatic insect community. To this end, I compared the relative abundance of individuals across streams types (rain vs. snowmelt and perennial vs. non-perennial) for each of the six traits (size, voltinism, occurrence in drift, female dispersal ability, thermal preference, and rheophilic preference).

5.2.0 Methods

I developed a heuristic streamflow typology that describes hydrologic variability in unregulated streams on the Colorado Plateau (Chapter 4). The typology separates streamflow into two ecologically-meaningful axes: flow permanence and flood predictability. Using a GIS databse I classified all Colorado Plateau stream segments into one of four classes: perennial-snowmelt, perennial-rain-driven, non-perennial-snowmelt, and non-perennial-rain-driven streams (Figure 5.5). Briefly, six hydrologic metrics that describe the magnitude, frequency, duration, and timing of high and flow flows were calculated at 139 stream gauges. Second, I used Ward's method in a hierarchical cluster analysis to assign the 139 stream sites to the four hydrologic classes. Third, a GIS database was developed to characterize several watershed variables, including monthly precipitation, contributing watershed area, elevation, and estimated stream discharge at all stream reaches (Theobald and Norman 2007). Fourth, a classification tree was built to link hydrologic classes and 12 GIS-derived watershed variables at the 139 gauges sites. Finally, this classification tree was used to predict the hydrologic class at ungauged sites based on their watershed variables.

Based on the training data at gauged sites, the stream class predictions from the GIS-variables are approximately 93% correct (see Chapter 3 for details). The accuracy of stream class predictions at ungauged sites can be further understood through an examination of a plot of Colorado Plateau streams in GIS-variable space (Figure 5.6). I conducted a Principle Components Analysis (PCA) on the 12 GIS-derived watershed variables that were used to assign ungauged stream segments to classes. I tested for significant differences in values of the first PCA axis among the four stream classes using

one-way ANOVA after square-root transforming the fist PCA axis to improve normality. I also tested for significant differences among transformed values for the perennial / non-perennial classes and the snowmelt / rain classes. I conducted these analyses in STATISTICA v. 6.0 (StatSoft Inc., Tulsa, OK).

5.2.1. Aquatic Insect Methods

The insect data used in this analysis came from two collections: the Utah State University BugLab data repository (Vinson 2001) and samples collected in 2004 and 2005. I limited my analysis to aquatic insect samples collected from free-flowing, wadeable streams in southern Utah and southwestern Colorado (Figure 5.5). Quantitative samples were collected from riffle habitats with a Hess net, Surber sampler, or kick net. Insects and detritus were preserved in the field and returned to the lab for processing. Insects were separated from detritus and identified to the lowest feasible taxonomic unit (Merritt and Cummins 1996). As I was interested in comparing taxonomic and functional descriptions of aquatic insect communities, I limited my analysis to aquatic insect families for which insect traits have been compiled (Poff *et al.* 2006a). I also excluded five insect families (Sericostomatidae, Corixidae, Haliplidae, Corduliidae, and Caenidae) from the analysis because they occurred at fewer than four sites. These criteria resulted in the inclusion of insect data from 180 sites (156 from U.S.U. and 24 from A.B.M, Chapter 3; details given in Appendix C) on 94 Colorado Plateau streams.

I examined the response of the aquatic insect community to stream hydrology based on community metrics and family-level insect functional traits. For this analysis, I selected six evolutionarily labile functional traits that describe aquatic insect ecology, life

history, and mobility (Table 5.1). I obtained the trait descriptions and states for insect families from Poff *et al.* (2006a). I conducted the statistical analyses on the relative abundance of individuals in a trait state. Trait states are alternate forms of a trait; for example, female dispersal ability may be high or low (two trait states).

5.2.2. Community Metrics, Similarity Analyses, and Functional Traits

The taxonomy-based community metrics that I considered in this analysis were insect density, %EPT (proportion of insects in the Ephemeroptera, Plecoptera, Trichoptera), % OCH (proportion of insects in the Odonata, Coleoptera, Hemiptera), % Diptera, and family-level richness. Even after transformation, the insect data do not meet the assumptions of parametric statistics. Therefore, I compared community metrics among stream classes with non-parametric Kruskal-Wallis tests. Kruskal-Wallis assumes that data are independent and drawn from populations whose distributions have the same shape and equal variances (Quinn and Keough 2002). In addition to the ANOVA analyses, I compared box plots of each trait states and families across stream classes.

I was also interested in the differences in the functional trait composition of the insect community among the stream classes. I used a similarity analysis procedure to determine whether communities within a stream class (e.g. insects in non-perennial-snowmelt streams) were more or less similar to communities among stream classes (e.g. non-perennial-snowmelt streams vs. perennial-snowmelt streams). If the among-class similarities were significantly greater than the within-class similarities, I concluded that the stream classification system accurately captured differences in the stream biota at the community level. I calculated five different similarity metrics (Bray-Curtis, Relative

Sorensen, Jaccard, Relative Euclidean, and simple correlation distance) on the community composition based on the six functional traits. These similarity metrics depend on the size of the species pool; therefore, analyses are typically compared through a standardized metric (Quinn and Keough 2002). I compared the standardized similarity metric (A) across the four stream classes with a Multi-Response Permutation Procedure (MRPP) in PC-ORD, v. 5.26 (MjM Software, Gleneden Beach, OR). MRPP calculates the observed delta (δ_{obs}), which is the average distance among sites based on the species abundances, for each group. It then calculates the value of delta that would be observed by random chance (δ_{exp}) based on Monte-Carlo permutation test of the original data (10,000 replications). The observed and expected delta values are compared through a test statistic (T) that is similar to a Student's t-test (McCune and Mefford 1999). The test statistic (T) has an associated p-value that indicates whether the observed delta is greater than would be expected by chance. Finally, the test statistic is adjusted to remove the effect of sample size; this adjustment results in a second test statistic (A). A is a measure of the within group/among group similarity: $A = 1$ when all items are identical within groups, $A = 0$ when heterogeneity within groups equals expectation by chance, and $A < 0$ with more heterogeneity within groups than expected by chance (McCune and Mefford 1999).

I tested for differences in the insect density in each trait state over the four stream classes with one-way Kruskal-Wallis ANOVA (Gotelli and Ellison 2004). As I was interested in the relative response of the insect community to the flood predictability and flow permanence axes, I also tested for differences between the number of individuals in each trait state for perennial / non-perennial classes and rain / snowmelt classes.

In order to gain an understanding of the interactions among functional traits in the different stream classes, I constructed classification trees to differentiate stream types based on insect functional traits. I constructed classification trees for two-class and four-class systems. I constructed the classification trees in STATISTICA v. 6.0 (StatSoft Inc., Tulsa, OK). Trees were constructed based on the Gini measure, with classification and regression tree style exhaustive search for univariate splits (Breiman *et al.* 1984). The prior probabilities were estimated from the proportion of training sites in each stream class. I employed FACT style direct stopping, which requires that terminal nodes (stream class predictions) contain no more than 20% of stream sites (Loh and Vanichestakul 1988). I tested the accuracy of the stream class predictions with a three-fold cross validation. This cross-validation technique builds a classification tree from 2/3 of the data (120 randomly selected streams in this case) and then tests the classification tree with the remaining 1/3 of the data; it repeats this procedure three times so each third of the data is used to test the tree (StatSoft 2001). The cross-validation procedure results in a misclassification matrix and a cross-validation cost. A lower value for the cross-validation cost indicates a tree with stronger predictive ability.

I also conducted Indicator Species Analysis (Dufrene and Legendre 1997) to determine the value of insect families and functional traits to indicate snowmelt and rain-driven stream classes. Indicator Species Analysis combines information on the faithfulness of a species (taxon or trait in this case) to a stream group and the concentration of abundance of that species in a stream group (McCune and Grace 2002). A good indicator species is one that is always present in a particular group and occurs only in that group. Indicator Species Analysis calculates the indicator value for each

species (or trait or family) by combining the relative frequency and abundance of a species in each group that is being compared (McCune and Grace 2002). I calculated indicator values for Colorado Plateau rain-driven and snowmelt streams using 17 trait states (for 6 traits) and 42 insect families using PC-ORD. PC-ORD calculates the significance of indicator values with a Monte Carlo method (1000 permutations). The Monte Carlo method determines how many times the indicator value is greater than expected by random chance. Very rare taxa (those that occur at one or two sites) are never selected as indicator species because they are so likely to be included in randomizations (i.e., the probability of selecting a species that occurs at only one site is 100%, McCune and Grace 2002).

Insect traits do not occur in isolation because an individual must have a full complement of traits. For example, a caddisfly may be univoltine and rare in the drift and small in size and have low dispersal ability. In order to understand the occurrence of trait combinations in Colorado Plateau insect families, I tabulated the number of taxa with certain combinations (e.g., univoltine, small, and rare in drift). I was interested if certain trait combinations occurred more frequently in Colorado Plateau aquatic insect families than would be expected by random chance. To this end, I calculated the probability of trait combinations occurring in insect taxa based on the frequency of occurrence for each single trait in Colorado Plateau insect families.

5.3.0 Results

The first Principle Components Analysis axis explained 49% of the variation in the data and was most highly correlated with GIS-variables that describe average monthly precipitation May and the coefficients of variation of precipitation for February and December (Table 5.2). The first axis was statistically significant based on the broken stick method (observed eigenvalue = 5.9, expected eigenvalue = 3.1, Jackson 1993). The second axis explained 16% of the variation in the GIS-data and was highly correlated with the watershed area coefficient of variation of precipitation in February and December and the coefficients of variation of precipitation for February and December. However, based on the broken stick method, the second axis was not statistically significant (observed eigenvalue = 1.9, expected eigenvalue = 2.1). The ordination plot of the gauged stream sites and ungauged insect collection sites in GIS-variable space revealed a stronger separation between rain and snowmelt classes than perennial and non-perennial classes (Figure 5.6). The first PCA axis can be thought of as a hydrologic gradient that ranges from harsh non-perennial-rain-driven sites to less harsh perennial-snowmelt driven sites. There were significant differences in this hydrologic gradient (PCA Axis 1) among the four stream classes at ungauged sites for which I had insect data (ANOVA; $F = 82.5$, d.f. = 3, 176, $p < 0.001$), between the perennial and non-perennial classes ($F = 10.0$, d.f. = 1, 178, $p < 0.001$), and between the snowmelt and rain classes ($F = 201.6$, d.f. = 1, 178, $p < 0.001$).

5.3.1. Community Metrics, Similarity Analyses, and Functional Traits

Three insect families (Chironomidae, Baetidae, and Simuliidae) comprised 62% of the total abundance over all sites. There were no differences in insect density among the four stream classes, but there were differences in the percentages of EPT taxa, OCH taxa, and Diptera among groups (Table 5.3). The significant difference in %EPT among the four classes was due to greater %EPT in snowmelt, compared to rain-driven, streams. The ephemeropteran family Leptohyphidae was especially common in snowmelt-driven streams, where it comprised 20% of the total insect abundance compared to 9% for all stream types combined. The difference in %OCH among the four classes ($p = 0.05$) was driven by the higher proportion of OCH in snowmelt-driven streams. This was probably due to the abundance of Elmidae, which comprised 6% of the total insect abundance but comprised 9% of the total abundance in snowmelt streams. Diptera were significantly more common in rain-driven streams than snowmelt streams. This may have been due to very high numbers of Chironomidae and Simuliidae. There was also a significant difference in family-level richness among the four stream classes. Family-level richness was highest in perennial-snowmelt streams, but there was considerable variation in richness over all sites (Table 5.3).

For insect functional traits, the similarity analysis revealed that the composition of in the four stream types (perennial-snowmelt, non-perennial-snowmelt, perennial-rain, non-perennial-rain) was not significantly different from random chance. Specifically, the test statistic (A) that was calculated in the MRPP analysis, which measures the ratio of within group to among group similarity, was very close to zero (min = 0.004, max =

0.042) for all similarity metrics (Table 5.4). A value of zero indicates that the heterogeneity among groups is equal to what would be expected by random occurrence.

Five of the six traits showed a significant difference in insect density among the four stream classes for at least one trait state (Kruskal-Wallis ANOVA; Table 5.5); only thermal preference showed no difference among stream classes. When the three most abundant families (Chironomidae, Simuliidae, and Baetidae) were removed from the analysis, all six traits were significantly different among the four classes. At the level of the trait state, less than half were significant (7/17) when all insects were analyzed. When Chironomidae, Simuliidae, and Baetidae were excluded, the number of significant trait states was approximately the same (8/17) but the composition of significant traits was different, which indicates that three dominant families are driving some of the functional community response. Chironomidae, Simuliidae, and Baetidae are multivoltine and small and thus influence the voltinism and size traits.

The univariate Kruskal-Wallis ANOVA results indicate that the flood predictability axis has a stronger influence on the insect community than the flow permanence axis. The insect density was significantly different in rain- and snow-driven streams for all six traits (10/17 trait states). It appears that the difference between rain- and snowmelt-dominated streams is driving the majority of significant differences in the four class model. Snowmelt streams had significantly higher densities of taxa that were dispersal limited (low female dispersal ability and rare/common in the drift). Snowmelt streams also had more insects that were cold/cool stenothermal obligates; however, the abundance of individuals in this trait state was not correlated to elevation ($r^2 = 0.001$, $p=0.7$). Insects that prefer depositional habitats were more common in snowmelt

streams, while insects that prefer erosional streams were significantly more abundant in rain-driven streams. This may be due to the substrate size distribution of the two stream types, but rheophilic abundance ($r^2 = 0.005$, $p=0.3$) and depositional abundance ($r^2 = 0.0002$, $p=0.8$) was not correlated with stream gradient. Univoltine and semivoltine insects are significantly more abundant in snowmelt streams. On the Colorado Plateau body size is inversely correlated to the number of generations per year (small-multivoltine: $r^2 = 0.9$, $p < 0.001$; medium-univoltine: $r^2 = 0.8$, $p < 0.001$; large-semivoltine: $r^2 = 0.4$, $p < 0.001$).

No functional traits differed significantly between perennial and non-perennial sites when insect density from all families was compared. However, when I excluded the abundant taxa (Chironomidae, Simuliidae, Baetidae) from the analysis, there were significantly more individuals that are "abundant in the drift" in perennial than non-perennial streams.

The CART model predicted site membership based on insect functional traits in the four stream classes slightly better than would be expected by random chance. Three insect functional traits (medium size, univoltine, and rare-in-drift) were the most important stream class predictors. The model predicted class membership with 32% accuracy (based on three-fold cross validation) and a random assignment of streams to classes would have produced 25% accuracy (Table 5.6). Site membership in rain and snowmelt streams was predicted by the CART model with 76% accuracy for training data and 61% accuracy for the three-fold cross validation. This model indicated that snowmelt streams are characterized by medium-sized, univoltine, taxa that are rare in the drift.

The Indicator Species Analysis on insect functional traits resulted in four traits (five trait states) that had significant ($p < 0.05$) indicator values (Table 5.7). All of the significant traits were indicators for snowmelt streams; no traits were significant for rain-driven streams. Voltinism (semivoltine and univoltine states), occurrence in the drift (rare), rheophily (depositional habitats preferred), and size (medium) were all significant trait indicators. Although each of these individual trait states is an indicator of snowmelt streams, traits do not occur in snowmelt streams by themselves; they must occur in combination within insect taxa. The proportional occurrence of trait states and trait combinations in Colorado Plateau insect families shows that some trait states, such as a univoltine life cycle, are common and some are rare, such as a semivoltine life cycle.

The Indicator Species Analysis of Colorado Plateau insect families resulted in nine significant indicator families for snowmelt streams and one rain-driven stream indicator (Table 5.8). Six of the nine snowmelt stream indicators were EPT taxa. In looking at which functional trait combinations are present in the indicator families, univoltine life history and low female dispersal ability are present in nearly all snowmelt indicators. Heptageniidae are snowmelt stream indicators and they contain all four indicator traits previously mentioned (univoltine, rare-in-drift, depositional, and small). The indicator families came in all size ranges (small, medium, and large) and all with rheophilic preferences (depositional, erosional, and both). The one rain-driven stream indicator, the microcaddisflies (Hydroptilidae), has functional traits that overlap with the snowmelt-indicator traits. These results suggest that while indicator traits are more common in certain stream types, they are not limited to a single type.

5.4.0. Discussion

Compared to the flow regimes of streams across the world (Poff *et al.* 2006b), Colorado Plateau stream hydrology exists at the harsh end of the spectrum (Poff and Ward 1989; Poff 1996). Given the region's extreme hydrologic variability, it is not surprising that disturbance-adapted aquatic insect taxa are common in perennial, non-perennial, snowmelt- and rain-driven streams. Dieterich and Anderson (2000) found higher richness in seasonally dry streams than in nearby perennial headwaters streams, which suggests that a large number of species are adapted to adverse conditions. Chironomidae, Simuliidae, and Baetidae are rapid colonists to recently disturbed stream habitats (Vieira *et al.* 2004) and these three families comprised over 60% of the insects collected on the Plateau. High larval and adult mobility, as evidenced by presence in the drift and female dispersal ability, are probably generalized adaptations by Colorado Plateau aquatic insects to frequent flood disturbance and climatic variation over decades to millennia. Insects with strong female dispersal ability were common in all Colorado Plateau stream types. Gray (1981a) found that approximately 65% of colonists to a recently flooded Sonoran Desert stream arrived from aerial stages; the majority of this recolonization was due to oviposition by aerial females. Another 20-35% of the colonists to the Sonoran desert stream arrived through drift (Gray 1981a); Colorado Plateau generalists are also abundant in the drift. In addition to being relatively mobile, disturbance-adapted taxa on the Colorado Plateau commonly produce more than one generation per year and are typically small as adults. Rapid development reduces the amount of time that aquatic larval stages are susceptible to hydrologic disturbances (Cushing and Gaines 1989).

The overall abundance of disturbance-adapted insect taxa in all streams may explain why I did not find different community assemblages in the four Colorado Plateau stream types. Other stream ecologists working in disturbance-prone regions have found an abundance of weedy insect taxa (Beche *et al.* 2006). It is also possible that there are community differences but I could not detect them due to the uncertainty inherent in this analysis. First, it is possible that the assignment of sites to the stream classes was not accurate and, therefore, I cannot detect a difference among insect communities because the communities are not correctly attributed to the appropriate stream classes. We know that the stream class assignments based on GIS-derived watershed variables were approximately 15% incorrect overall, which may be sufficient to mask significant differences among community types; however, this is unlikely. Second, dividing continuous flow variability into four classes may be too coarse grained to detect the response of the insect community to the habitat template. The flood timing axis is a gradient from streams that only flood during snowmelt to streams that do not receive any snowmelt runoff. Most Colorado Plateau streams exist somewhere between these two extremes and their hydrographs (Figure 5.3) constitute a snow + rain stream class (*sensu* Poff and Ward 1989) rather than snow versus rain classes. Due to the scarcity of streamflow data on the Plateau, the GIS-based site classification could not correctly identify these snow + rain sites into a separate group. Perhaps if more data were available, more subtle differences among insect adaptations to the flood timing axis could be detected. Third, aquatic insects on the Colorado Plateau may not be as responsive to changes in flow permanence as flood timing. Even in non-perennial streams, flood events probably occur more frequently than stream drying events, especially at the scale

of aquatic insect lifetimes (Lake 2000). Therefore, flooding may exert a stronger selective pressure on aquatic insect evolutionary than stream drying (Lake 2000; Lytle 2001). Alternately, it may be more effective at "filtering" certain traits that are not adaptive in non-perennial-rain-driven streams. It is also likely that even perennial streams on the Colorado Plateau dry frequently enough to select for aquatic insect taxa that can recover quickly from droughts. Fourth, I did not have data to test what habitat refugia from floods and droughts are available to the aquatic insects at these sites. The 180 one-time point samples that I analyzed may not be adequate to capture the insect community dynamics on the Colorado Plateau. Fifth, it is possible that the streamflow typology adequately captures the hydrologic variation on the Plateau and that sites are accurately assigned to stream classes, but that other habitat gradients are overriding the influence of hydrology in structuring aquatic communities. Poff and Ward (1990) suggested that streamflow, substrate, and thermal regime are the minimum elements needed to characterize the habitat template in streams. I did not have adequate substrate or temperature data at the site-scale in order to test how Colorado Plateau stream insect communities respond to these environmental variables. In an analysis of the 25 streams that I sampled (Chapter 3), I found significant relationships between mean particle size and insect density and richness, which suggest that other habitat gradients are important on the Colorado Plateau.

Prior to this analysis, I believed that I would find mountain and desert specialists. I expected that Rocky Mountain taxa would be adapted to high gradient, snowmelt-driven, cool water streams, whereas desert taxa would be characterized by desiccation resistance, strong dispersal ability, asynchronous emergence, and multivoltine life

histories. It appears, however, that the Colorado Plateau insect fauna consists of a small number of snowmelt-adapted taxa nested within a larger assemblage of disturbance-adapted generalists (Figure 5.7). Bonada *et al.* (2007) found a similar pattern in northern Spain where most insects are multivoltine and have short life spans, presumably as an adaptation to the Mediterranean climate. Insects with Mediterranean life histories showed different physiological traits in streams with different flow regimes, such that strong aerial dispersal was more common in intermittent streams and desiccation resistant stages were more common in ephemeral streams (Bonada *et al.* 2007) . According to Nelson (1994), the most common biogeographic pattern for Colorado Plateau insects is a widespread range that extends east and west of the Plateau; the second most common biogeography is to range in the Colorado Plateau and Rocky Mountains. In general, Ephemeroptera, Plecoptera, and Trichoptera are common and Diptera are rare in snowmelt-fed streams on the Colorado Plateau (Table 5.3). Odonata, Coleoptera, and Hemiptera were slightly more common in snowmelt streams than rain-driven streams.

Several different analyses (Tables 5.5, 5.6, 5.7) suggest that snowmelt-adapted taxa are semi/univoltine, medium size at maturity, and scarce in the drift. Snowmelt-fed streams are typically cold and winter snow cover can reduce food resources available to larval insects through a reduction of organic inputs matter to streams, which have been shown to result in slower larval growth (Schutz *et al.* 2001) and later emergence adult in snowmelt-fed mountain streams (Gregory *et al.* 2000). Snowmelt-adapted taxa on the Plateau tend to be rare in the drift. Insect taxa that prefer depositional habitats were significantly more common in snowmelt-streams than rain-driven streams on the Colorado Plateau (Tables 5.5, 5.7). The abundance of depositional taxa in snowmelt

streams may be due to the high co-occurrence of this trait with semivoltine ($r^2 = 0.57$, $p < 0.001$) and univoltine life cycles ($r^2 = 0.98$, $p < 0.001$) in the insects that I analyzed. These trait combinations may be common because they are adaptive or they may be common because they are evolutionarily or physiologically linked (Poff *et al.* 2006a).

High elevation streams on the Colorado Plateau have a low incidence of flash floods (Thomas *et al.* 1997) compared to rain-driven streams. The seasonally predictable, ramped floods that occur in snowmelt streams have several evolutionary implications for aquatic insect taxa on the Plateau. First, snowmelt adapted taxa on the Colorado Plateau have limited mobility (low frequency in the drift and low female dispersal ability) compared to their rain-driven counterparts (Table 5.5). Low dispersal ability in mountain environments results in limited gene flow among stream insects populations (Finn *et al.* 2006). Limited gene flow coupled with a predictable disturbance regime should lead to locally-adapted populations (Lytle 2001). Second, the timing of adult emergence should minimize insect mortality due to spring floods and maximize the reproductive ability of snowmelt-adapted taxa (Lytle 2002). Synchronous emergence is favored when the probability of flood-induced mortality is greater than the probability of mortality due to long distance dispersal (Iwasa and Levin 1995). Because flood predictability is high in snowmelt-fed streams on the Plateau and snowmelt-adapted taxa tend to have limited dispersal ability, synchronous emergence should be common in these insects but there was no difference in the synchronicity of emergence between snowmelt- and rain-driven streams at the Colorado Plateau sites (ANOVA: $F=0.03$, d.f.=1, 178, $p = 0.86$). This may be due to the low evolutionary lability of this trait (Poff *et al.* 2006a).

Perennial streams on the Colorado Plateau are and have been susceptible to diversions, dikes, and exotic invasion (Tuhy *et al.* 2002). All western streams are vulnerable to changes in stream discharge, flood timing, and frequency due to global climate change. In the Colorado River basin, the timing of peak snowmelt runoff has already started to shift earlier into the spring (Dettinger 2005). Anthropogenic streamflow alteration will probably not affect the disturbance-adapted generalist taxa that comprise the majority of the insects on the Colorado Plateau. Snowmelt-adapted taxa, however, appear to be particularly susceptible to changes in hydrology. Experimental reductions in streamflow suggest that insect communities from high-gradient (step-pool) channels are more susceptible to flow alteration than insects from lower gradient (riffle-pool) streams (Albano 2006). Snowmelt indicator taxa, such as Heptageniidae, Glossosomatidae, and Rhyacophilidae (Table 5.8), have limited mobility and local populations may be genetically distinctive. These sensitive taxa may be locally extirpated from Colorado Plateau snowmelt streams as they are forced to move further uphill due to climate change and eventually run out of high-elevation thermal refugia as alpine temperatures rise (Hauer *et al.* 1997). Local extirpation of genetically unique Belostomatidae, probably due to climatic warming, have been identified in the mountain stream habitats of the Sky Islands in Arizona (Finn *et al.* 2007; Finn *et al.* In Press) and the upward migration of stoneflies has been documented in the in the Smoky Mountains of Tennessee (Sheldon 2007). The ecology of Colorado Plateau insect fauna is not well studied, but research in the Sky Islands indicates that there are distinct insect species that occupy high elevation streams during the dry and rainy seasons (Bogan and Lytle 2007). Snowmelt-adapted insects on the Colorado Plateau have functional traits (low dispersal,

univoltine life cycles) that make them particularly susceptible to streamflow changes. Aquatic conservation efforts on the Plateau should consider the how the habitat template pre-disposes aquatic organisms to be susceptible or resilient to anthropogenic change.

5.5.0. Literature Cited

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Table 5.1. Descriptions of evolutionarily labile insect traits used in this analysis. Harsh sites on the Colorado Plateau are non-perennial, rain-driven sites. Perennial-snowmelt sites are hydrologically more benign. Traits and descriptions are from Poff *et al.*(2006).

	Trait	Predicted Response	Code	Categories
1	Female Dispersal	High dispersal at harsh sites	Disp1	Low (< 1 km flight before laying eggs)
			Disp2	High (> 1 km flight before laying eggs)
2	Voltinism	Multivoltine life cycle common at harsh sites	Volt1	Semivoltine (< 1 generation / year)
			Volt2	Univoltine (1 generation / year)
			Volt3	Multivoltine (1+ generation / year)
3	Occurrence in drift	Drift-prone organisms more common at harsh sites	Drft1	Rare (Catastrophic only)
			Drft2	Common (Typically observed)
			Drft3	Abundant (Dominant in drift samples)
4	Rheophily	Rheophilic taxa more rare at harsh sites	Rheo1	Depositional
			Rheo2	Depositional & Erosional
			Rheo3	Erosional
5	Thermal Preference	Taxa that prefer cool/cold water common at benign sites	Therm1	Cold stenothermal/cool eurythermal
			Therm2	Cool/warm eurythermal
			Therm3	Warm eurythermal
6	Size at Maturity	Small size common at harsh sites	Size1	Small
			Size2	Medium
			Size3	Large

Table 5.2. Correlation coefficients (r^2) between PCA axes and the GIS-derived variables used to generate the axes. PCA axis 1 was significant based on the Broken Stick method (Jackson 1993) but axis 2 was not. See text for details.

	PCA Axis 1		PCA Axis 2	
	r^2	p	r^2	p
Estimated flow (cms)	0.11	$p < 0.001$	**0.16**	$p < 0.001$
Contributing watershed area	0.06	$p < 0.001$	**0.20**	$p < 0.001$
Av. March Precipitation	0.08	$p < 0.001$	0.01	p=.08
Av. April Precipitation	0.14	$p < 0.001$	0.06	$p < 0.001$
Av. May Precipitation	0.74	$p < 0.001$	0.00	$p = 0.4$
Acc. January Precipitation	0.11	$p < 0.001$	0.01	$p = 0.2$
Acc. April Precipitation	0.16	$p < 0.001$	0.06	$p < 0.001$
Acc. May Precipitation	0.12	$p < 0.001$	0.06	$p < 0.001$
Acc. July Precipitation	0.07	$p < 0.001$	0.04	$p < 0.001$
C.V. February Precipitation	0.20	$p < 0.001$	0.24	$p < 0.001$
C.V. October Precipitation	0.16	$p < 0.001$	0.15	$p < 0.001$
C.V. December Precipitation	0.31	$p < 0.001$	0.23	$p < 0.001$

* ln (x+1) transformed to improve normality.

Table 5.3. Summary of one-way nonparametric Kruskal-Wallis ANOVA results for the general insect community metrics. Density was measured as the number of individuals per m^2. Family-level richness was calculated for insect families only. %Ephemeroptera, Plecoptera, Trichoptera (%EPT) is the number of EPT individuals divided by the total number of individuals. %Odonata, Coleoptera, Hemiptera (%OCH) and %Diptera were calculated in the same manner as %EPT. The four class ecological model includes non-perennial-snowmelt, non-perennial-rain-driven, perennial-snowmelt, and perennial-rain-driven stream types. The flood predictability axis divides streams into snowmelt and rain-driven stream types; flow permanence dives streams into perennial and non-perennial stream types.

	Four-class Ecological Model		**Flood Predictability**		**Flow Permanence**	
	K-W Test	**p-value**	**K-W Test**	**p-value**	**K-W Test**	**p-value**
Density	4.42	0.22	3.14	0.08	0.44	0.51
Family-richness	9.37	**< 0.05**	6.48	**< 0.05**	0.49	0.49
% EPT	10.03	**< 0.05**	9.63	**< 0.05**	0.74	0.79
% OCH	7.80	0.050	3.49	0.06	0.27	0.61
% Diptera	13.85	**< 0.05**	13.58	**< 0.01**	0.02	0.88

Table 5.4. Test of similarity within vs. across four groups (perennial-snowmelt, non-perennial-snowmelt, perennial-rain, non-perennial rain) for traits (abundance of all insects). Tested with Multi-Response Permutation Procedures (MRPP) in PC-ORD, Version 4.26. T = raw test statistic (similar to Student's t), δ_{obs} = observed within group similarity, δ_{exp} = within group similarity expected by random chance, A = test statistic adjusted for group size, p-value = significance test for δ_{obs}. A = 0 indicates that there is more heterogeneity within groups than expected by chance. See text for more details.

	T	δ_{obs}	δ_{exp}	Var. of δ	Skew. of δ	A	p-value
Bray-Curtis	-1.29	0.695	0.699	0.72E-05	-0.96	0.005	0.11
Rel. Sorensen	-9.49	0.290	0.310	0.18E-05	-0.93	0.042	< 0.001
Jaccard	-1.28	0.793	0.796	0.47E-05	-0.86	0.004	0.11
Rel. Euclidean	-7.32	0.556	0.574	0.58E-05	-0.92	0.031	< 0.001
Correlation	-6.77	0.395	0.406	0.28E-05	-0.91	0.028	< 0.001

Table 5.5. Summary of one-way nonparametric ANOVA results for the insect density in functional trait states for streams on the Colorado Plateau. a) All insects and b) These data have had Chironomidae, Baetidae, Simuliidae excluded, which comprise 62% of the individual insects collected among all sites.

a)

All Insects		Four-class Ecological Model		Flood Predictability		Flow Permanence	
		K-W Test	p-value	K-W Test	p-value	K-W Test	p-value
Female Dispersal	Displ	9.13	**0.03**	4.97	**0.03**	2.60	0.11
	Disp2	2.32	0.51	0.57	0.45	0.22	0.64
Voltinism	Voltl	8.60	**0.04**	4.01	**0.05**	1.09	0.29
	Volt2	12.50	**0.01**	10.90	**0.00**	0.64	0.42
	Volt3	1.07	0.78	0.67	0.41	0.01	0.93
Occurrence in Drift	Drftl	14.60	**0.00**	11.80	**0.00**	1.14	0.29
	Drft2	7.59	0.06	5.13	**0.02**	1.76	0.18
	Drft3	1.67	0.64	0.97	0.33	0.06	0.81
Rheophily	Rheol	9.97	**0.02**	7.28	0.01	0.92	0.34
	Rheo2	3.21	0.36	2.06	0.15	0.02	0.88
	Rheo3	6.37	0.09	4.97	**0.03**	0.90	0.34
Thermal Preference	Therml	6.75	0.08	4.88	**0.03**	1.14	0.28
	Therm2	4.14	0.25	3.00	0.08	0.43	0.51
	Therm3	3.21	0.36	0.13	0.72	2.69	0.10
Size at Maturity	Sizel	2.28	0.52	1.24	0.26	0.08	0.78
	Size2	21.00	**0.00**	19.10	**0.00**	0.77	0.38
	Size3	11.70	**0.01**	6.63	**0.01**	2.86	0.09

b)

Insects without CBS		Four-class Ecological Model		Flood Predictability (RvS)		Flow Permanence (NPvP)	
		K-W Test	p-value	K-W Test	p-value	K-W Test	p-value
Female Dispersal	Displ	8.02	0.05	6.75	**0.01**	0.47	0.49
	Disp2	5.44	0.14	0.02	0.88	0.26	0.61
Voltinism	Voltl	6.91	0.07	2.49	0.11	1.06	0.30
	Volt2	8.39	0.04	7.28	**0.01**	0.45	0.50
	Volt3	2.60	0.46	1.98	0.16	0.48	0.49
Occurrence in Drift	Drftl	10.10	0.02	8.02	**0.00**	0.87	0.35
	Drft2	4.50	0.21	4.40	**0.04**	0.10	0.75
	Drft3	16.50	**0.00**	10.20	**0.00**	5.72	**0.02**
Rheophily	Rheol	7.58	**0.06**	4.78	0.03	0.74	0.39
	Rheo2	6.80	0.08	4.23	0.04	0.02	0.90
	Rheo3	4.67	0.20	3.95	0.05	0.14	0.71
Thermal Preference	Therml	7.98	0.05	7.73	**0.01**	0.04	0.84
	Therm2	8.08	0.04	4.85	0.03	1.43	0.23
	Therm3	3.36	0.34	0.07	0.79	2.76	0.10
Size at Maturity	Sizel	3.71	0.29	0.29	0.59	0.01	0.93
	Size2	16.10	**0.00**	14.70	**0.00**	0.52	0.47
	Size3	9.63	**0.02**	4.94	**0.03**	2.60	0.11

* These traits have a different result (significant differences became non-significant or vice versa) when Chironomidae, Baetidae, Simuliidae are removed from the analysis.

Table 5.6. Confusion matrices for the classification trees constructed from insect functional trait states to differentiate among the a) four stream classes and between b) rain-driven and snowmelt streams on the Colorado Plateau (Predicted class (row) x observed (column)). These classification trees were constructed with prior probabilities estimated from the training data, the Gini measure of fit, univariate splits, and FACT style direct stopping with no more than 20% of the training data in a terminal node.

a) The classification tree for the four stream classes contained 17 terminal nodes and had a Global CV-cost of 0.683 ±0.035.

	Learning Sample					*Cross-validation Data*				
	Non-Perennial		**Perennial**			**Non-Perennial**		**Perennial**		
	Rain	**Snow**	**Rain**	**Snow**	**mean**	**Rain**	**Snow**	**Rain**	**Snow**	**mean**
NonPerennial-Rain	27	4	3	3		11	1	14	11	
NonPerennial-Snowmelt	6	25	6	10		11	13	7	16	
Perennial-Rain	7	3	33	10		14	7	12	6	
Perennial-Snowmelt	5	3	4	31		9	14	13	21	
Correct Classification	60%	71%	72%	57%	**64%**	24%	37%	26%	39%	**32%**

b) The classification tree for rain- and snowmelt-driven streams contained 6 terminal nodes and had a Global CV-cost of 0.389 ±0.036.

	Learning Sample			*Cross-validation Data*		
	Rain	**Snow**	**mean**	**Rain**	**Snow**	**mean**
Rain	72	21		54	33	
Snow	19	68		37	56	
Correct Classification	79%	76%	**78%**	59%	63%	**61%**

Table 5.7. Number of Colorado Plateau insect families and genera with combinations of snowmelt-driven stream indicator traits. These traits are significantly more common in **snowmelt streams than rain** streams (Indicator Species Analysis; significance based on a Monte-Carlo test with 1000 permutations). The Colorado Plateau regional species pool includes 50 families and 105 genera.

Indicator Traits for Snowmelt Streams	Families	Exp.	Obs.
Single Traits			
Semivoltine (Volt 1)	8	-	16%
Univoltine (Volt2)	37		74%
Rare in Drift (Drift 1)	39	-	78%
Depositional (Rheo 1)	10	-	20%
Medium Size (Size 2)	19	-	38%
Two Trait Combinations			
Volt 1/2 & Drift 1	37	70%	74%
Volt 1/2 & Rheo 1	8	18%	16%
Volt 1/2 & Size 2	19	34%	38%
Drift 1 & Rheo 1	9	16%	18%
Drift 1 & Size 2	16	30%	32%
Rheo 1 & Size 2	4	8%	8%
Three Trait Combinations			
Volt 1/2 & Drift 1 & Rheo 1	7	14%	14%
Volt 1/2 & Drift 1 & Size 2	16	27%	32%
Volt 1/2 & Rheo 1 & Size 2	4	7%	8%
Drift 1 & Rheo 1 & Size 2	4	5%	8%
Four Trait Combinations			
Volt 1/2 & Drift 1 & Rheo 1 & Size 2	4	5%	8%

Table 5.8. Indicator taxa (families) for snowmelt and rain-driven streams on the Colorado Plateau. Indicator species analysis indicated that these taxa are significantly more common in **snowmelt or rain-driven** streams (significance based on a Monte-Carlo test with 1000 permutations). The dominant trait states are given for each taxon; see Table 2 for codes and text for details.

Indicator Taxa	**Functional Trait States**					
Snowmelt Streams	***Disp***	***Volt***	***Drift***	***Rheo***	***Ther***	***Size***
Chloroperlidae	1	2	2	2	1	2
Elmidae	1	1	2	2	2	1
Ephemerellidae	1	2	2	2	2	2
Glossosmatidae	1	2	1	3	1	1
Heptageniidae	1	2	1	1	2	2
Nemouridae	1	2	2	2	1	1
Perlidae	2	2	2	3	2	3
Rhyacophiladae	1	2	1	3	1	2
Tipulidae	1	2	1	2	2	2
Rain-driven Streams						
Hydroptilidae	2	2	1	3	2	1

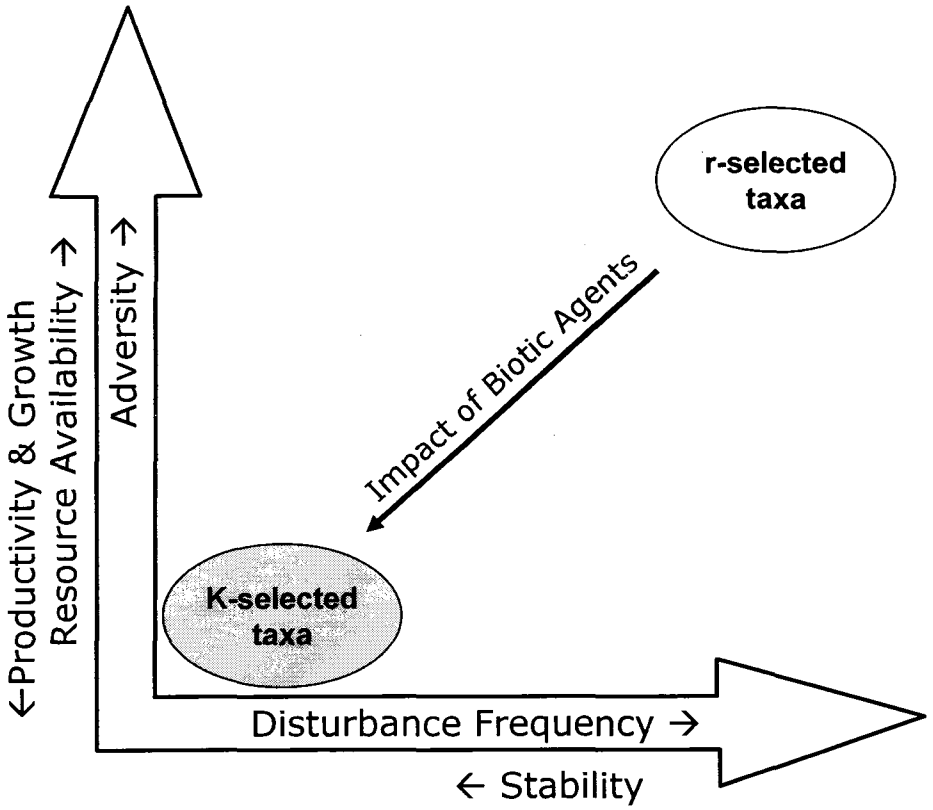


Figure 5.1. The habitat template concept modified from Southwood (1988).

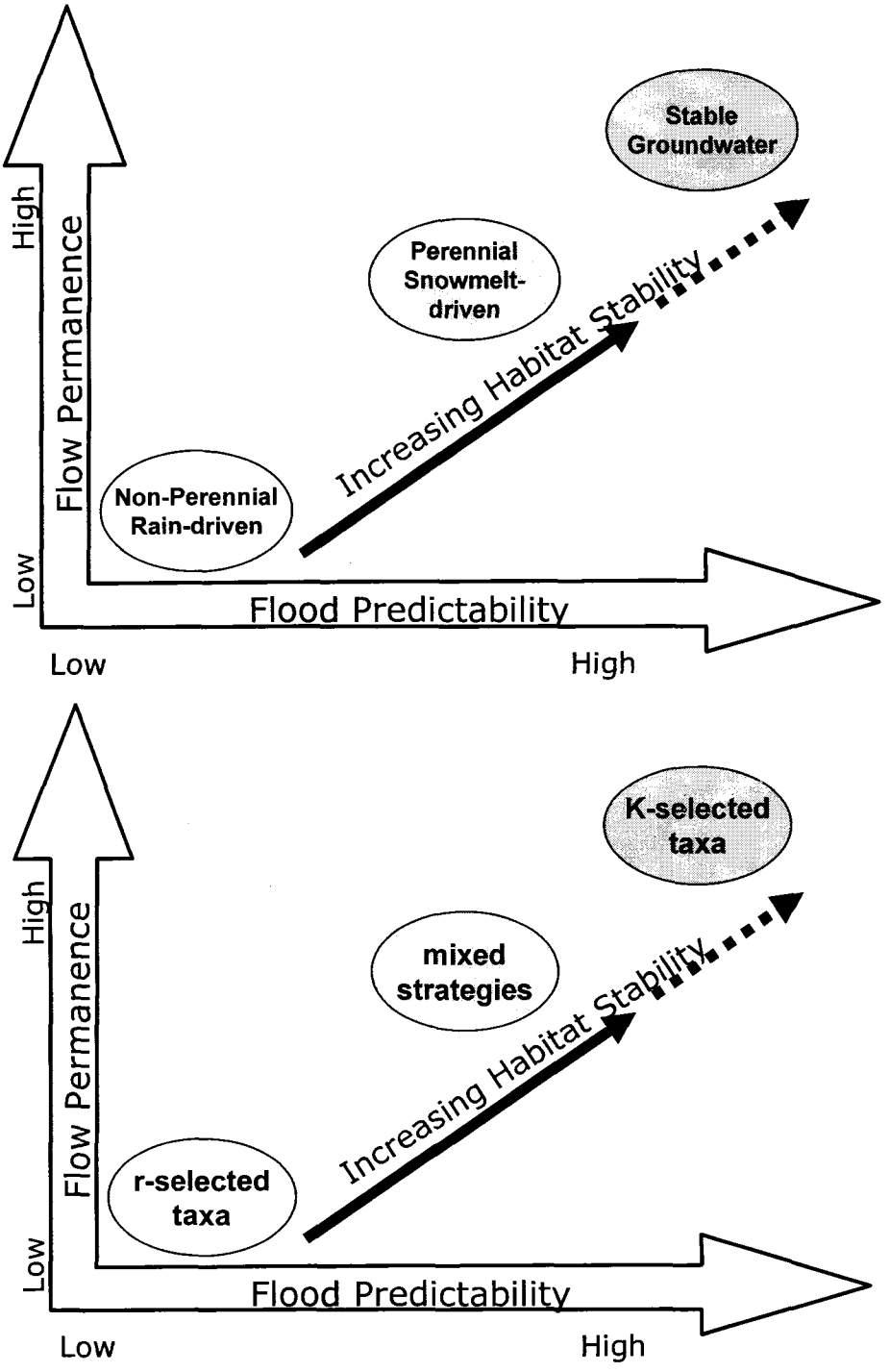


Figure 5.2. top) The habitat template of ecologically-relevant stream hydrology on the Colorado Plateau. Flow permanence and flood predictability are thought to be the two major drivers of lotic communities on the Plateau. bottom) Predicted life-history strategies that Colorado Plateau insects have to adapt to the hydrologic variability.

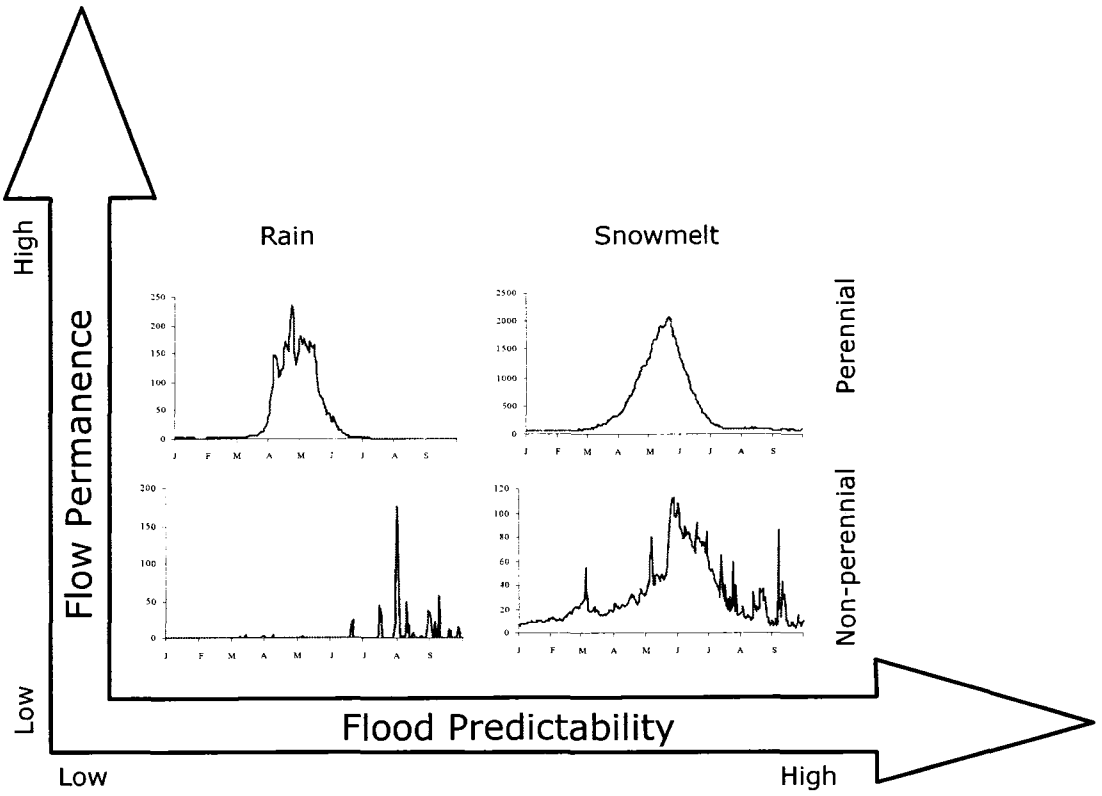


Figure 5.3. Stream hydrology (output from chapter 2) on the Colorado Plateau stream community. The inset hydrographs are an example of what the flow regime looks like. Flow regimes on the Plateau exist along a continuum from perennial streams to streams that flow only during snowmelt or after rain events. The two major sources of floods are snowmelt and summer convective rain events. Snowmelt tends to occur at higher elevations, whereas summer convective storms occur mostly below 2,286 m / 7,500 ft. (Thomas *et al.*, 1997). These stream classes correspond to classes suggested by Poff (1996) as follows: snowmelt-perennial stream = snowmelt, summer convective-perennial = perennial flashy, snowmelt-non-perennial = none, summer convective-non-perennial = harsh intermittent.

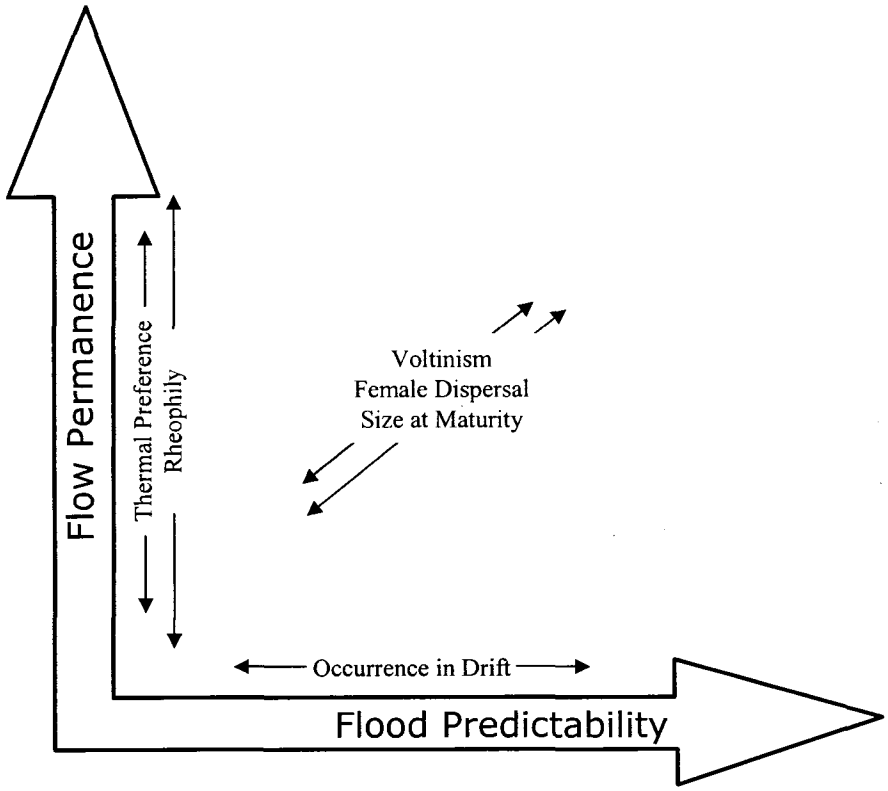


Figure 5.4. Evolutionarily labile insect traits that are believed to confer a survival advantage to insects in streams across two gradients of hydrologic variability on the Colorado Plateau.

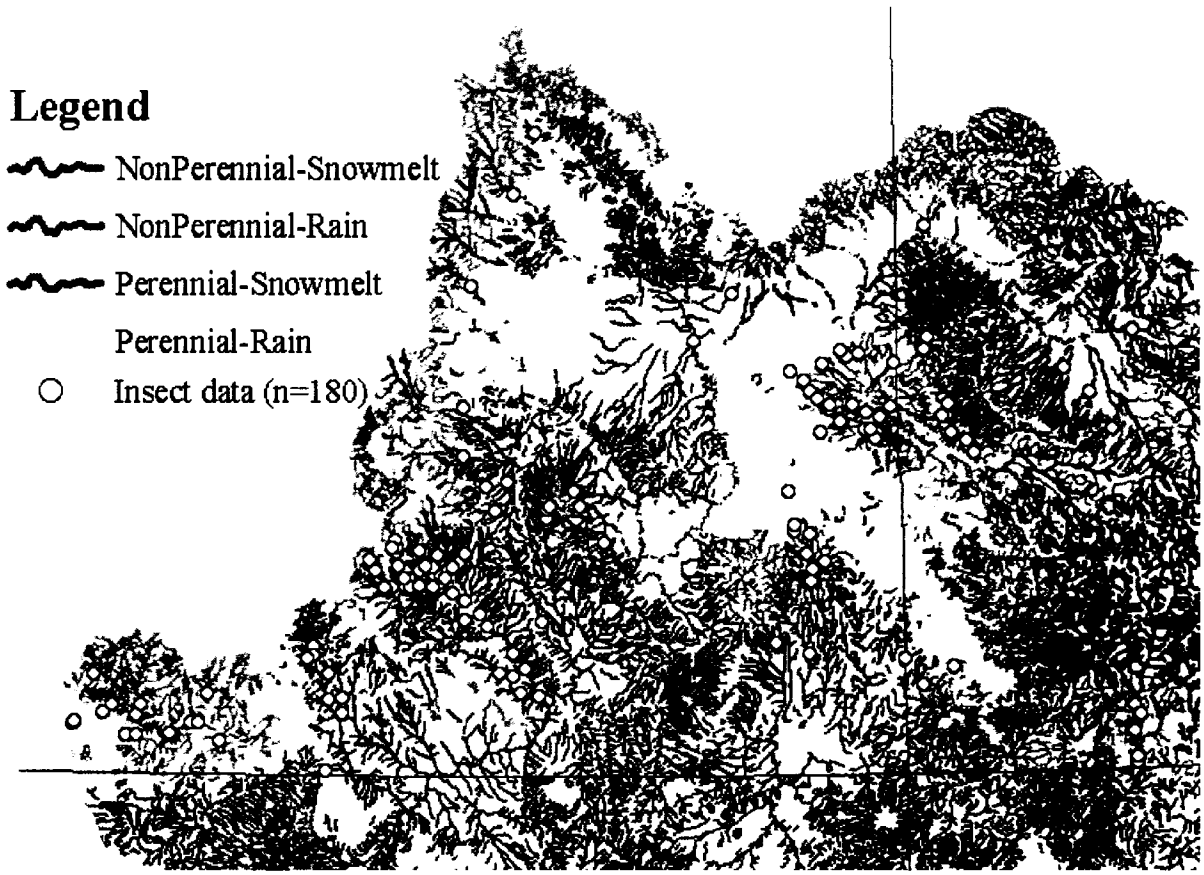
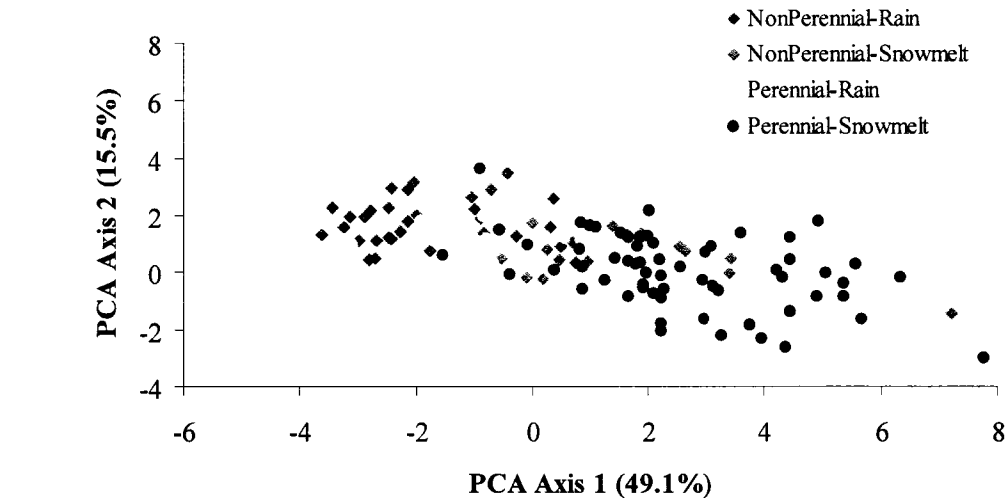
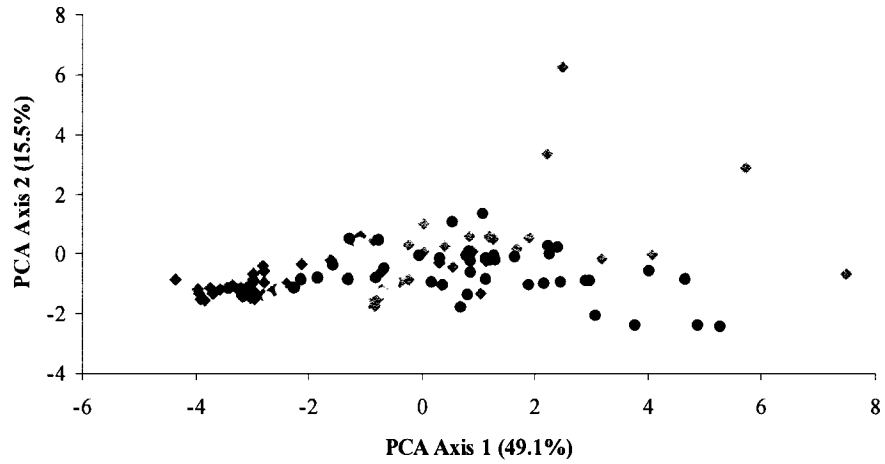


Figure 5.5. Map of stream classification on the Colorado Plateau with insect collection locations



a)



b)

Figure 5.6. Plot of Principle Components Analysis output for gauged and ungauged stream sites in GIS-derived watershed variables space. The first axis was significant by the Broken Stick method (Jackson 1993) but the second axis was not. The first axis shows the distribution of stream types along a continuous hydrologic gradient from harsh (left) to less harsh (right). a) The plot of gauged sites (n = 139) illustrate the difficulty of classifying perennial and non-perennial streams based on daily streamflow data. b) The plot of ungauged sites from which I analyzed insect data (n = 180) illustrates the distinct line between rain-driven and snowmelt-driven stream sites.

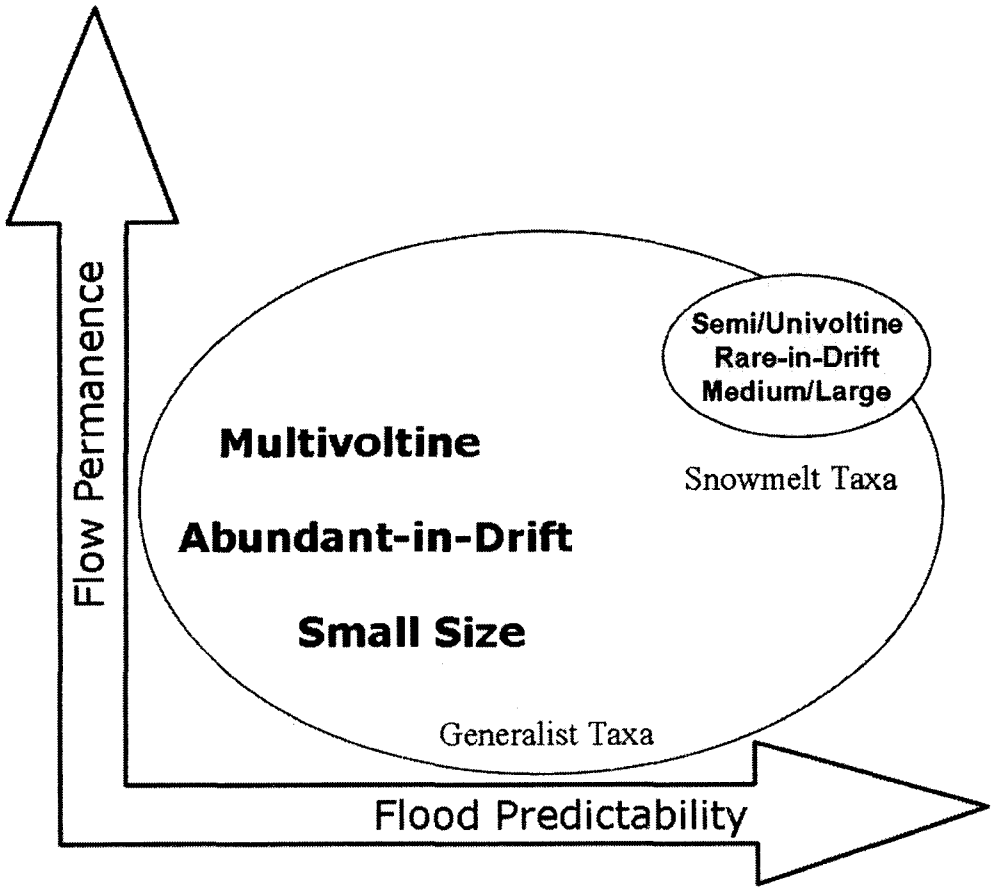


Figure 5.7. Distribution of insect functional traits across the habitat template of hydrologic variability on the Colorado Plateau. Generalist taxa are common in all stream types, probably because of the overall unpredictability of streamflow in this region, but snowmelt specialists exist in slightly more benign higher elevation sites that are dominated by snowmelt runoff.

Appendix A: Definitions and statistical transformations for hydrologic metrics used in the Statistical and Ecological Models (Chapter 4). Metric abbreviations and definitions are from Olden and Poff (2003). a) Hydrologic metric abbreviation, b) dimension adjustment, c) dimensions of the hydrologic metric after adjustment (none = dimensionless), d) transformation to improve normality, linearity, and homogeneity of variance, and e) metric definition.

a)	b)	c)	d)	e)
Magnitude Metrics				
M_L3	M_L3/M_A1	none	none	Mean minimum flows for March across all years (ft^3/s.– temporal).
M_H20	M_H20/M_A1	none	log (x + 1)	Specific mean annual maximum flow. M_H20 is the mean of the annual maximum flows divided by the drainage area (ft^3/s per square mile – temporal).
Frequency Metrics				
F_L3	none	number / year	none	Frequency of low pulse spells. Compute the average number of flow events with flows below a threshold equal to 5 percent of the mean flow value for the entire flow record. F_L3 is the average number of events (number of events/year – temporal).
Duration Metrics				
D_L11	D_L1/M_A1	none	none	Annual minimum daily flow. Compute the minimum 1-day average flow for each year. D_L1 is the mean of these values (ft^3/s. – temporal).
D_L15	none	none	square root	Low exceedence flows. Compute the 90 percent exceedence value for the entire flow record. DL14 is the exceedence value divided by the median for the entire record (dimensionless – spatial).
D_L16	none	days	log (x + 1)	Low flow pulse duration. Compute the average pulse duration for each year for flow events below a threshold equal to the 25th percentile value for the entire flow record. DL16 is the median of the yearly average durations (number of days – temporal).
D_L18	none	days	square root	Mean annual number of zero-flow days. Count the number of zero-flow days for the entire flow record (number of days/year – temporal).
D_L20	none	percent	square root	Number of zero-flow months. While computing the mean monthly flow values, count the number of months in which there was no flow over the entire flow record (percent – spatial).
D_H20	none	days	none	Average high flow duration. Compute the 75th percentile value for the entire flow record. Compute the average duration of flow events with flows above a threshold equal to the 75th percentile value for the median annual flows (days – temporal).
Timing Metrics				
T_H1	$T_H1/365$	none	none	Julian date of annual maximum. Determine the Julian date that the maximum flow occurs for each year; calculated on a circular scale as in T_L1. (Julian day – spatial).

Appendix B: USGS stream gauge data. **Table 1)** USGS gauging stations used as training data for the stream classification system (Chapter 4). All sites are located on the Colorado Plateau and have at least 8 years of continuous flow data. Data are given for a) USGS gauge number, b) gauge name, c) longitude, d) latitude, e) mean daily flow in cubic-feet per second, f) watershed area in square miles, g) first year of stream data, h) last year of stream data, and i) the longest continuous period of streamflow in years.

a)	b) Station Name	c)	d)	e)	f)	g)	h)	i)
9095000	ROAN CREEK NEAR DE BEQUE, CO.	-108.3170	39.4533	25.5	321.0	1962	1972	10
9096800	BUZZARD CREEK BL OWENS CREEK, NR HEIBERGER, CO.	-107.6340	39.2361	25.2	49.7	1956	1970	14
9097500	BUZZARD CREEK NEAR COLLBRAN, CO.	-107.8420	39.3250	46.6	143.0	1922	1980	58
9097600	BRUSH CREEK NEAR COLLBRAN, CO.	-107.8420	39.3250	6.8	9.6	1956	1967	11
9124500	LAKE FORK AT GATEVIEW, CO.	-107.2300	38.2989	233.5	334.0	1938	2005	67
9125000	CURECANTI CREEK NEAR SAPINERO, CO.	-107.4150	38.4878	32.3	35.0	1946	1972	26
9127500	CRYSTAL CREEK NEAR MAHER, CO.	-107.5060	38.5519	29.1	42.2	1946	1955	9
9129600	SMITH FORK NEAR LAZEAR, CO.	-107.7100	38.7075	38.8	166.0	1977	1987	10
9132900	WEST HUBBARD CREEK NEAR PAONIA, CO.	-107.6140	39.0322	3.5	2.3	1961	1973	12
9135900	LEROUX CREEK AT HOTCHKISS, CO.	-107.7320	38.7980	28.8	66.7	1977	1996	19
9137050	CURRANT CREEK NEAR READ, CO.	-107.9390	38.7847	14.6	56.9	1977	1987	10
9140200	KISER CREEK NEAR GRAND MESA, CO.	-107.9440	38.9866	8.2	5.4	1958	1969	11
9140700	COTTONWOOD CREEK NEAR GRAND MESA, CO.	-107.9510	38.9272	1.3	2.2	1958	1968	10
9146400	WEST FORK DALLAS CREEK NEAR RIDGWAY, CO.	-107.8510	38.0736	12.8	14.1	1956	1970	14
9146500	EAST FORK DALLAS CREEK NEAR RIDGWAY, CO.	-107.8140	38.0933	26.4	16.8	1961	1970	9
9146600	PLEASANT VALLEY CREEK NEAR NOEL, CO.	-107.9200	38.1455	2.2	8.2	1956	1967	11
9147000	DALLAS CREEK NEAR RIDGWAY, CO.	-107.7580	38.1778	39.4	97.2	1980	2005	25
9147100	COW CREEK NEAR RIDGWAY, CO.	-107.6450	38.1494	62	45.4	1956	1973	17
9150500	ROUBIDEAU CREEK AT MOUTH, NEAR DELTA, CO.	-108.1620	38.7350	126.3	242.0	1940	1954	14
9151500	ESCALANTE CREEK NEAR DELTA, CO.	-108.2600	38.7566	60.4	209.0	1977	1989	12
9152600	ORCHARD MESA DRAIN AT GRAND JUNCTION, CO.	-108.5720	39.0469	7.7	3.7	1974	1983	9
9152650	LEACH CREEK AT DURHAM, CO.	-108.6080	39.0908	31.4	24.8	1974	1983	9
9152900	ADOBE CREEK NEAR FRUITA, CO.	-108.6970	39.1369	21.9	15.4	1974	1983	9
9153290	REED WASH NEAR MACK, CO.	-108.8040	39.2114	44.4	15.7	1976	2000	24
9153300	REED WASH NEAR LOMA, CO.	-108.7870	39.1836	97.1	29.3	1974	1983	9
9153400	WEST SALT CREEK NEAR MACK, CO.	-108.9840	39.3086	0.9	168.0	1974	1983	9
9163050	BADGER WASH NEAR MACK, CO.	-108.9340	39.2933	6.9	6.5	1974	1982	8
9163310	EAST SALT CREEK NEAR MACK, CO.	-108.8670	39.2972	5.8	197.0	1974	1982	8
9163340	MACK WASH NEAR MACK, CO.	-108.8430	39.2658	25.5	15.9	1974	1982	8
9163490	SALT CREEK NEAR MACK, CO.	-108.8930	39.2216	93.8	436.0	1974	1983	9
9165000	DOLORES RIVER BELOW RICO, CO.	-108.0600	37.6389	135.5	105.0	1952	1996	44
9166950	LOST CANYON CREEK NEAR DOLORES, C0.	-108.4690	37.4461	21.3	71.3	1985	2005	20
9168100	DISAPPOINTMENT CREEK NEAR DOVE CREEK, CO.	-108.5830	37.8767	21.6	147.0	1958	1986	28

a)	b) Station Name	c)	d)	e)	f)	g)	h)	i)
9172000	FALL CREEK NEAR FALL CREEK, CO.	-108.0060	37.9583	24.6	33.4	1942	1959	17
9172500	SAN MIGUEL RIVER NEAR PLACERVILLE, CO.	-108.1320	38.0425	236.4	310.0	1943	2005	62
9173000	BEAVER CREEK NEAR NORWOOD, CO.	-108.1960	37.9700	18.4	40.6	1942	1961	19
9174000	SAN MIGUEL RIVER NEAR NUCLA, CO.	-108.3980	38.2630	249.3	649.0	1954	1962	8
9174500	COTTONWOOD CREEK NEAR NUCLA, CO.	-108.3630	38.2736	4.7	38.8	1943	1951	8
9174600	SAN MIGUEL RIVER AT BROOKS BRIDGE NEAR NUCLA CO	-108.5020	38.2442	243	736.0	1996	2005	9
9175500	SAN MIGUEL RIVER AT NATURITA, CO.	-108.5660	38.2178	308.9	1069.0	1941	1981	40
9175900	DRY CREEK NEAR NATURITA, CO.	-108.6220	38.0922	2.6	78.6	1967	1978	11
9177000	SAN MIGUEL RIVER AT URAVAN, CO.	-108.7130	38.3572	319.6	1499.0	1961	1982	21
9179500	DOLORES RIVER AT GATEWAY, CO.	-108.9800	38.6814	938.4	4347.0	1937	1954	17
9182000	CASTLE CREEK ABOVE DIVERSIONS, NEAR MOAB, UTAH	-109.2660	38.5928	1	7.6	1954	1968	14
9183000	COURTHOUSE WASH NEAR MOAB, UTAH	-109.5800	38.6128	1.7	162.0	1967	1989	22
9183500	MILL CREEK AT SHELEY TUNNEL, NEAR MOAB, UT.	-109.4040	38.4830	12.1	26.8	1983	2000	17
9184000	MILL CREEK NEAR MOAB, UT	-109.5140	38.5622	13.3	74.9	1973	1993	20
9185500	HATCH WASH NEAR LA SAL, UTAH	-109.4400	38.2433	1.6	378.0	1951	1971	20
9186500	INDIAN C AB COTTONWOOD CREEK, NR MONTICELLO, UT	-109.5190	37.9722	4.4	31.2	1950	1971	21
9310000	GOOSEBERRY CREEK NEAR SCOFIELD, UT	-111.3000	39.7158	19	16.8	1941	2003	62
9310500	FISH CREEK ABOVE RESERVOIR, NEAR SCOFIELD, UT	-111.1910	39.7744	48.2	60.1	1939	2005	66
9310700	MUD CREEK BL WINTER QUARTERS CANYON AT SCOFIELD,UT	-111.1610	39.7216	14.8	29.1	1991	2005	14
9312500	WHITE RIVER NEAR SOLDIER SUMMIT, UTAH	-111.0580	39.9222	19.4	52.8	1940	1967	27
9312600	WHITE RIVER BL TABBYUNE C NEAR SOLDIER SUMMIT, UT	-111.0370	39.8758	26.8	75.6	1968	2005	37
9312700	BEAVER CREEK NEAR SOLDIER SUMMIT, UTAH	-110.9690	39.8305	4.6	26.1	1961	1989	28
9312800	WILLOW CREEK NEAR CASTLE GATE, UTAH	-110.7920	39.7769	9.6	62.8	1963	1989	26
9314280	DESERT SEEP WASH NEAR WELLINGTON, UTAH	-110.6460	39.4211	30.1	191.0	1973	1986	13
9315500	SALERATUS WASH AT GREEN RIVER, UTAH	-110.2470	38.9814	3	180.0	1949	1970	21
9316000	BROWNS WASH NEAR GREEN RIVER, UTAH	-110.1300	38.9861	1	75.0	1950	1968	18
9318000	HUNTINGTON CREEK NR HUNTINGTON, UTAH	-111.0640	39.3713	95.3	187.0	1940	1973	33
9328000	SAN RAFAEL RIVER NEAR CASTLE DALE, UTAH	-110.8980	39.1436	113.7	930.0	1948	1964	16
9328100	SAN RAFAEL R AT SAN R BR CAMPGROUND NR C DALE,UT	-110.6660	39.0808	170.9	1284.0	1976	1986	10
9328500	SAN RAFAEL RIVER NEAR GREEN RIVER, UT	-110.3700	38.8583	114.9	1628.0	1946	2005	59
9330500	MUDDY CREEK NEAR EMERY, UT	-111.2490	38.9819	38.2	105.0	1949	2005	56
9331500	IVIE CREEK ABOVE DIVERSIONS NR EMERY, UTAH	-111.4220	38.7583	3.9	50.0	1951	1961	10
9332100	MUDDY CREEK BL I-70 NR EMERY, UTAH	-111.1990	38.8122	31.8	418.0	1974	1986	12
9332500	MUDDY CREEK BELOW IVIE CREEK NR EMERY, UTAH	-111.1290	38.7666	15.4	440.0	1951	1961	10

a)	b) Station Name	c)	d)	e)	f)	g)	h)	i)
9332700	MUDDY CREEK AT DELTA MINE NR HANKSVILLE, UTAH	-110.9540	38.5630	32.7	841.0	1976	1986	10
9333500	DIRTY DEVIL R ABV POISON SP WASH NR HANKSVILLE, UT	-110.4070	38.0942	99.7	4159.0	1949	1992	43
9334000	NORTH WASH NEAR HANKSVILLE (HITE), UTAH	-110.4490	37.8986	1.2	136.0	1951	1970	19
9334500	WHITE CANYON NEAR HANKSVILLE UTAH	-110.3770	37.7986	5.1	276.0	1951	1970	19
9337000	PINE CREEK NEAR ESCALANTE, UT	-111.6360	37.8625	5.5	68.1	1958	2005	47
9337500	ESCALANTE RIVER NEAR ESCALANTE, UT	-111.5750	37.7780	11	320.0	1973	2005	32
9338000	EAST FORK BOULDER CREEK NEAR BOULDER, UTAH	-111.4500	38.0419	24	21.4	1958	1972	14
9340500	WF SAN JUAN R AB BORNS LAKE,NR PAGOSA SPGS, CO.	-106.9300	37.4856	83.3	41.2	1938	1953	15
9341500	WEST FORK SAN JUAN RIVER NR PAGOSA SPRINGS, CO.	-106.9070	37.3919	157	85.4	1937	1960	23
9342500	SAN JUAN RIVER AT PAGOSA SPRINGS, CO.	-107.0110	37.2661	367.8	298.0	1936	2004	68
9344000	NAVAJO R AT BANDED PEAK RANCH, NEAR CHROMO, CO.	-106.6890	37.0853	110	69.8	1938	1994	56
9344300	NAVAJO RIVER ABOVE CHROMO, CO.	-106.7330	37.0320	115.9	96.4	1957	1970	13
9346000	NAVAJO RIVER AT EDITH, CO.	-106.9080	37.0028	119.1	172.0	1935	1995	60
9346400	SAN JUAN RIVER NEAR CARRACAS, CO.	-107.3120	37.0136	612.5	1230.0	1963	2005	42
9354500	LOS PINOS RIVER AT LA BOCA, CO.	-107.6000	37.0094	238.2	520.0	1952	2005	53
9355000	SPRING CREEK AT LA BOCA, CO.	-107.5970	37.0111	31.7	58.2	1952	2005	53
9357500	ANIMAS RIVER AT HOWARDSVILLE, CO.	-107.6000	37.8330	101.6	55.9	1936	1982	46
9358000	ANIMAS RIVER AT SILVERTON, CO.	-107.6590	37.8111	128.5	70.6	1993	2005	12
9358550	CEMENT CREEK AT SILVERTON, CO	-107.6640	37.8197	37.2	20.1	1995	2005	10
9359020	ANIMAS RIVER BELOW SILVERTON, CO	-107.6680	37.7903	276.8	146.0	1992	2005	13
9359500	ANIMAS RIVER ABOVE TACOMA, CO.	-107.7810	37.5703	522.4	348.0	1946	1956	10
9361000	HERMOSA CREEK NEAR HERMOSA, CO.	-107.8450	37.4219	128.2	172.0	1941	1980	39
9361500	ANIMAS RIVER AT DURANGO, CO.	-107.8800	37.2792	787	692.0	1928	2005	77
9362000	LIGHTNER CREEK NEAR DURANGO, CO.	-107.8940	37.6039	22.6	66.0	1928	1949	21
9363100	SALT CREEK NEAR OXFORD, CO.	-107.7530	37.1397	12.5	17.7	1968	1983	15
9363200	FLORIDA RIVER AT BONDAD, CO.	-107.8700	37.0567	75.4	221.0	1968	1983	15
9363500	ANIMAS RIVER NEAR CEDAR HILL, NM	-107.8740	37.0381	924.4	1090.0	1935	2005	70
9364500	ANIMAS RIVER AT FARMINGTON, NM	-108.2020	36.7214	834.7	1360.0	1931	2005	74
9365000	SAN JUAN RIVER AT FARMINGTON, NM	-108.2260	36.7228	2042.3	7240.0	1931	2005	74
9365500	LA PLATA RIVER AT HESPERUS, CO.	-108.0410	37.2897	44	37.0	1918	2005	87
9366000	CHERRY CREEK NEAR RED MESA, CO.	-108.1990	37.1189	9.5	66.0	1929	1950	21
9366500	LA PLATA RIVER AT COLORADO-NEW MEXICO STATE LINE	-108.1890	36.9997	34.8	331.0	1921	2005	84
9367500	LA PLATA RIVER NEAR FARMINGTON, NM	-108.2480	36.7397	27.6	583.0	1939	2003	64
9367561	SHUMWAY ARROYO NEAR WATERFLOW, NM	-108.4410	36.7733	1.5	73.8	1975	1989	14
9367680	CHACO WASH AT CHACO CANYON NATIONAL MONUMENT, NM	-107.9180	36.0286	4.3	578.0	1977	1989	12
9367950	CHACO RIVER NEAR WATERFLOW , NM	-108.5910	36.7244	47.9	4350.0	1977	1994	17

a)	b) Station Name	c)	d)	e)	f)	g)	h)	i)
9368500	WEST MANCOS RIVER NEAR MANCOS, CO.	-108.2580	37.3817	38.1	39.4	1939	1953	14
9369000	EAST MANCOS RIVER NEAR MANCOS, CO.	-108.2310	37.3703	10.7	11.9	1938	1951	13
9369500	MIDDLE MANCOS RIVER NEAR MANCOS, CO.	-108.2310	37.3739	7.5	12.1	1939	1951	12
9371000	MANCOS RIVER NEAR TOWAOC, CO.	-108.7420	37.0275	47.3	526.0	1956	2005	49
9371420	MCELMO CREEK ABOVE ALKALI CANYON, NR CORTEZ, CO.	-108.6490	37.3272	27.4	147.0	1973	1986	13
9371492	MUD CREEK AT STATE HIGHWAY 32, NEAR CORTEZ, CO.	-108.6610	37.3128	7.9	33.6	1985	1997	12
9371500	MCELMO CREEK NEAR CORTEZ, CO.	-108.6730	37.3228	61.5	230.0	1983	1993	10
9371520	MCELMO CREEK ABOVE TRAIL CANYON NEAR CORTEZ, CO	-108.7010	37.3267	55.2	234.0	1994	2005	11
9371700	MCELMO CREEK BELOW CORTEZ, CO.	-108.8060	37.3405	41.6	283.0	1973	1983	10
9372000	MCELMO CREEK NEAR COLORADO-UTAH STATE LINE	-109.0160	37.3242	50.4	346.0	1952	2005	53
9378170	SOUTH CREEK ABOVE RESERVOIR NEAR MONTICELLO, UT	-109.3700	37.8467	1.8	8.6	1986	2005	19
9378200	MONTEZUMA CREEK AT GOLF COURSE AT MONTICELLO, UT	-109.3420	37.8605	3.5	17.6	1980	1992	12
9378630	RECAPTURE CREEK NEAR BLANDING, UT	-109.4770	37.7556	1.3	3.8	1966	2005	39
9378650	RECAPTURE CR BL JOHNSON CR NR BLANDING,UT.	-109.4630	37.6808	8.6	50.2	1976	1993	17
9378700	COTTONWOOD WASH NR BLANDING UTAH	-109.5790	37.5606	9	205.0	1965	1987	22
9379000	COMB WASH NEAR BLUFF, UTAH	-109.6760	37.2661	2.8	278.0	1960	1968	8
9379200	CHINLE CREEK NEAR MEXICAN WATER, ARIZ.	-109.7110	36.9439	28	3650.0	1965	2005	40
9386030	LITTLE COLORADO RIVER AB ZION RES NR ST JOHNS	-109.4070	34.5836	7	1007.0	1976	2005	29
9386950	ZUNI RIVER ABV BLACK ROCK RESERVOIR, NM	-108.7510	35.1009	8.8	848.0	1970	2005	35
9394000	SILVER CR NR WOODRUFF ARIZ	-110.0340	34.7334	19.4	966.0	1936	1946	10
9400562	ORAIBI WASH NR TOLANI LAKE	-110.7740	35.5797	2.8	635.0	1996	2005	9
9400568	POLACCA WASH NR SEC MESA	-110.5620	35.6558	2.7	905.0	1995	2005	10
9400583	JEDDITO WASH NR JEDDITO	-110.4620	35.5764	0.4	147.0	1994	2005	11
9401110	DINNEBITO WASH NR SAND SPRINGS	-110.9330	35.7811	3.7	473.0	1994	2005	11
9401260	MOENKOPI WASH AT MOENKOPI	-111.2020	36.1050	9.7	1629.0	1977	2005	28
9401280	MOENKOPI WASH NEAR TUBA ARIZ	-111.2020	36.1050	23.3	1904.0	1927	1940	13
9401400	MOENKOPI WASH NR TUBA CITY, ARIZ.	-111.3970	36.0236	16.6	2492.0	1941	1953	12
9401500	MOENKOPI WASH NEAR CAMERON, ARIZ.	-111.4220	35.9250	13.8	2662.0	1954	1964	10
9404208	DIAMOND CREEK NEAR PEACH SPRINGS, AZ	-113.3680	35.7650	4.3	279.5	1994	2005	11
9404450	EAST FORK VIRGIN RIVER NEAR GLENDALE, UT	-112.6040	37.3386	18	74.2	1967	2005	38
9404700	EAST FK VIRGIN RIVER NR MOUNT CARMEL JUNCTION, UT	-112.6880	37.2083	16.9	163.0	1993	2002	9
9404900	EAST FORK VIRGIN RIVER NEAR SPRINGDALE, UT	-112.9590	37.1642	57.7	395.0	1992	2005	13
9405420	N FK VIRGIN R BLW BULLOCH CANYON NR GLENDALE	-112.8000	37.4183	19.8	29.6	1975	1984	9
9405500	NORTH FORK VIRGIN RIVER NEAR SPRINGDALE, UT	-112.9790	37.2097	103.6	344.0	1928	2005	77
9406700	SOUTH ASH CREEK BELOW MILL CREEK NEAR PINTURA, UT	-113.3340	37.3639	6.9	11.0	1967	1982	15
9409500	MOODY WASH NEAR VEYO, UTAH	-113.7430	37.4333	2.8	33.0	1956	1968	12

Appendix B - Table 2) USGS gauging stations used as validation data for the stream classification system (Chapter 4). All sites are located on the Colorado Plateau and have less than 8 years of continuous flow data. Data are given for a) USGS gauge number, b) gauge name, c) longitude, d) latitude, and e) watershed area in square miles.

a)	b)	c)	d)	e)
09092800	WEST FORK PARACHUTE CREEK NEAR PARACHUTE, CO.	-108.1430	39.5869	48.10
09094200	ROAN CREEK ABOVE CLEAR CREEK, NEAR DE BEQUE, CO.	-108.3550	39.4911	151.00
09095400	DRY FORK NEAR DE BEQUE, CO.	-108.2620	39.3689	109.00
09124000	HENSON CREEK AT LAKE CITY, CO.	-107.3350	38.0197	83.10
09129000	SMITH FORK AT CRAWFORD, CO.	-107.5760	38.7105	63.10
09129800	CLEAR FORK NEAR RAGGED MOUNTAIN, CO.	-107.4310	39.1433	38.50
09132700	MAIN HUBBARD CREEK NEAR PAONIA, CO.	-107.6300	39.0569	1.33
09132800	MIDDLE HUBBARD CREEK NEAR PAONIA, CO.	-107.6210	39.0494	1.36
09132920	HUBBARD CREEK NEAR BOWIE, CO.	-107.5670	39.0447	20.70
09145500	CANYON CREEK AT OURAY, CO.	-107.6760	38.0197	25.80
09146550	BEAVER CREEK NEAR RIDGWAY, CO.	-107.8180	38.1164	12.20
09167000	LOST CANYON CREEK AT DOLORES, CO.	-108.5020	37.4614	73.50
09170500	WEST PARADOX CREEK NEAR PARADOX, CO.	-108.9970	38.3833	23.60
09171000	WEST PARADOX CREEK NEAR BEDROCK, CO.	-108.8720	38.3300	55.30
09171200	SAN MIGUEL RIVER NEAR TELLURIDE, CO.	-107.8770	37.9481	42.80
09172100	LEOPARD CREEK AT NOEL, CO.	-107.9230	38.1017	9.03
09175400	MAVERICK DRAW NEAR NORWOOD, CO.	-108.3320	38.1755	41.30
09179000	ROC CREEK NEAR URANIUM, CO.	-108.9230	38.4353	75.80
09179200	SALT CREEK NEAR GATEWAY, CO	-108.9710	38.5330	31.20
09181000	ONION CREEK NEAR MOAB, UTAH	-109.3450	38.7250	18.80
09182900	COURTHOUSE WASH AT ARCHES HWY CROSS NR MOAB, UT	-109.5990	38.6486	143.00
09184500	PACK CREEK AT M4 RANCH, NR MOAB, UTAH	-109.3550	38.4361	15.80
09185000	PACK CREEK NEAR MOAB, UTAH	-109.5010	38.5403	57.40
09186000	INDIAN CREEK NEAR MONTICELLO, UTAH	-109.5190	37.8444	4.70
09187000	COTTONWOOD CREEK NEAR MONTICELLO, UTAH	-109.5740	38.0625	115.00
09187500	INDIAN CREEK ABV HARTS DRAW, NR MONTICELLO, UT	-109.6260	38.1517	258.00
09312000	NORTH FORK WHITE RIVER NEAR SOLDIER SUMMIT, UTAH	-111.0670	39.9333	23.30
09314340	GRASSY TRAIL CREEK AT SUNNYSIDE, UTAH	-110.3800	39.5555	40.10
09317000	BOULGER CREEK NEAR FAIRVIEW, UTAH	-111.2670	39.6333	1.90
09325100	SAN RAFAEL R ABOVE FERRON CR NR CASTLE DALE, UT	-110.9090	39.1500	680.00
09330410	BULL CREEK NEAR HANKSVILLE, UT	-110.7600	38.1219	7.53
09331950	CHRISTIANSEN WASH NEAR EMERY, UTAH	-111.2530	38.8614	13.60
09332800	MUDDY CREEK AT MOUTH NR HANKSVILLE, UTAH	-110.7010	38.4028	1552.00
09338500	EAST FORK DEER CREEK NEAR BOULDER, UTAH	-111.3900	38.0014	1.90
09339000	BOULDER CREEK NEAR BOULDER, UT	-111.3840	37.8000	175.00
09339500	ESCALANTE RIVER AT MOUTH NEAR ESCALANTE, UTAH	-110.9040	37.3142	1770.00
09347200	MIDDLE FORK PIEDRA RIVER NR PAGOSA SPRINGS, CO.	-107.1630	37.4867	32.20
09347205	MIDDLE FORK PIEDRA RIVER NEAR DYKE, CO.	-107.1760	37.4528	34.10
09361400	JUNCTION CREEK NEAR DURANGO, CO.	-107.9100	37.3342	26.30

a)	b)	c)	d)	e)
09362550	WILSON GULCH NEAR DURANGO, CO	-107.8430	37.2433	6.50
09367555	SHUMWAY ARROYO NEAR FRUITLAND, NM	-108.3960	36.8064	62.80
09367660	CHACO WASH NR STARLAKE TRADING POST, NM	-107.5280	35.9353	
09367685	AH-SHI-SLE-PAH WASH NEAR KIMBETO, NM	-107.9470	36.1550	8.21
09367710	DE-NA-ZIN WASH NR BISTI TRADING POST, NM	-108.2000	36.2309	183.00
09367930	HUNTER WASH AT BISTI TRADING POST, NM	-108.2540	36.2770	45.60
09367934	TEEC-NI-DI-TSO WASH NR BURNHAM, NM	-108.4570	36.3072	
09367936	BURNHAM WASH NR BURNHAM, NM	-108.4550	36.3531	
09367938	CHACO RIVER NR BURNHAM, NM	-108.5660	36.3658	
09370000	MANCOS RIVER NEAR MANCOS, CO.	-108.2550	37.3572	71.50
09371400	HARTMAN DRAW AT CORTEZ, CO.	-108.6150	37.3239	34.00
09376900	SPRING CREEK ABV DIVERSIONS, NR MONTICELLO, UTAH	-109.4350	37.9194	4.95
09378100	NORTH CREEK ABV. RANGER STAT NR MONTICELLO, UTAH	-109.3670	37.8731	8.68
09378600	MONTEZUMA CREEK NEAR BLUFF, UTAH	-109.3010	37.3000	1154.00
09404115	HAVASU CREEK ABV MOUTH NR SUPAI, ARIZ.	-112.7610	36.3058	
09405200	DEEP CREEK NEAR CEDAR CITY, UT	-112.8840	37.5216	6.72
09405250	EAST FORK DEEP CREEK NR CEDAR CITY, UT	-112.8840	37.5097	7.82
09405300	CRYSTAL CREEK NEAR CEDAR CITY, UTAH	-113.0240	37.5222	10.20
09405400	NF VIRGIN RIVER NEAR GLENDALE, UTAH	-112.7790	37.4728	5.65
09405450	N FK VIRGIN R ABV ZION NARROWS NR GLENDALE	-112.8260	37.3905	41.50
09405900	NORTH CREEK NEAR VIRGIN, UT	-113.1510	37.2372	96.60
09406150	LA VERKIN CREEK NEAR LA VERKIN, UTAH	-113.2850	37.2047	91.30
09406640	LEAP CREEK BELOW MAPLE HOLLOW, NEAR PINTURA, UT	-113.2940	37.3833	9.19
09406900	WET SANDY CREEK NEAR PINTURA, UT	-113.3570	37.3242	5.02

Appendix C: Insect collection locations for Chapter 5. a) sample identification number (1XXXXX are from the USU BugLab and 9999XX are Moline samples), b) site name, c) state, d) latitude, e) longitude, f) sample date, g) sample method (S = surber net, K = kick net, H = Hess net), and h) invertebrate density.

a)	b)	c)	d)	e)	f)	g)	h)
103647	Animas River	CO	37.271	-107.883	10/21/1996	S	131
103649	Animas River	CO	37.268	-107.881	10/21/1996	S	12
103659	Animas River	CO	37.229	-107.852	10/30/1996	S	250
103681	Animas River	CO	37.051	-107.876	11/8/1996	S	203
123966	Animas River at Purple Cliffs	CO	37.222	-107.863	10/7/2004	K	494
123962	Animas River at Weaselskin	CO	37.152	-107.885	10/14/2004	K	487
121014	Arch Creek	UT	37.546	-109.690	9/23/2003	S	23
102601	Beaver Creek	UT	38.676	-109.075	9/14/1994	S	268
117792	Beaver Creek	UT	38.378	-109.175	7/10/2001	S	661
109097	Beaver Creek, Site 1	UT	38.405	-109.190	5/26/1998	S	162
109100	Beaver Creek, Site 2	UT	38.388	-109.169	5/26/1998	S	51
110349	Birch Creek	UT	37.764	-111.696	5/10/1999	K	235
999901	Birch Creek, Zion NP	UT	37.241	-112.969	10/28/2004	H	32
110167	Blue Spring Creek at Hell's Backbone Road	UT	37.963	-111.656	6/13/1999	K	384
114070	Boulder Creek at Hwy 12	UT	37.901	-111.437	7/4/2000	K	533
116933	Boulder Creek, off Hwy 12 near Calf Creek CG	UT	37.812	-111.394	4/12/2001	S	580
100418	Bull Creek	UT	38.100	-110.700	8/25/1993	S	144
102731	Bull Creek	UT	38.100	-110.850	9/13/1995	S	137
108862	Bull Creek	UT	38.168	-110.740	7/8/1997	S	31
111386	Calf Creek above upper falls	UT	37.854	-111.453	2/19/2000	K	610
999902	Calf Creek in Calf Creek Campground, GSENM	UT	37.799	-111.413	10/26/2004	H	1833
121431	Calf Creek, at mouth	UT	37.776	-111.419	5/12/2003	S	672
111837	Calf Creek, downstream from bridge, near HWY 12	UT	37.793	-111.413	3/28/2000	K	537
119501	Calf Creek, downstream from Lower Falls	UT	37.829	-111.419	6/24/2002	S	575
114093	Calf Creek, just downstream from upper falls	UT	37.855	-111.451	9/12/2000	K	534
121012	Castle Creek, below 2nd trail crossing	UT	38.661	-109.441	8/27/2003	S	306
119890	Castle Creek, downstream from second trail sign	UT	38.663	-109.440	8/14/2002	S	317
121013	Castle Creek, just above diversion	UT	38.670	-109.449	8/27/2003	S	98
119891	Castle Creek, upstream from diversion	UT	38.672	-109.449	8/14/2002	S	175
109108	Chicken Creek, Site 1	UT	38.405	-109.165	5/27/1998	S	26
109111	Chicken Creek, Site 2	UT	38.395	-109.163	5/26/1998	S	3
999904	Cottonwood Creek downstream site	UT	37.250	-111.917	11/18/2004	H	0
999905	Courthouse Wash Arches NP	UT	38.648	-109.602	10/11/2005	H	53
110870	Coyote Gulch at mouth	UT	37.428	-111.981	5/26/1999	K	31
111811	Coyote Gulch downstream from Hamblin Arch	UT	37.420	-111.040	4/2/2000	K	70
999906	Coyote Gulch GSENM	UT	37.430	-111.112	11/2/2005	H	10
115746	Cross Canyon	CO	37.478	-109.042	4/12/2001	S	630
110171	Death Hollow Creek at Boulder Mail Trail	UT	37.844	-111.521	6/14/1999	K	340
110876	Death Hollow Creek, 2 mi upstream Escalante River	UT	37.805	-111.511	5/28/1999	K	382
110173	Deep Creek, 2 miles E of Posy Lake	UT	37.936	-111.666	6/13/1999	K	378
102322	Deer Creek	UT	38.500	-111.300	7/13/1982	S	1187

a)	b)	c)	d)	e)	f)	g)	h)
114087	Deer Creek, downstream from campground	UT	37.855	-111.355	9/11/2000	K	226
124115	Dry Creek	CO	38.535	-108.064	5/26/2004	S	1426
100424	Dugout Creek	UT	38.093	-110.876	8/26/1993	S	72
117497	East Fork Virgin River	UT	37.334	-112.601	3/28/2001	H	598
999908	East Fork Virgin River (Parunaweep Zion NP)	UT	37.161	-112.970	11/16/2004	H	52
110304	Escalante River	UT	37.500	-111.042	5/17/1999	S	72
110306	Escalante River	UT	37.333	-110.917	5/19/1999	S	295
114391	Escalante River	UT	37.660	-111.215	9/15/2000	S	567
114393	Escalante River	UT	37.449	-110.980	9/14/2000	S	186
119100	Escalante River @ mouth of Fence Canyon	UT	37.023	-111.992	10/9/2002	S	197
111203	Escalante River above Sand Crk.	UT	37.776	-111.459	1/4/2000	K	45
110350	Escalante River at Birch Creek and North Creek	UT	37.765	-111.684	5/10/1999	K	213
114102	Escalante River at Boulder Creek confluence	UT	37.758	-111.350	9/13/2000	K	26
111849	Escalante River at bridge north of Escalante town	UT	37.776	-111.593	3/29/2000	K	55
119486	Escalante River at Hwy 12 Bridge	UT	37.776	-111.419	6/18/2002	S	497
119504	Escalante River at the mouth of Fence Canyon	UT	37.613	-111.178	6/25/2002	S	485
119488	Escalante River near Escalante Cemetery trailhead	UT	37.776	-111.579	6/19/2002	S	471
115130	Escalante River upstream from Calf Creek	UT	37.776	-111.418	10/12/2000	K	566
999909	Escalante River upstream from Calf Creek confluence	UT	37.778	-111.423	10/27/2004	H	80
110351	Escalante River upstream from Mamie Creek	UT	37.781	-111.523	5/12/1999	K	342
120158	Escalante River, 3.5 mi west of town at wier gage	UT	37.773	-111.666	10/9/2002	H	62
123969	Florida Creek Mouth	CO	37.050	-107.867	10/19/2004	K	478
103688	Florida River	CO	37.050	-107.874	11/9/1996	S	358
110189	Forty Mile Creek	UT	37.342	-111.006	6/11/1999	K	347
109113	Geyser Creek, Site 1	UT	38.479	-109.211	9/15/1998	S	22
109117	Geyser Creek, Site 2	UT	38.465	-109.143	5/27/1998	S	21
109120	Geyser Creek, Site 2A	UT	38.460	-109.145	5/27/1998	S	71
109127	Geyser Creek, Site 3	UT	38.493	-109.096	9/15/1998	S	57
120186	Gordon Creek	UT	39.613	-110.935	8/30/2002	S	65
120189	Gordon Creek	UT	39.617	-110.949	8/30/2002	S	25
117036	Gulch Creek upstream from Burr Trail bridge	UT	37.865	-111.313	9/20/2001	S	80
999910	Hackberry Canyon at mouth GSENM	UT	37.260	-111.916	11/19/2004	H	0
116981	Hackberry Creek	UT	37.322	-111.916	5/7/2001	K	429
999911	Halls Creek upstream of narrows Capitol Reef NP	UT	37.634	-110.891	10/24/2004	H	2
111847	Harris Wash at mouth	UT	37.663	-111.215	3/30/2000	K	23
110873	Harris Wash, 0.5 near NRA boundary	UT	37.642	-111.290	5/27/1999	K	334
116983	Hogeye Creek	UT	37.312	-111.987	5/8/2001	K	189
111003	Hungry Creek upstream from Pine Creek	UT	37.917	-111.645	6/26/1999	K	319
120173	Huntington Creek	UT	39.362	-111.043	10/27/2002	H	729
121451	Indian Creek	UT	37.492	-109.521	4/8/2003	S	230
999913	Indian Creek upstream of bridge to Canyonlands NP	UT	38.151	-109.626	10/3/2004	H	219
999912	Indian Creek upstream of Newspaper Rock Campground	UT	37.987	-109.518	10/4/2004	H	48
123524	Johnson Creek	UT	37.798	-109.511	10/22/2004	S	465
999914	Kanab Creek upstream of Animal Friends Shelter	UT	37.148	-112.539	11/15/2004	H	30
119888	Kane Springs Creek near hole in the rock	UT	38.392	-109.455	8/1/2002	S	654
117793	La Sal Creek above fish barrier	UT	38.392	-109.208	7/12/2001	S	613

a)	b)	c)	d)	e)	f)	g)	h)
999915	La Verkin Creek Zion NP	UT	37.405	-113.182	10/18/2005	H	173
110855	Lake Creek	UT	37.923	-111.524	5/22/1999	K	312
110175	Lake Creek at confluence with Sand Creek	UT	37.868	-111.495	6/15/1999	K	395
109087	LaSal Creek, Site 2	UT	38.385	-109.209	9/14/1998	S	101
109093	LaSal Creek, Site 3	UT	38.368	-109.179	5/26/1998	S	35
118921	LaVerkin Creek upstream of confluence with Virgin River	UT	37.216	-113.279	6/14/2002	S	100
999916	Left Fork of North Creek Zion NP	UT	37.290	-113.085	10/20/2005	H	493
121467	Lower Floy Wash	UT	38.962	-109.906	4/10/2003	S	8
123526	Lower Indian Creek at Shay Mountain Road	UT	37.900	-109.533	10/21/2004	S	96
110980	Lower Steep Creek	UT	37.866	-111.317	6/22/1999	K	332
111833	Mamie Creek at mouth	UT	37.781	-111.505	3/31/2000	K	526
124038	Mesa Creek	CO	38.451	-108.823	5/28/2003	S	965
102602	Mill Creek	UT	38.500	-109.400	9/29/1994	S	315
123530	Mill Creek	UT	38.509	-109.286	10/20/2004	S	638
121006	Mill Creek - north fork above 1st waterfall	UT	38.559	-109.501	7/29/2003	S	81
999917	Mill Creek (south fork) near Moab UT	UT	38.563	-109.508	10/7/2004	H	66
121021	Mill Creek above diversion at new gauging station	UT	38.480	-109.404	10/9/2003	S	178
121010	Mill Creek at Hidden Valley	UT	38.537	-109.466	7/30/2003	S	192
999918	Mill Creek below waterfall (north fork) near Moab UT	UT	38.566	-109.506	11/21/2004	H	281
121455	Mill Creek upstream from diversion	UT	38.484	-109.408	4/8/2003	S	953
123531	Muddy Creek	UT	38.997	-111.261	10/15/2004	S	121
119889	Negro Bill Canyon	UT	38.609	-109.533	8/2/2002	S	7
121463	Negro Bill Canyon	UT	38.608	-109.531	4/9/2003	S	517
999919	Negro Bill Canyon near Moab UT	UT	38.610	-109.532	10/8/2004	H	19
121028	North Cottonwood Creek at Beef Basin Road Crossing	UT	37.997	-109.596	11/20/2003	S	147
999920	North Cottonwood Creek near Indian Creek UT	UT	38.030	-109.590	10/6/2004	H	40
100509	North Creek	UT	37.254	-113.131	10/23/1984	S	145
100516	North Creek	UT	37.250	-113.139	9/22/1982	S	451
117790	North Creek	UT	37.876	-109.446	7/3/2001	S	634
119496	North Creek	UT	37.778	-111.708	6/21/2002	S	620
110177	North Creek, upstream from reservior	UT	37.847	-111.758	6/13/1999	K	392
121449	North Fork Cottonwood Creek	UT	37.990	-109.599	4/8/2003	S	567
124043	North Fork Mesa Creek	CO	38.504	-108.790	5/22/2003	S	1093
999921	Oak Creek upstream of diversion in Capitol Reef NP	UT	38.084	-111.139	10/6/2005	H	21
121461	Onion Creek - Upper	UT	38.711	-109.324	4/9/2003	S	16
121027	Onion Creek #1 just above Hwy 128 bridge	UT	38.727	-109.348	11/12/2003	S	17
121018	Onion Creek #2 at 6th road crossing	UT	38.713	-109.328	9/24/2003	S	3
121026	Onion Creek #3, 100' above narrows entrance	UT	38.704	-109.314	11/7/2003	S	4
121004	Onion Creek #4, where road leaves canyon	UT	38.713	-109.255	7/25/2003	S	123
121459	Onion Creek upstream from bridge	UT	38.730	-109.347	4/9/2003	S	11
123534	Pack Creek	UT	38.435	-109.353	10/20/2004	S	258
121060	Parunuweap East Fork of Virgin River - Downstream #1	UT	37.177	-112.786	6/5/2003	S	96
121062	Parunuweap East Fork of Virgin River - Downstream #2	UT	37.176	-112.792	6/5/2003	S	107
121054	Parunuweap East Fork of Virgin River - Upstream #1	UT	37.219	-112.648	6/5/2003	S	23
121057	Parunuweap East Fork of Virgin River - Upstream #2	UT	37.219	-112.680	6/5/2003	S	50
111005	Pine Creek at Lower Box Trailhead	UT	37.864	-111.635	6/27/1999	K	480

a)	b)	c)	d)	e)	f)	g)	h)
121444	Pine Creek below lower box trailhead	UT	37.816	-111.608	5/15/2003	S	502
111001	Pine Creek between upper and lower trailheads	UT	37.934	-111.643	6/26/1999	K	342
121442	Pine Creek near upper trailhead	UT	37.963	-111.652	5/15/2003	S	781
102759	Pleasant Creek	UT	38.200	-111.070	9/12/1995	S	36
999922	Pleasant Creek upstream of 4WD road, Capitol Reef NP	UT	38.181	-111.183	10/9/2004	H	31
124047	Potter Creek	CO	38.634	-108.194	5/20/2003	S	465
124035	Roubideau Creek upstream from Potter Creek	CO	38.638	-108.194	5/27/2003	S	458
121871	Salt Creek	CO	39.226	-108.893	10/29/2003	H	290
124041	San Miguel River at Tabeguache	CO	38.358	-108.708	7/21/2003	S	17
999923	San Miguel River at TNC Tabeguache Preserve Ranch	CO	38.304	-108.661	11/14/2004	H	247
124049	San Miguel River upstream from Dolores	CO	38.388	-108.787	9/24/2003	S	362
124034	San Miguel River upstream from Tabequache Creek	CO	38.339	-108.702	5/30/2003	S	627
110169	Sand Creek at Lake Creek confluence	UT	37.867	-111.495	6/15/1999	K	435
110354	Sand Creek at mouth	UT	37.775	-111.458	5/12/1999	K	243
110179	Sand Creek upstream from Boulder Mail Trail	UT	37.867	-111.496	6/15/1999	K	346
110994	Sheep Creek upstream from spillway	UT	37.496	-112.066	6/25/1999	K	245
100440	South Creek	UT	38.053	-110.871	9/1/1993	S	1124
109095	South Fork Beaver Creek	UT	38.393	-109.190	5/26/1998	S	73
124037	South Fork Mesa Creek	CO	38.450	-108.803	5/29/2003	S	264
119290	Spring Creek	CO	38.381	-107.954	5/30/2002	S	774
999924	Sulfur Creek upstream of confluence Capitol Reef NP	UT	38.303	-111.306	10/6/2005	H	63
117044	Sweetwater Creek	UT	37.868	-111.494	9/2/2001	S	232
111819	The Gulch at mouth	UT	37.725	-111.296	4/4/2000	K	544
999925	Trachyte Creek upstream of highway	UT	37.958	-110.578	10/8/2005	H	78
999907	tributary to Deer Creek GSENM	UT	37.846	-111.373	11/3/2005	H	807
123970	Twin Crossing on Animas River, up from Florida Creek	CO	37.030	-107.879	10/18/2004	K	480
124036	Upper Gunnison River downstream of confluence with NF	CO	38.783	-107.836	6/12/2003	S	65
117791	Upper Indian Creek above Blanding Tunnel	UT	37.844	-109.500	7/8/2001	S	302
121453	Upper Kane Springs	UT	38.393	-109.454	4/8/2003	S	368
109083	Upper LaSal Creek	UT	38.404	-109.228	9/14/1998	S	198
116975	Upper Sand Creek	UT	37.863	-111.489	5/6/2001	K	247
110978	Upper Steep Creek	UT	37.873	-111.323	6/22/1999	K	376
110988	Vinson Creek, trib to Deer Creek, off Burr Trail	UT	37.848	-111.374	6/24/1999	K	294
118490	Virgin River downstream from Zion Narrows	UT	37.285	-112.948	10/17/2001	H	530
123739	Virgin River upstream from Laverkin Creek	UT	37.203	-113.287	11/2/2004	S	39
118493	Virgin River, East Fork upstream from North Fork	UT	37.163	-113.010	10/18/2001	H	384
110982	Water Canyon Creek	UT	37.915	-111.292	6/23/1999	K	207
110984	Water Canyon Creek upstream from The Gulch	UT	37.904	-111.285	6/23/1999	K	386
121618	West Creek	CO	38.724	-108.910	12/5/2003	S	922
121619	West Creek	CO	38.775	-108.891	12/5/2003	S	832
116188	White Creek, Dixie N.F.	UT	37.886	-111.784	8/23/2000	S	458
116930	Willis Creek above Skutumpah Road	UT	37.483	-112.097	4/12/2001	S	8
116973	Willow Patch Creek	UT	37.824	-111.450	5/5/2001	K	199
110995	Yellow Creek upstream from old homestead	UT	37.535	-112.063	6/25/1999	K	26
115744	Yellow Jacket Creek	CO	37.439	-108.790	4/10/2001	S	662
121424	Yellow Jacket Creek	CO	37.365	-108.950	5/24/2003	S	626
115745	Yellow Jacket Creek - Lower	CO	37.363	-108.953	4/12/2001	S	553

Appendix D: .Presence / absence of insect taxa at 24 stream sites. Location details are given in Table 3.1. Sites: 1 Birch Creek, 2 Calf Creek, 3 Cottonwood Creek #2, 4 Courthouse Wash, 5 Coyote Gulch, 6 Deer Creek, 7 East Fork Virgin River, 8 Escalante River, 9 Hackberry Canyon, 10 Hall's Creek, 11 Indian Creek #1, 12 Indian Creek #2, 13 Kanab Creek, 14 La Verkin Creek, 15 Left Fork of North Creek, 16 Mill Creek, 17 Left Fork of Mill Creek, 18 Negro Bill Canyon, 19 North Cottonwood Creek, 20 Oak Creek, 21 Pleasant Creek, 22 San Miguel River, 23 Sulfur Creek, and 24 Trachyte Creek.

Order	Family	Genus and Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Ephemeroptera																										
	Baetidae					X	X					X									X	X				
		Acentrella sp.								X			X											X		
		Baetis sp.				X		X					X			X	X	X			X	X	X	X	X	
		B. bicaudatus		X			X	X	X	X			X	X		X	X				X		X	X		
		B. flavistriga																X	X				X	X		
		B. notos																	X				X			
		B. tricaudatus	X	X			X	X	X	X			X	X		X	X	X		X	X	X	X	X	X	X
		Callibaetis sp.	X	X		X	X										X		X		X		X			
	Ephemerellidae								X													X				X
		Drunella grandis											X										X			
		Ephemerella sp.											X										X	X		
	Leptohyphidae	*Tricorythodes minutus*		X						X							X							X		
	Leptophlebiidae		X																X							
	Heptageniidae							X					X											X		
		Rhithrogena sp.											X										X			
		R. hageni																					X			
Odonata																										
	Aeshnidae	*Anax sp.*	X																							
	Calopterygidae	*Hetaerina sp.*	X																							
	Coenagrionidae																									
		Argia sp.	X															X	X							
		Enallagma sp.	X												X				X		X					X
	Corduliidae	*Somatochlora sp.*	X																							
	Gomphidae	*Ophiogomphus severus*		X																						

Order	Family	Genus and Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Plecoptera																										
	Capniidae												X	X		X	X		X				X	X	X	
	Chloroperlidae									X			X						X				X			
	Leuctridae			X																			X			
	Nemouridae															X			X							
	Perlidae	*Claassenia sabulosa*																						X		
	Perlodidae																		X					X		
		Isogenoides sp.																					X	X		
		Isoperla sp.																					X	X		
	Taeniopterygidae								X	X														X		
		Taenionema sp.		X						X									X					X		
Hemiptera																										
	Corixidae																				X					
	Veliidae																									
		Microvelia sp.					X																			
		Rhagovelia sp.								X									X							
Megaloptera																										
	Corydalidae	*Corydalus cornutus*							X									X	X							
Trichoptera																										
	Brachycentridae																									
		Brachycentrus americanus		X				X		X							X						X			
		Micrasema sp.															X					X				
	Glossosomatidae								X																	
		Culoptila sp.																					X			
	Hydropsychidae			X						X			X					X					X	X	X	X
		Cheumatopsyche sp.	X														X							X		
		Hydropsyche sp.						X	X				X	X	X	X				X		X		X	X	X

Order	Family	Genus and Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Trichoptera cont.																										
	Hydroptilidae							X											X	X			X			
		Hydroptila sp.		X				X					X											X		
		Leucotrichia pictipes						X												X				X		
	Hydroptilidae	*Ochrotrichia sp.*						X																		
	Leptoceridae	*Oecetis sp.*	X														X						X			
	Limnephilidae							X											X							
		Grammotaulius sp.																X								
	Philopotamidae	*Chimarra sp.*																	X				X			
	Polycentropodidae	*Polycentropus sp.*	X														X									
	Psychomyiidae																X									
		Tinodes sp.		X																						
Lepidoptera																										
	Pyralidae	*Petrophila sp.*		X					X									X		X				X		
Coleoptera																										
	Dytiscidae	*Dytiscidae sp.*	X					X																		
	Elmidae			X						X							X				X					
		Dubiraphia sp.																	X							
		Heterelmis sp.	X														X		X							
		Ordobrevia nubifera		X															X					X		
	Gyrinidae	*Dineutus sp.*	X																							
Diptera																										
	Ceratopogonidae	*Bezzia/Palpomyia sp.*				X							X								X			X		
	Chironomidae		X	X		X	X	X		X	X	X	X	X	X	X	X	X			X		X	X	X	X
	Empididae	*Hemerodromia sp.*	X	X												X			X				X		X	
	Muscidae					X		X								X										
	Simuliidae		X	X		X	X	X	X	X		X		X	X	X	X	X	X	X	X	X	X	X	X	