

DISSERTATION

THE DISTRIBUTION OF LOTIC INSECT TRAITS IN RELATION TO REFERENCE
CONDITIONS AND PROJECTED CLIMATE CHANGE IN THE WESTERN UNITED
STATES

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ABSTRACT

THE DISTRIBUTION OF LOTIC INSECT TRAITS IN RELATION TO REFERENCE CONDITIONS AND PROJECTED CLIMATE CHANGE IN THE WESTERN UNITED STATES

The use of species traits (e.g., life history, morphological, physiological, or ecological characteristics of an organism) to describe community responses to environmental change has become a common practice in stream ecosystems, with over 900 papers describing macroinvertebrate trait-environment relationships in streams. The use of traits provides some advantages over traditional taxonomic metrics, such as providing a mechanistic link between an organism and its environment, but also presents some challenges, such as many traits being correlated with other traits and multiple environmental variables. Various methods have been recommended to address these challenges, such as using multiple traits, posing *a priori* hypotheses, and evaluating streams across large-spatial scales. The vast majority of studies have not incorporated these recommendations, however, particularly in North America. My research had two general objectives: 1) describe the dominant trait-environmental relationships in natural streams in the western United States and 2) use two distinct traits-based methods to evaluate how stream aquatic insect communities are currently distributed in terms of multiple environmental variables and how species and communities may respond to climate change.

Traits are often used to evaluate the ecological integrity of streams and a baseline understanding of aquatic insect trait-environment relationships is needed for the western United States. I used logistic regression, multinomial regression, and redundancy analysis to explore the

relationships between 20 trait distributions and 83 environmental variables in 253 least-disturbed streams across 12 western states. Traits had the strongest relationships with regional climate and local stream habitat conditions (e.g., air temperature, conductivity, mean annual runoff) rather than elevation, land use, or measures of extreme hydrological events. Traits such as thermal tolerance, size, swimming strength, rheophily, voltinism, and armoring exhibited strong relationships with the environmental data and would be ideal for large-scale stream assessments.

Aquatic insect communities contain many taxa that are sensitive to temperature increases and changes to runoff. Two traits, cold water preference and erosional obligate (i.e., needs to live in fast-water habitat) have been used in the past to estimate the effect of climate change on stream insect communities, but no study has accounted for both climatic and non-climatic effects on these two traits. I developed a Bayesian path analysis describing how the distributions of these two traits respond to multiple environmental gradients, not just temperature, and discovered that the distribution of cold-adapted taxa was strongly correlated with changes in air temperature in the wet, cool ecoregions, but was correlated with thermal buffers and refuges in most dry, warm ecoregions, indicating that temperature-sensitive taxa are likely on the brink of their thermal tolerance in those ecoregions. A second approach to assess community sensitivity to climate change is to determine the specific thermal tolerance of each taxon individually. I computed the thermal and stream runoff thresholds of common stream taxa and compared the World Climate Research Programme's climate model predictions to these thresholds. I found that the stream communities most at risk to climate change were found in some dry ecoregions, concurring with the previous results, and in wet, warm ecoregions with a high proportion of spatially restricted and endemic taxa, such as northern California. These two approaches describe possible mechanisms of climate change resistance and identify sensitive ecoregions.

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CHAPTER 1: THE USE OF MACROINVERTEBRATE TRAITS IN LOTIC SYSTEMS: A
SHORT REVIEW OF THE HISTORY OF TRAIT RESEARCH IN STREAMS AND AN
ASSESSMENT OF STUDY CHARACTERISTICS

Summary

Traits-based descriptors of communities (e.g., proportion of taxa in the community that are small, breathe with gills, or are predators) have some distinct advantages over more traditional taxonomic descriptors (e.g., proportion of individuals in the community that are of the genus *Baetis*). Traits provide a mechanistic, causal link between biology and environment, are more spatially and temporally consistent, and have the ability to distinguish the effects of multiple environmental variables on the stream community. There are specific challenges that arise from using traits-based approaches, however, including correlations with other traits and environmental variables, issues with trait assignment and trait designation, and trait tradeoffs. These challenges can be mitigated by using multiple traits, multiple environmental variables, multivariate statistical analyses, *a priori* predictions, the appropriate spatial scale, and incorporating natural or near-natural stream conditions. Studies comparing aquatic insect trait distributions to environmental conditions in streams have been around for almost 40 years. Many of these studies have aimed to use trait distributions in an applied context by discriminating the effect of human disturbance on stream systems. I reviewed 905 trait studies in lotic ecosystems and found that the majority of studies were conducted in small or medium streams and found in one geo-political region, usually the temperate climatic regions in North America and Europe. The vast majority of studies focused on the Functional Feeding Group trait and measures of human disturbance, possible food sources, and habitat or substrate

characteristics. Very few studies (6) incorporated the suggested techniques (e.g., multiple traits, multivariate statistics) to deal with the challenges of using traits.

Introduction

One of the fundamental goals of ecology is to comprehend the underlying causes of species distribution and abundance (Begon et al. 2006). Organismal, population, community, and ecosystem ecology have developed various approaches to address this goal, most incorporating some component of species interactions with their abiotic or biotic environment (Begon et al. 2006, McGill et al. 2006, but see Hubbell 2001). If an organism's fitness, and ultimately the evolutionary success of the species, is determined by its interactions with the surrounding environment and other biota, then the organism's traits will arbitrate the effect of those interactions. Traits are behavioral, morphological, physiological, or ecological characteristics of an organism and can be continuous characteristics (e.g., size), but are often defined categorically (e.g., small, medium, large) with each trait category referred to as a state. Traits have long been important components of ecological theory since the earliest developments of ecology as a formal discipline. Stutzner et al. (2001b) highlighted three historical and theoretical pathways that integrated species traits. First, early ecologists understood that traits are constrained by environmental conditions and biological interactions (Forbes 1887, Steinmann 1907). Second, the relationship between a species traits and environmental conditions determines the spatial and temporal niche in which the species can operate (Shelford 1913, Grinnell 1917, Pearse 1926, Elton 1927). Third, early demographic studies formalized the concepts of growth and resource use and lead to the concept of traits-based ecological strategies, such as the r-K concept by MacArthur and Wilson (1967). Stutzner et al. (2001b) contended that

these three theoretical pathways culminated in the habitat template concept by Southwood (1977, 1988). Southwood argued that the spatial and temporal habitat provides a template that selects for specific species traits and drives evolution. Traits and ecological strategies evolve from organisms adapting to variations in habitat stability and resource availability, resulting in organisms sorted along environmental gradients according to their traits (Webb et al. 2010).

Species traits have long been an important component of ecological theory, but traits have traditionally been used in conjunction with taxonomy. For example, the traits of an individual organism or a species may have been used to evaluate that organism's fitness or distribution. In this case, traits were an important component of the analysis, but the focus was on the taxonomic unit. Recently, however, community-level measures of traits have been proposed as an alternative to taxonomic-based approaches in community ecology (McGill et al. 2006), focusing on the distribution and abundance of specific traits or trait states in a community instead of the distribution or fitness of a taxonomic unit. The use of traits *in lieu* of taxonomy is appealing because it is theoretically grounded in niche theory (Chase and Leibold 2003, McGill et al. 2006) and has the potential to develop a more universal theoretical understanding of community composition. For example, while taxonomic composition in a community type, such as stream systems, changes over a landscape due to geographic and evolutionary constraints, traits are omnipresent by definition, and should be more closely aligned to changes to environmental conditions in streams. Therefore, community trait distributions should be similar in streams or rivers with similar environmental conditions, irrespective of proximity between sites. The one exception to this argument is the presence of phylogenetically constrained traits, traits found only in particular groups of taxa, where trait distributions become dependent on taxa present in the community Poff et al. (2006). But, the general application of phylogenetically

unconstrained traits would allow for the possibility of predicting community responses along existing gradients of environmental conditions or to new environmental conditions facilitated by anthropogenic disturbance, climate change, or taxa invasion, irrespective of the specific taxonomic designations. McGill et al. proposed this concept in 2006, but traits have been used in this fashion in streams for over 40 years.

Early examples exist of trait usage in stream ecology, particularly with feeding groups (e.g., Nelson and Scott 1962, Minshall 1967) and organic pollution tolerance (e.g., Kolkwitz and Marsson 1909), but the formalized use of community-level, traits-based analyses in stream ecosystems stems from two distinct developments in stream ecology. The first was the development of functional feeding groups (FFG) by K. W. Cummins (Cummins 1973, Cummins and Klug 1979) and their incorporation into the theoretical framework of the River Continuum Concept (RCC; Vannote et al. 1980). Taxa were assigned to functional feeding groups based on mouth morphology and food acquisition and were included in the first edition of *An introduction to the aquatic insects of North America* (Merritt and Cummins 1978), which became the standard text in aquatic insect identification for North America and many other parts of the world. The RCC incorporated Southwood's ideas into stream systems and predicted distributions of FFGs along a stream continuum, from small, heavily shaded streams to large, open rivers. Thus, FFGs and the RCC provided the first widely available trait database and the first specific, theoretical, *a priori* predictions to test trait-environmental relationships in streams. The 1980s saw a series of studies that tested RCC predictions of FFG distributions, particularly predictions related to stream order (e.g., Hawkins and Sedell 1981, Marchant et al. 1985, Bruns et al. 1987), habitat type (e.g., Benke et al. 1984, Huryh and Wallace 1987), and food availability/distribution (e.g., Hawkins et al. 1982, Cowan and Oswood 1984, McDowell and Naiman 1986, Dudgeon 1989).

Studies also began to look at the influence of anthropogenic disturbance on functional feeding group distributions (e.g., Hawkins et al. 1982, Kondratieff et al. 1984, Specht et al. 1984, Rabeni et al. 1985). Functional Feeding Groups also became an integral component in U.S. stream bioassessment protocols (Plafkin et al. 1989, Barbour et al. 1999) and the use of FFG in conjunction with taxonomic metrics in bioassessment is a common practice today, often used in a univariate fashion, tracking the response of a single trait-state to a single environmental stressor.

The second development that expanded and formalized the use of traits in streams was the adaptation of Southwood's habitat template theory to stream disturbance by Townsend and Hildrew (1994), which made specific theoretical predictions about trait distributions in streams according to a spatial and temporal disturbance template (see also Poff and Ward 1990). The habitat concept was further adapted to the structure of stream systems by Poff (1997), filtering the regional species pool according to the interactions between traits and the hierarchical structure of streams. These papers provided a theoretical framework to test *a priori* hypotheses about trait distributions according to variation in natural environmental conditions as well as anthropogenic influences. The theoretical developments at this time focused on detecting the responses of multiple traits to multiple natural and anthropogenic disturbance gradients. Additionally, multiple trait databases were developed during this time period (e.g., Tachet et al. 1991, Thorp and Covich 1991, Moog 1995, Merritt and Cummins 1996, Tachet et al. 2000, Poff et al. 2006), making trait data more accessible. Theoretical underpinnings and abundant trait data provided ideal conditions for an explosion in trait research and applications to stream bioassessment.

Townsend and Hildrew's application of the habitat template was first tested in New Zealand (Scarsbrook and Townsend 1993, Townsend et al. 1997) and along the Rhône River in Europe (Juget and Lafont 1994, Marmonier et al. 1994, Resh et al. 1994, Richoux 1994, Tachet et al. 1994, Usseglio-Polatera 1994, Usseglio-Polatera and Tachet 1994). While these multi-trait, often multivariate, analyses had mixed results, the researchers from the 1994 Rhône study began to test the merits of applying traits-based metrics to bioassessment techniques. Charvet et al. (1998) and Dolédec et al. (1999) compared traits-based metrics to more traditional taxonomic metrics in small regional systems in Europe and found that traits-based metrics performed as well or better than taxonomic metrics, indicating that traits may be a more effective bioassessment tool. The next step in applying traits-based metrics to bioassessment was to determine how traits respond to environmental gradients in natural or semi-natural streams, establishing a baseline understanding of trait distributions against which anthropogenic disturbances may be judged. Charvet et al. (2000) assessed environment-trait relationships and trait stability across sites in semi-natural French streams and Statzner et al. (2001a, 2005) expanded this research to least-impacted or near-natural streams across Europe. From these baseline studies, more recent studies have focused on the impact of various forms of disturbance on the trait composition of stream communities in Europe and New Zealand (e.g., Gayraud et al. 2003, Bonada et al. 2006, Dolédec et al. 2006, Lecerf et al. 2006, Bonada et al. 2007b, Dolédec and Statzner 2008, Statzner et al. 2008, Dolédec et al. 2011, Feio and Dolédec 2012). This multi-trait approach has been used, to lesser extent, in North America (e.g., Richards et al. 1997, Finn and Poff 2005, Bêche et al. 2006, Griswold et al. 2008, Tullos et al. 2009), although the majority of these studies have covered small areas, usually within a single ecoregion or state.

These two developmental pathways of trait research in streams has resulted in two distinct approaches in stream bioassessment, 1) a univariate approach incorporating one or two traits, usually as a small part of an overall bioassessment index, and 2) an often standalone traits-based bioassessment, incorporating multiple traits and multiple environmental gradients, often assessed using multivariate statistics. Traits-based community ecology research in streams has recently been reviewed by multiple authors, although most reviews focus solely on the multivariate, multiple trait development process in Europe. Wallace and Webster (1996) summarized the then current theoretical underpinnings of functional feeding group distribution, Resh and Rosenberg (2010) highlighted the development and use of traits in life history research, and Statzner and Bêche (2010) discussed technical aspects of trait research in streams (e.g., development of trait databases, trait syndromes, taxonomic resolution, etc.). Finally, Menezes et al. (2010), Dolédec and Statzner (2010), and Culp et al. (2011) reviewed the major steps in developing traits-based analyses as a tool to monitor and assess stream health. Each review has provided a unique contribution to trait research in streams, often reviewing the theoretical constructs of traits-based stream research, major developments, and a selection of examples. But, no review has attempted to provide a comprehensive coverage of trait research in streams, accounting for all papers using traits as indicators of environmental change in stream systems, particularly the univariate FFG approach, which has become prevalent in stream ecology research, not just bioassessment. I have collected every published paper that has used macroinvertebrate traits in a community-level assessment of stream ecosystems. My goal with this data is to understand: 1) when and where these studies have occurred, 2) what traits have been used, 3) what environmental gradients have been used, 4) how have these relationships be analyzed, 5) what deficiencies there are in our understanding of trait research, and 6) what has

been learned (i.e., what trait-environment relationships have been detected in stream systems). The purpose of this review is to study the ‘demographics’ of stream trait studies, dealing with points 1, 2, 3, 4, and part of point five above. An additional forthcoming review will deal with point 6: the results of these studies, what has been learned.

Advantages, challenges, and recommendations of trait research in streams

Previous reviews of trait research in streams have argued that traits-based research and bioassessment provides a series of distinct advantages over more traditional taxonomic-based research and bioassessment. They also acknowledge various challenges to trait research and make recommendations to deal with those challenges.

Traits provide the following advantages over traditional taxonomic metrics:

1. A mechanistic, causal link between biology and environment (Culp et al. 2011). This causal relationship would allow for specific *a priori* predictions of community response to natural and anthropogenic disturbance (Dolédec and Statzner 2010).
2. Spatial and temporal consistency. Traits occur in each taxon, but a specific taxon is constrained by geographic and temporal limitations. Thus, traits-based metrics can be applied across regions, while many taxonomic-based metrics cannot (Dolédec and Statzner 2010, Culp et al. 2011)
3. Ability to distinguish multiple environmental variables, including multiple anthropogenic stressors (Feio and Dolédec 2012), with greater detection sensitivity to mild impairment than taxonomic metrics (Culp et al. 2011).

Challenges from a traits-based approach include:

1. Disentangling a true trait-environment relationship from correlations with other traits and environmental variables (Culp et al. 2011). Traits may be correlated through physiological constraints, similar responses to the same environment gradient, evolutionary history, or through a trait syndrome. Syndromes are groups of traits that may respond, in concert, to an environmental stressor. Additionally, an environmental variable may be correlated with or only a component of the true environmental condition eliciting a trait response. Trait and environmental correlations may lead to the use of variables tangentially related to a true trait-environment relationship and possibly reducing the predictive power (Chessman 2012).
2. Trait assignment. Most macroinvertebrate trait databases are categorical and do not capture trait variation within the genus or species (Culp et al. 2011). A fuzzy coding approach (Chevenet et al. 1994) attempts to address this problem by assigning multiple trait states proportionally to taxa. For example, if taxon consumes detritus as an early instar, but adopts a predatory lifestyle as a mature larva, then each record of this larva in a dataset would be partitioned into the two feeding groups based on established proportions, such as 40% detritivore and 60% predator. The fuzzy approach is advantageous if the intra-taxon trait state variation is static or linked to physiology or life history development and not environmental gradients, but it requires detailed life history knowledge of each taxon, unavailable in most parts of the world. If intra-taxon trait state variability is correlated to an environmental conditions, then the fuzzy approach may be as inaccurate as a binary assignment (i.e., each taxon assigned a single trait state).

3. Trait designation. Some traits cannot be easily binned into categories or are often misapplied. For example, Resh and Rosenberg (2010) point out that functional feeding groups were originally based on mouthpart morphology and method of food acquisition. Many studies now assign functional feeding groups based on food type, which may or may not correspond with mouthpart morphology, resulting in a possible misapplication of the original trait. Additionally, they point out that many macroinvertebrates are omnivores and cannot be easily assigned a functional feeding group (Mihuc 1997). Taxa are often broken in to 4-5 functional groups, such as predators, shredders, grazers, or collectors of detritus. If a taxon is a true omnivore, it would not adequately belong in any of the trait states.
4. Trait tradeoffs. Multiple traits may provide solutions to a fitness constraint imposed by an organism's environment, but an organism may not incorporate all traits due to physiological or evolutionary constraints, resulting in a trait tradeoff. In trait syndromes, described above, multiple traits work together to increase fitness under particular environmental conditions. Thus, most taxa would possess that particular syndrome and community-level measures of trait abundance would reflect that syndrome's dominance. Traits involved in a trait tradeoff also increase fitness under particular environmental conditions, but no single trait may become dominant since different organisms employ different traits to survive. In such cases, the traits may not be correlated and attempts to measure the strength of single trait-environment relationships may be confounded, where no single trait exhibits a strong correlative relationship with that environmental condition (Menezes et al. 2010).

Recommendations to deal with challenges:

1. Use multiple traits. Since traits are often correlated or may exhibit tradeoffs, it has been argued that a multiple traits should be used to fully capture a community's response to an environmental gradient (Menezes et al. 2010, Statzner and Bêche 2010, Verberk et al. 2013).
2. Use multiple environmental variables. Traits simultaneously interact with multiple environmental variables. For example, stream ecological theory posits that prevalence of multivoltinism (having more than one generation per year) should be related to temperature, latitude, stream nutrients, pH, land use, stream flashiness, drought, substrate size, stream scouring, and predation intensity. Using multiple environmental variables in an analysis gives the ability tease out the most dominant relationships from multiple natural and anthropogenic stressors (Menezes et al. 2010).
3. Use multivariate statistical analyses. This approach accounts for multiple trait-environment relationships (Culp et al. 2011) and gives the ability to detect the strongest trait-environment relationships.
4. Establishment of specific *a priori* predictions. The complex interactions between multiple traits with multiple environmental gradients can result in a single trait responding to many different environmental gradients. Establishment of *a priori* predictions based on ecological theory will allow for a mechanistic understanding of trait responses (Statzner and Bêche 2010), however many studies conduct a more *à la carte* approach, using every trait available, resulting in many correlatins, but few explanations.
5. Use appropriate spatial scale. One of the major debates concerning trait use in stream bioassessment has revolved around what appropriate scales should be used to build traits-

based bioassessment tools. Much of this development in Europe has been based on the assumption that trait distributions are similar in least-impacted streams across ecoregions and even continents (Bonada et al. 2007a, Statzner and Bêche 2010). If this is true then a single, universal bioassessment protocol could be developed for a nation or continent (Statzner and Bêche 2010). This viewpoint has recently been challenged, however, with some evidence that trait distributions are constrained at the scale of ecoregions (Poff et al. 2010, Zuellig and Schmidt 2012, Heino et al. 2013). Ideally, a traits-based bioassessment protocol should be developed to detect anthropogenic disturbances across at a large-scale and across a wide range of habitats and such protocols have been developed in Europe, (Bis and Usseglio-Polatera 2004) and the U.S. (Barbour et al. 1999), but such large-scale analyses should reflect specific *a priori* predictions and bioassessment objectives, which is often not done in stream ecology (Heino et al. 2013).

6. Incorporate reference condition trait responses. The goal of traits-based ecology is not the mere prediction of trait distributions along environmental gradients, but to also understand how and why trait patterns deviate from natural conditions due to anthropogenic disturbance. Trait patterns must first be established under reference or semi-natural conditions in order to provide a baseline response in which to judge potential traits-based community responses to anthropogenic disturbances on stream systems (Statzner et al. 2001a, Statzner et al. 2005).

The last two recommendations are often made in the context of incorporating traits into a large-scale (i.e., continental) bioassessment and are not applicable to every situation. For example, Cowell et al. (2004) compared FFG between reclaimed mining sites and sites under

agricultural or mining use. To address their particular question there was no need to work at large-scale or incorporate natural streams into the study. As I review the when, where, and how of stream trait studies below, I will discuss how many incorporated the recommendations listed above.

Review of Studies

The amount of literature incorporating stream macroinvertebrate traits is immense. For example, I found 7505 papers listed in the Web of Science[®] database [Institute for Scientific Information; <http://apps.isiknowledge.com/>, checked on June 15, 2014] which refer to 1) macroinvertebrates (using the search terms TS=macroinvert* or TS=invert*), 2) a freshwater system (TS=stream* or TS=river* or TS=reservoir* or TS=lake* or TS=wetland* or TS=pond*), and to 3) some iteration of functional feeding groups, trophic groups, or traits (TS=guild* or TS=functional feeding or TS=shred* or TS=graz* or TS=scrap* or TS=collecto* or TS=filter* or TS=troph* or TS=trait* or TS=function* or TS=burrow* or TS=voltin* or TS=size*). The goal of my review is determine how aquatic macroinvertebrate communities respond to lotic conditions using traits as the metric of response, so I refined my search by reviewing titles and abstracts, scanning figures and tables in the text, and searching text for terms that incorporate the following criteria:

- They derived a community-level, trait metric for aquatic macroinvertebrates, such as richness, abundance, or diversity of taxa with a particular trait state.
- They conducted the study in a freshwater, lotic systems (e.g., streams, rivers)
- They measured a trait response to a specific abiotic or biotic condition, gradient, or disturbance.

- Studies published up to and including 2012.

These criteria excluded a wide range of studies incorporating traits in aquatic systems, including those which use lentic habitats (e.g., Cereghino et al. 2008, Verberk et al. 2008, Gallardo et al. 2009), lack a distinct trait-environment relationship (e.g., Yanoviak and McCafferty 1996, Gayraud et al. 2003, González et al. 2003, Statzner et al. 2008, Jiang et al. 2010), or only focus on one or a few taxa instead of a community-wide response (e.g., Hill and Knight 1987, Bastian et al. 2007, López-Rodríguez et al. 2009, Silveri et al. 2009, Wellnitz and Poff 2012). I also did not include studies that measure the flow of energy through a trait group, often using isotope analyses (e.g., Li and Dudgeon 2008, Riva-Murray et al. 2013), since these studies do not measure how trait distributions change across the stream environment. I did not include studies that use a general metric, possibly based on multiple traits, which cannot discern relationships between individual traits and environmental gradients. This type of metric includes biological indices, tolerance scores, ratios of functional groups, or functional diversity, which describes the overall trait diversity, but provides no measure of individual trait responses (e.g., Cushing et al. 1983, Cummins et al. 2005, Heino 2005, Bressler et al. 2006, Angradi et al. 2009, Bêche and Statzner 2009, Dang et al. 2009). Finally, I did not incorporate studies that clustered taxa according multiple traits, but used many traits wholesale and did not select traits based on the underlying theory (e.g., Usseglio-Polatera et al. 2001, Carlisle and Hawkins 2008, Merigoux et al. 2009). The two latter approaches incorporate the simultaneous analysis of multiple traits and can be important in detecting synergistic trait combinations, but also make it difficult or impossible to detect the relationship between a given environmental condition and specific trait, which is the goal of this review.

I found 905 studies that met the criteria above. The earliest study was published in 1975 and the number of studies has increased exponentially (Figure 1.1), at a rate similar to the growth rate in overall publication numbers in my initial publication search. Many of the studies occurring in the 1980s dealt with validating the River Continuum Concept. The number of papers dealing with trait-environment relationships had a marked increase in the early to mid-1990s, with a greater focus on bioassessment following the incorporation of functional feeding groups and habits into bioassessment protocols in the United States (e.g., Plafkin et al. 1989, Barbour et al. 1999) and adaptation of the habitat template concept to stream systems in conjunction with the 1994 Rhône study (Resh et al. 1994, Townsend and Hildrew 1994).

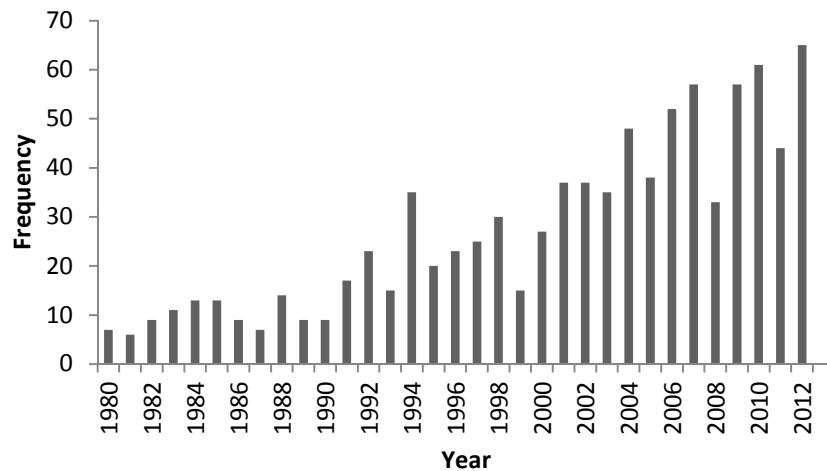


Figure 1.1: Number of studies per year addressing a trait-environment relationship at the community-level.

Early emphasis on approaches developed in the United States and Europe has, not surprisingly, resulted in a geographic distribution of studies heavily skewed towards northern temperate regions, particularly in the U.S. and western Europe, followed by southern temperate regions such as Argentina, southeastern Australia, and New Zealand (Figure 1.2). Three hundred

and ninety (43.1%) papers included at least one location in the U.S., followed by France, with 63 papers, Canada (49), Spain (47), New Zealand (43), Portugal (40), and Australia (37).

Conversely, 20 (2.2%) papers included sites from Africa and 40 papers included sites from Asia. Additionally, the vast majority of papers conducted studies within limited spatial scope. Eight hundred and twenty-five (91.2%) studies were conducted within a single political region (which I define here as a country except in the five largest countries, which I define as their component states, provinces, territories, or federal districts). Of these papers, 568 used ten sites or less. Eighteen papers included sites from more than ten regions. Classifying sites according to general climate demonstrated a bias towards temperate and cold climates. Using the Köppen climate classification (Peel et al. 2007), I found 384 papers included sites from the maritime temperate climate (Cfa, Cfb, Cfc); 382 papers included humid continental climate (Dfa, Dfb, Dfc) sites; and 158 included Mediterranean sites (Csa, Csb). Conversely, only two papers included sites from the polar tundra (but, 39 papers incorporated alpine tundra), while 17 papers included desert (Bwh, Bwk), and 53 included tropical climates (Af, Am, Aw).

These studies included a wide range of stream sizes and environmental characteristics, but were biased towards small streams. Six hundred and seventy-eight papers included streams that they defined as small (or 1st-3rd Strahler order), 241 included medium streams (or 4th-6th order), 69 included large rivers (> 6th order), 31 included intermittent streams, and four included ephemeral streams. Thirty-six papers did not list stream size, but included a large number of sites (>50) and probably incorporated a diverse array of stream sizes. I could not determine stream size for an additional 109 papers. A wide variety of stream conditions were also represented. I did not attempt to formally define an undisturbed or disturbed stream, but rather recorded the authors' own assessments of stream condition. For those papers with no condition

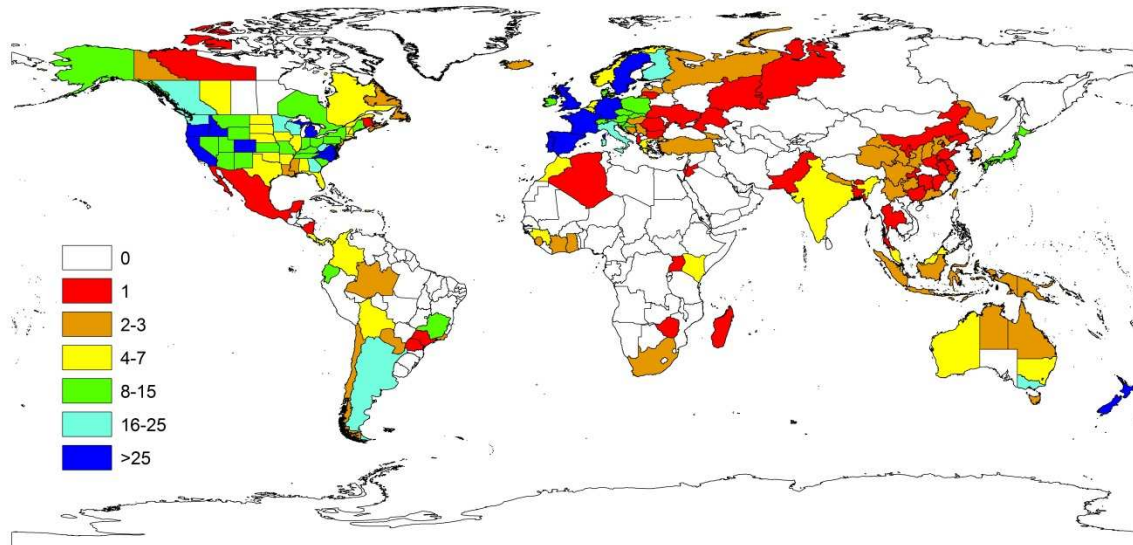


Figure 1.2: The number trait-environment studies according to country. The five largest countries (Australia, Canada, China, the Russian Federation, and the United States of America) were divided into their component states, provinces, territories, or federal districts (in the case of Russia).

stated, I attempted to detect major anthropogenic influences (e.g., roads, urbanization, agriculture, dams) within the watershed using a Geographic Information System (GIS; ArcMap™ 9.3, ESRI, Redlands, California) and Google Earth (Google, Mountain View, California) if spatial coordinates were given. Given these criteria, 263 papers used only streams relatively free from anthropogenic disturbance, 220 used only disturbed streams, and 356 used both. I could not determine stream condition for 62 papers.

A wide variety of environmental variables have also been used to assess and predict trait distributions in streams. I recorded over 500 different environmental variables, with over 10,000 recorded relationships with traits. The most commonly used type of environmental variable was some measure of stream size, such as stream order or distance from headwaters, which was used in 98 papers. This metric was commonly used in the 1980s and 1990s to assess the predictive

capabilities of the River Continuum Concept. Measures of stream habitat type (92 papers) were also commonly used, followed by leaf litter (91), detritus or organic matter (80), and discharge, velocity or stream power (66). I further binned each environmental variable into one of 17 general categories, including chemistry (e.g., pH, nitrogen), human disturbance (e.g., logging, chemical exposure), food (e.g., organic matter, leaf litter, invertebrate prey), and natural disturbance (e.g., glaciation, channel stability). Human disturbance, food, and substrate/habitat were the most common environmental variables (Figure 1.3). The majority of studies, 546, analyzed a single environmental variable, while only 14 studies measured relationships for >10 environmental variables. Some studies measured more than ten variables, but only recorded trait-environment relationships for less than ten variables. For example, Poff et al. (2010) included 45 environmental variables in their analysis, but their classification and regression tree analyses only selected a few of these variables. Other papers had a large number of environmental variables, but only described the few strong relationships highlighted by multivariate techniques (e.g., Minshall and Robinson 1998, Weigel and Robertson 2007).

A total of 77 different traits were used in these analyses. Most research has focused on the distribution of functional feeding groups in streams with 706 papers exclusively using this trait, while an additional 133 included FFG with other traits. Functional habit (101 papers), size (81), voltinism (64), and respiration (51) were other commonly used traits. The use of many traits in an analysis was uncommon, with only 86 studies using more than three traits with 49 of these in Europe alone (North America had 22).

The majority of studies (620) used univariate statistics, with 54 using multivariate approaches and 172 using no statistical analysis, instead opting for non-statistical comparisons. Many of the studies lacking statistical analyses were performed in the 1980s. Fifty-nine studies

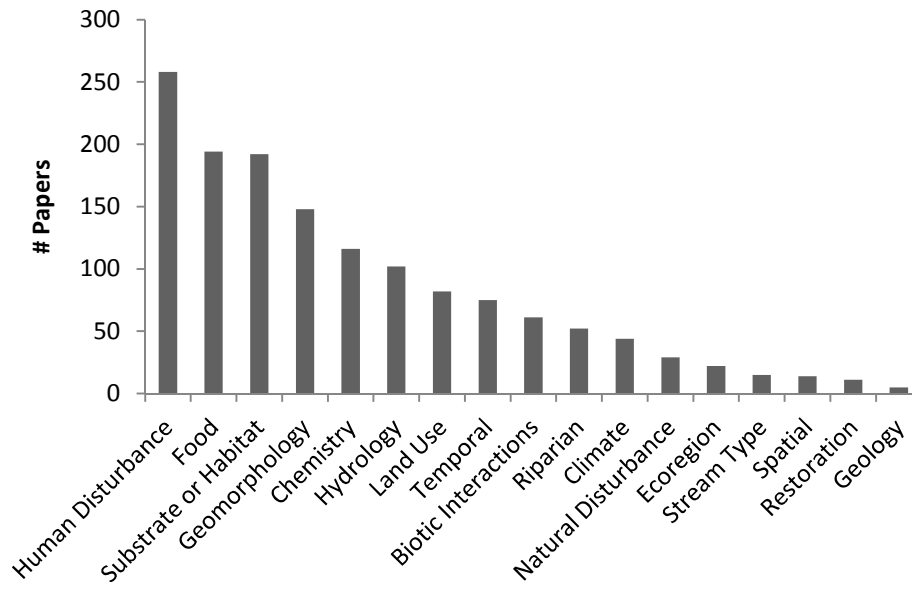


Figure 1.3: The number of papers that included an environmental variable from these general categories.

used some combination of none, multivariate, or univariate statistical approaches. Dividing up statistical preferences according to continent showed an inclination toward multivariate approaches in Europe, with 15% of European studies including a multivariate approach opposed to only 7% in North America. The use of multivariate statistics did not necessarily mean that a multi-trait approach was used. A multi-trait approach incorporated multiple traits into a single analysis. Often multivariate techniques were used on multiple states from a single trait or, if multiple traits were used, each trait was analyzed separately. I did not define these approaches as multi-trait. A multi-trait approach can incorporate traits in one of two ways. The most common technique, which I will call the multivariate multi-trait approach, is to include multiple states from multiple traits as response variables in a multivariate analysis (e.g., Usseglio-Polatera and Tachet 1994, Statzner et al. 2004, Finn and Poff 2005, Bêche et al. 2006, Tomanova et al. 2008). This approach can account for trait syndromes, but not trait tradeoffs. A much less common

approach is to integrate multiple trait states into a new composite trait, which was described as the Functional Trait Niche (FTN) in Poff et al. (2006) or a life history strategy in Verberk et al. (2013). These approaches are different from creating a tolerance score or other multiple trait metrics because the composite trait retains the mechanistic link between the environment and the organism by selecting trait states, *a priori*, based on ecological theory. For example, Rader (1997) used multiple traits, including size, emergence behavior, mobility, and habitat preference, to develop a drift propensity index for macroinvertebrates. The ecological understanding as to why the organism would have a high or low drift propensity was maintained. The composite trait can be derived for a very specific environmental gradient or ecological question (in the case of the FTN) or in terms of a general fitness strategy (in the case of Verberk et al.'s life history strategies). A simple tolerance score, in contrast, details if an organism is resistant to pollution or disturbance, but cannot explain why that organism is resistant. Either the multivariate multi-trait or the composite multi-trait approach was only used in 46 studies with 28 occurring in Europe. While a multi-trait approach has been recommended by multiple reviews, it is not necessarily appropriate for all situations. If a study is trying to capture the total community response to multiple environmental factors, then a multi-trait approach would be preferred, but many of the studies I reviewed in this paper addressed specific ecological questions that required only one trait or trait-state.

So, how many studies have used the recommendations stated above to deal with challenges of traits-based research, namely using multiple traits, multiple environmental variables, a large spatial scale (> one region), multivariate analyses, incorporating some reference sites, and using a multi-trait approach? Eighty-one papers used more than one trait and more than one environmental variable, 34 from Europe, 31 from North America, 13 from

Australia/Oceania, one from South America, one from Asia, and one from multiple continents. Fifteen of those studies included sites from more than one region. Seven of the 15 studies (Corkum and Ciborowski 1988, Statzner et al. 2001a, Brabec et al. 2004, Lecerf et al. 2007, Poff et al. 2010, Vandewalle et al. 2010, Carlisle et al. 2011) described trait-environment relationships for 2-6 traits and 2-8 environmental variables Europe and North America, but used univariate approaches to describe trait-environment relationships. Zuellig and Schmidt (2012) described trait-environment relationships across 46 U.S. states (20 traits, two environmental variables) and incorporated a multivariate ANOSIM analysis, but did not use a multi-trait approach. The seven remaining studies did include a multi-trait, multivariate statistical approach. Morais et al. (2009) compared 11 traits to 11 environmental variables across western Europe and Israel using a multi-trait, multivariate approach, but did not incorporate any reference condition streams in their analysis. The remaining six studies did include reference streams. Four studies are from Europe (Usseglio-Polatera and Beisel 2002, Bis and Usseglio-Polatera 2004, Haybach et al. 2004, Statzner et al. 2004), describing trait-environment relationships for 7-17 traits and 2-4 environmental variables. The two remaining studies are from the Great Lakes region and Canada in North America (Horrigan and Baird 2008, Hutchens et al. 2009) describing trait-environment relationships for 5-20 traits and 8-10 environmental variables. If the goal of traits-based community ecology in streams is to understand the complex interactions between multiple environmental factors and multiple traits across a wide range of climatic, habitat, and disturbance conditions and incorporate that knowledge into large-scale bioassessment, then much work needs to be done.

The contribution of each of the remaining studies should not be discounted, either. In some studies, some recommendations simply do not apply. For example, the recommendations

to assess streams across multiple geo-political regions or in multiple climates make no sense for New Zealand streams, a climatically homogenous (in terms of our climate classifications) island nation. In other studies, the nature of the ecological question in the paper precluded the incorporation of some recommendations. The goal of most small studies was not to develop a large-scale multi-use bioassessment technique, but address specific question. A typical trait study in this review would have compared the distribution of functional feeding groups to one environmental variable (commonly human disturbance, food type, or substrate/habitat type) in a single country using a univariate analysis. Some have argued that the univariate approach may not as ecologically meaningful nor be as effective in discriminating human impact in stream systems (Statzner et al. 2001a), but the statistics are more tractable and interpretations are often more straight-forward, making it a vital component of many stream bioassessment techniques. Single trait responses, if consistent across a wide variety of stream types and conditions, may be all that is needed for a biomonitoring metric. For example, 24 studies (e.g., Sedell et al. 1975, Gessner et al. 1991, Albariño and Balseiro 2002, Gonçalves et al. 2012) compared the distributions of functional feeding groups, particularly the distribution of shredders, to different types of leaves found in streams. Each study consisted of a small-scale experiment using leaf packs at 1-3 sites used to answer a single question: does the distribution of shredders change if different leaves are introduced in the stream? A univariate, single-trait approach is appropriate. But, if the question is expanded to ask if distribution of shredders is affected by leaf type in the context of different land use, habitat types, and climatic regions, the use of a large-scale, multivariate, multi-trait approach would be more appropriate. The influence of environmental conditions, both natural and anthropogenic, on trait distributions is still poorly understood, particularly at large-scales (Heino et al 2013). This review showed that few studies have been

performed in streams ecosystems using the six recommendations for effective traits-based bioassessments and further studies are needed to provide a holistic understanding of trait responses in streams.

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CHAPTER 2: LOTIC INSECT TRAIT-ENVIRONMENT RELATIONSHIPS IN REFERENCE STREAMS ACROSS THE WESTERN UNITED STATES

Summary

Species trait distributions are increasingly used in stream research and in bioassessments to evaluate stream health, but bioassessments require a baseline understanding of how traits respond to environmental conditions in least impacted streams in order to detect trait distribution deviations due to anthropogenic disturbance. Large-scale assessments of trait distributions across multiple environmental gradients for least impacted streams have mainly occurred in Europe, while North American assessments have mostly focused on a few traits, such as Functional Feeding Groups, and small-scale studies. We used macroinvertebrate and environmental data from 253 least-impacted sites to establish a baseline understanding of how traits are distributed across highly variable stream environments in the western U.S. We compared 20 life history, morphology, mobility, and ecology traits to 81 environmental variables encompassing major aspects of the stream environment using logistic regression, multinomial regression, and redundancy analysis. We also compared our results to *a priori* predictions for 11 environmental variables taken from 108 publications in stream ecology. Mean annual runoff, catchment precipitation, conductivity, mean July air temperature of catchment, total nitrogen and phosphorus, substrate size, slope, and coefficient of variation in daily flows had the strongest relationships with trait states, while thermal tolerance, size, swimming strength, rheophily, voltinism, armoring, synchronization of emergence, and female dispersal had the strongest relationships with environmental variables. Except for runoff and daily flow variability, other measures of hydrological timing, duration, and limits (e.g., frequency of low flows, duration of

flood free days) did not exhibit strong relationships with traits. Elevation was also not a strong predictor of trait distributions. While some traits, such as thermal tolerance, matched most *a priori* predictions, most traits had mixed results, with many not matching any predictions. Our results indicate that for large-scale analyses, traits may be effective in detecting changes in stream flow magnitude and daily variability, habitat, climate, chemistry, and geomorphology, but not for measures of natural hydrological extremes. While some trait distributions shift along large-scale environmental gradients, small-scale studies may be needed to detect the effect of some types of hydrological disturbance. One approach would be to account for climate and stream habitat variation in their analyses or constrain site selection by climatic or ecoregion regionalization.

Introduction

The study of species trait distributions for communities of benthic invertebrates is an increasingly integral part of stream community ecology (Heino et al. 2013, Verberk et al. 2013). Analysis of the distribution of traits in response to changes in stream conditions has some advantages over more traditional analysis of taxonomic distributions. Traits provide the ecological link between an organism and its environment, encapsulating the process of how the environment affects the fitness of the organism, resulting in species sorting across environmental gradients (Poff 1997, Chase and Leibold 2003, McGill et al. 2006, Webb et al. 2010, Culp et al. 2011). Taxonomically-based distributions are constrained by biological, environmental, and regional factors, but every organism can be described according to its biological attributes, making traits a general feature of species across diverse regions (Dolédec and Statzner 2010, Culp et al. 2011). This leads to traits being more spatially and temporally consistent than

taxonomic descriptors. These two factors, a strong theoretical connection between the trait and the environment and the ubiquitous distribution of traits, should give traits-based, community-level metrics greater ability to detect multiple natural and anthropogenic disturbances in stream systems than taxonomically-based approaches (Pollard and Yuan 2010, Culp et al. 2011, Feio and Dolédec 2012). Traits-based metrics should be good candidates for bioassessment of stream disturbance, since they are tied to ecological theory, have potential to discriminate human impacts, and can be applied across regions (Poff 1997, Dolédec et al. 1999, Bonada et al. 2006, Culp et al. 2011).

The use of traits in an applied context, such as bioassessment, has generated a considerable amount of interest and application (Charvet et al. 1998, Usseglio-Polatera et al. 2000, Statzner et al. 2001, Carlisle and Hawkins 2008, Dolédec 2009, Menezes et al. 2010). But, using traits in an applied context requires that we have a good baseline understanding of how they are distributed along reference or semi-natural environmental gradients in order to make proper inference about changes due to anthropogenic disturbance (Statzner et al. 2001, 2005, Poff et al. 2010). Inferences about anthropogenic impacts on trait distributions are sensitive to the number and type of traits and environmental variables used in the analysis and the scale of the analysis. Traits can be correlated or exhibit tradeoffs and environmental variables are often correlated (Poff et al. 2006, Verberk et al. 2013). The use of multiple traits and a wide array of environmental variables can provide insight into how communities are structured along large environmental gradients and how they may change with new conditions (Menezes et al. 2010, Statzner and Bêche 2010).

Development and application of large-scale, multivariate, traits-based biomonitoring has occurred mostly in Europe (for a detailed timeline of major developments, see Menezes et al.

2010). The results of these studies indicate that trait distributions can be effective indicators of stream condition, but they require the use of multiple traits to assess the effect of multiple environmental factors (Menezes et al. 2010, Statzner and Bêche 2010). Additionally, studies should account for the effect of natural variation in stream conditions across large spatial extents (Statzner et al. 2001, Statzner et al. 2005, Bonada et al. 2007a, Poff et al. 2010, Heino et al. 2013). Many European studies have had a wide range of trait data and large biological databases, but were limited by the number of available environmental variables and thus did not capture the full variation in stream conditions. For example, Statzner et al. (2004) compared seven traits to only four environmental variables (water hardness, elevation, stream width, and latitude) across 17 countries in Europe.

The use of traits in spatially extensive studies in North America has focused less on incorporating and understanding a wide range of traits, and more on the application of a few traits, especially Functional Feeding Groups (FFG), in bioassessment protocols (Plafkin et al. 1989, Barbour et al. 1999). Hundreds of studies in the United States have incorporated a FFG metric, and the majority of these studies have been small spatial scale. A few studies have used traits-based metrics to assess stream condition in streams across more than one or two U.S. states or Canadian provinces in North America. Of these studies, most used only one trait, typically FFG (e.g., Benke and Wallace 2003, Weigel et al. 2003, Angradi et al. 2009a, Pollard and Yuan 2010, Yuan 2010, Cuffney et al. 2011, Qian et al. 2012) or one environmental variable (e.g., Astin 2006, Angradi et al. 2009b, Bêche and Statzner 2009). Four studies incorporated multiple sites across large regions, multiple traits, and multiple environmental variables. Corkum and Ciborowski (1988) compared two traits, size and functional habit of Ephemeroptera, to eight environmental characteristics across western Canada and Alaska. Horrigan and Baird (2008)

compared 20 traits (the same used in this paper) to ten environmental variables describing climate, hydrology, chemistry and geomorphology across four Canadian provinces. Poff et al. (2010) compared two traits (thermal tolerance and rheophily) to 45 environmental variables across 253 sites in 12 western U.S. states. They also categorized sites according to the dominance of eight traits at each site, but did not compare these traits individually to environmental gradients. Zuellig and Schmidt (2012) compared 20 traits (the same used in this paper) to two environmental variables, ecoregion and land use type, across 1987 minimally-disturbed sites in 46 U.S. states. They also compared trait similarity between sites to a similarity matrix derived from nine environmental variables, but there were no direct comparisons between traits and environmental variables (except for the two listed above).

All of these studies have contributed to our understanding of how traits are distributed in North American streams, but no single study has compared a large number of traits to a diverse array of environmental variables encompassing most major aspects of the stream environment across a large geographic extent. The objective of this paper is to compare multiple insect traits across many major environmental gradients for streams in the western United States and compare our results to those found the published literature. Specifically, we aim to establish a baseline understanding of how traits are distributed across highly variable stream environments in 253 relatively undisturbed streams in 12 western states where data were available (covering over 3,100,000 km², an area roughly equal to 30% of the European continent). Further studies in western North America can use this understanding to account for natural variation in trait distributions and predict how anthropogenic perturbations may disrupt these distributions.

Methods

For this study, we selected sites in the U.S. Environmental Protection Agency's (USEPA) Environmental Monitoring and Assessment Program – Western Pilot Study (WEMAP), which collected samples from 1340 perennial streams and rivers in the western U.S. from 2000 to 2004 (Stoddard et al. 2005a). Streams in this region are diverse, reflecting the complex topographic, geologic and climatic conditions prevailing across the western U.S. WEMAP streams were selected using a stratified random design, described in Stoddard et al. (2005a) as being stratified according to state, Strahler order (Strahler 1957) and an ecoregion classification modified from Omernik (1987). Sites were selected in the states of Arizona, California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, South Dakota, Utah, Washington, and Wyoming.

At each site, biological, chemical, and physical habitat data were collected following the procedures in Peck et al. (2006). Streams were sampled mostly during the summer (June–September) with a few sites sampled in May or October. Stoddard et al. (2005a) assessed the reference condition of each stream site using phosphorus, nitrogen, chloride, sulfate concentration, pH, turbidity, a riparian disturbance index, % fine substrates, and canopy density. Of the 1340 sites, 326 (24%) met their criteria for “reference” conditions; however, we were concerned that these definitions might be too liberal because they did not incorporate catchment-scale anthropogenic influences, particularly influences associated with hydrologic disturbance. Using a geographic information system (GIS; ArcMapTM 9.3, ESRI, Redlands, California), we quantified various anthropogenic disturbances for each catchment (e.g., dams, reservoirs, canals, roads, land use) and removed 11 sites that showed a relatively high proportion of these disturbances relative to the remaining dataset. We also examined the sites and found 50 that did not have biological samples or well defined catchments.

An unavoidable issue with this dataset, and with most large stream datasets, is the lack of complete site independence. Although sites were selected randomly, the large number of sites and dendritic nature of stream systems resulted in some cases where a site was nested within the catchment of another site further downstream. Although streams may be in the same hydrologic unit (i.e., HUC), we only focused on sites with overlapping upstream catchments. To determine if nested sites are more similar than sites from separate watersheds (i.e., independent sites), we computed the Bray-Curtis similarity index (Bray and Curtis 1957) between sites for each group of environmental variables (e.g., geology, land use, hydrology). We then performed two regression analyses between similarity values and geographic distance between sites, one for sites within the same catchment and one for independent sites. For catchment geomorphology, hydrology, land use, precipitation, and temperature, nested sites were distinctly more similar than independent sites if they less than 6 km apart. Nested sites and independent sites had the same similarity values for stream habitat regardless of distance while nested sites were consistently more similar for geology metrics, regardless of distance. Based on these results, if two sites resided in the same stream network, had overlapping catchments, and were ≤ 6 km apart, we randomly removed one of the sites from the dataset. We removed 12 such sites, resulting in a final dataset with 253 sites (Figure 2.1). Although these sites were selected randomly within the WEMAP study, the reference condition criteria restrictions resulted in underrepresentation of some stream types and conditions. For example, all lowland perennial streams in desert and Mediterranean ecosystems are substantially modified by agricultural and urban development in the contributing catchments. Reference sites in these ecosystems were found only where anthropogenic development is restricted, such as areas with steep slope. Thus, most of our sites in drier climates were found in mountain or foothill regions.

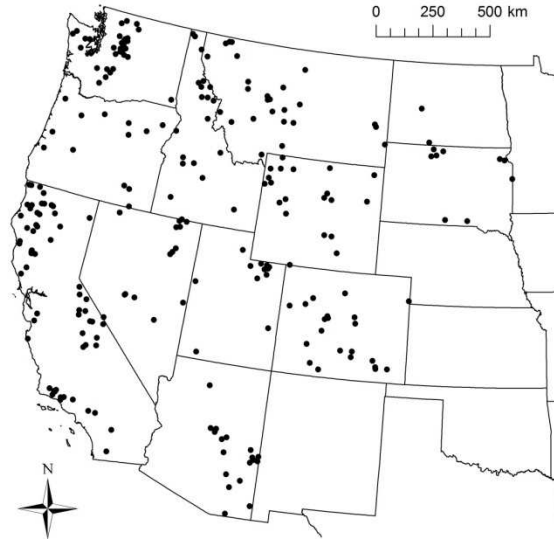


Figure 2.1: Location of the 253 reference-condition sites in the western United States.

Environmental variables

We selected our variables from an environmental database of 289 variables across three spatial scales. Reach-scale variables were collected at each EMAP site (Stoddard et al. 2005a, Stoddard et al. 2005b) and catchment and valley-scale variables were derived by at Colorado State University (Cuhaciyon 2006), or at the USGS (Carlisle et al. 2010), with measures of bed stability being derived elsewhere (Kaufmann et al. 2008). Catchment-scale variables were derived in a GIS following the delineation of the upstream contributing catchment area for each site from the National Elevation Dataset 30-meter resolution Digital Elevation Models (Gesch 2007). Catchment-scale precipitation and temperature data were derived from the 800-m-resolution Parameter-elevation Regressions on Independent Slopes Model (PRISM) database (30-y period of record from 1971–2000; PRISM Climate Group, Oregon State University, Corvallis, Oregon; <http://www.prismclimate.org>; extracted 5/17/2012), while soil metrics were derived from the U.S. general soil map (U.S. Department of Agriculture 2006), land use metrics from the 2001 National Land Cover dataset (Homer et al. 2004), geology from Reed and Bush

(2005), and habitat and geomorphology from DEMs using methods from Cuhaciyani (2006). Valley-scale geomorphology metrics were also derived from DEMs using methods from Cuhaciyani (2006). Catchment-scale hydrology was derived from catchment location, topography, geology, geomorphology, soil properties, land cover, and climate variables using a random forest method described in Carlisle et al. (2010). This method estimates long-term, average flow metrics (e.g., mean annual runoff, flood frequency, etc.) at each site based on models calibrated to regional, reference-quality U.S. Geological Survey (USGS) stream gauges (see Carlisle et al. 2010 for details). For the reference sites used in that study, the mean values of the estimated metrics were calibrated to within 0 to 3%, with standard deviations between 15 and 40%, of the 1272 observed values from existing streamflow gauge data. Reach-scale environmental variables were collected at the sampling site by the WEMAP collection team using the procedures from Peck et al. (2006), Kaufmann et al. (1999), and Kaufmann et al. (2008).

Our resulting dataset had 289 environmental variables, but we reduced their number by grouping them into their respective scale (e.g., reach, catchment) and category (e.g., hydrology, land use, geomorphology) and performing a PCA analysis on each group to assess the correlation between variables and determine which variables account for the most variation in each group. We selected variables from each scale/category that had highest loadings with the PCA axes. Our reduced dataset contained 81 variables (Table 2.1). We normalized the variables using power transformations and tested the normality of each environmental variable using the Lilliefors test (Thode 2002), D'Agostino-Pearson test (Zar 1999), and visual assessments.

Table 2.1: Environmental variable descriptions, codes, units of measure, data transformations, and descriptive statistics, including mean, standard deviation (SD), and range. If the variable's minimum value was <1, then the absolute value of the minimum value plus 1.01 were added to the data before transformation, except for arcsine transformed data, which have values between 0 and 1.

Description	Label	Unit	Tran.	Mean \pm SD	Range
Location					
Latitude	S.L.Lat	DD	None	42.00 \pm 4.63	31.44 - 48.84
Longitude	S.L.Long	DD	$x^{1/2}$	-114.92 \pm 6.65	-124.17 - -96.47
Catchment Scale					
Geology					
Prop. of crystalline rock underlying catchment	C.G.Cry	proportion	None	0.33 \pm 0.45	0.00 - 1.00
Prop. of sedimentary rock underlying catchment	C.G.Sed	proportion	None	0.47 \pm 0.47	0.00 - 1.00
Hydrology					
Median annual coefficient of variation of dailys	C.H.CV	unitless	$-1/x^2$	1.64 \pm 0.68	0.77 - 4.62
Estimated mean of daily flows in December	C.H.Dec	ft ³ /sec	$-1/x^{1/4}$	37.14 \pm 116.51	0.06 - 1,338.82
Mean flood-free days	C.H.FldFree	days/year	x^2	176.81 \pm 49.83	76.07 - 246.26
Mean high flood pulse count	C.H.HCnt	number/year	$-1/x^{1/2}$	5.49 \pm 2.75	2.30 - 16.78
Estimated mean of daily flows in July	C.H.Jul	ft ³ /sec	$-1/x^{1/8}$	45.76 \pm 118.40	0.12 - 1,359.51

Description	Label	Unit	Tran.	Mean ± SD	Range
Mean low flood pulse count	C.H.LCnt	number/year	$x^{1/2}$	5.21 ± 1.03	2.80 - 9.54
Mean total low flow pulse duration per year	C.H.LDurY	proportion	$-1/x^{15}$	0.32 ± 0.05	0.25 - 0.52
Mean annual runoff (Carlisle method)	C.H.MAR	ft ³ /sec/mile ²	$-1/x^{1/2}$	1.94 ± 1.96	0.04 - 9.47
Prop. of mean of daily flows - March-June	C.H.SprFl	proportion	x^4	0.57 ± 0.11	0.32 - 0.81
Prop. of mean of daily flows - July-October	C.H.SuFaFl	proportion	None	0.19 ± 0.08	0.03 - 0.40
Topographic wetness index	C.H.TopWet	ln(m)	$-1/x$	9.68 ± 1.20	7.07 - 13.17
Habitat					
Prop. of stream network that is plane-bed	C.Ha.PB	proportion	arcsin(x)	0.01 ± 0.01	0.00 - 0.05
Prop. of stream network that is pool-riffle	C.Ha.PR	proportion	$-1/x^4$	0.22 ± 0.23	0.00 - 0.97
Land Use					
Prop. of the catchment with barren	C.L.Bar	proportion	arcsin(x)	0.05 ± 0.11	0.00 - 0.64
Prop. of the catchment with evergreen forest	C.L.Ever	proportion	arcsin(x)	0.50 ± 0.31	0.00 - 1.00
Prop. of the catchment with mixed-forest	C.L.Mix	proportion	arcsin(x)	0.02 ± 0.07	0.00 - 0.43
Prop. of the catchment with wetland	C.L.Wet	proportion	arcsin(x)	0.01 ± 0.02	0.00 - 0.17

Description	Label	Unit	Tran.	Mean ± SD	Range
Geomorphology					
Catchment drainage area	C.M.Area	km ²	-1/x ^{1/8}	159.48 ± 543.04	0.66 - 5,864.54
Mean catchment elevation	C.M.Elev	meters	None	1,908.77 ± 812.97	231.87 - 3,821.61
Mean relief ratio	C.M.RR	unitless	x ^{1/2}	0.48 ± 0.09	0.18 - 0.85
Standard deviation of catchment elevation	C.M.SDElev	m	x ^{1/2}	202.71 ± 108.79	12.24 - 558.86
Mean catchment slope	C.M.Slp	%	None	28.76 ± 13.66	1.46 - 62.11
Precipitation					
Mean annual precipitation for the catchment	C.P.Ann	cm	-1/x ^{1/4}	114.68 ± 70.15	30.24 - 379.05
Mean July precipitation for the catchment	C.P.JulP	cm	x ^{1/2}	4.08 ± 2.93	0.00 - 16.82
Mean relative humidity of catchment	C.P.RH	proportion	None	0.59 ± 0.09	0.38 - 0.84
Soils					
Mean bulk density	C.S.Bulk	g/cm ³	exp(x)	1.33 ± 0.15	0.82 - 1.63
Prop. of soils in hydrologic group C	C.S.C	proportion	arcsin(x)	0.20 ± 0.15	0.00 - 0.81
Prop. of soils in hydrologic group D	C.S.D	proportion	-1/x	0.33 ± 0.20	0.00 - 1.00
Prop. organic matter content	C.S.Org	proportion	arcsin(x)	0.01 ± 0.01	0.00 - 0.05

Description	Label	Unit	Tran.	Mean ± SD	Range
Rainfall and Runoff factor	C.S.R	100s ft-tonf/h/ac/yr	ln(x)	88.13 ± 75.27	7.23 - 405.87
Prop. of soil, < 3 inches, passing a No. 200 sieve	C.S.Size20	proportion	-1/x	0.35 ± 0.15	0.01 - 0.75
Temperature (air)					
Mean annual air temperature of the catchment	C.T.Ann	degrees C	-1/x	1.45 ± 3.13	-0.89 - 15.00
Mean December air temp. of the catchment	C.T.DecT	degrees C	x ^{1/2}	-2.62 ± 5.03	-9.98 - 10.56
Mean July air temperature of the catchment	C.T.JulT	degrees C	x ^{1/2}	16.37 ± 3.92	8.64 - 25.88
Mean max. monthly air temp. of catchment	C.T.Max	degrees C	-1/x ²	3.79 ± 5.25	0.42 - 22.30
Valley Scale					
Geomorphology					
Mean hillslope connectivity	V.M.Conn	m	x ^{1/4}	5.70 ± 4.27	0.01 - 21.64
Coefficient of variation for hillslope connectivity	V.M.CVConn	unitless	-1/x ²	0.45 ± 0.30	0.00 - 2.48
CV for width based valley entrenchment	V.M.CVEntW	unitless	-1/x ^{1/2}	0.31 ± 0.14	0.00 - 0.99
Distance from site to 1 st tributary upstream ^a	V.M.Dist_1	m	None	110.91 ± 68.39	10.00 - 257.99
Mean valley entrenchment (width based)	V.M.EntW	unitless	-1/x ^{1/2}	15.76 ± 13.34	3.76 - 109.21
Catchment area of mainstem above tributary 1 ^a	V.M.MArea_1	km ²	-1/x ^{1/8}	163.93 ± 553.32	0.18 - 5,849.82

Description	Label	Unit	Tran.	Mean ± SD	Range
Mean slope of the valley above the outlet point	V.M.Slp	unitless	arcsin(x)	0.03 ± 0.03	0.00 - 0.17
Mean specific stream power, site valley (S*A ^{0.4})	V.M.SSP	km ^{0.8}	-1/x ⁶	0.11 ± 0.09	0.00 - 0.77
Reach Scale					
Chemistry					
Conductivity	R.C.Cond	uS/cm	-1/x ^{1/8}	286.04 ± 467.22	11.91 - 2,959.00
Dissolved Organic Carbon	R.C.DOC	mg/L	-1/x ²	1.67 ± 2.02	0.20 - 19.00
Nitrate	R.C.NO3	ueq/L	-1/x ^{1/8}	5.34 ± 13.74	0.00 - 181.33
pH	R.C.pH	unitless	x ⁴	7.82 ± 0.48	6.15 - 8.88
Silica	R.C.SiO2	mg/L	x ^{1/4}	14.71 ± 10.45	1.14 - 61.00
Total Nitrogen	R.C.TN	ug/L	-1/x ^{1/4}	188.89 ± 283.16	17.00 - 3,314.00
Total Phosphorous	R.C.TP	ug/L	-1/x ^{1/8}	16.75 ± 31.13	0.00 - 303.00
Total Suspended Solids	R.C.TSS	mg/L	-1/x ^{1/2}	4.44 ± 13.65	0.00 - 173.00
Dissolved Zinc	R.C.Zn	mg/L	x ^{1/4}	9.02 ± 12.22	0.00 - 88.00
Stream Flow ^a	R.H.Flow	ft ³ /sec	-1/x ^{1/2}	12.22 ± 43.08	0.00 - 429.37

Description	Label	Unit	Tran.	Mean ± SD	Range
Habitat and Land Use					
Mean fish cover from aquatic macrophytes	R.Ha.AqMac	proportion	arcsin(x)	0.06 ± 0.13	0.00 - 0.85
Mean fish cover from brush, small woody debris	R.Ha.Brsh	proportion	arcsin(x)	0.08 ± 0.10	0.00 - 0.88
Prop. of reach that is fast water habitat (≥ riffle)	R.Ha.Fast	proportion	arcsin(x)	0.52 ± 0.28	0.00 - 1.00
Prop. of reach that consists of Pools (all types)	R.Ha.Pool	proportion	-1/x ³	0.19 ± 0.17	0.00 - 1.00
Presence of all human disturbance along reach	R.L.Hum	index	None	0.37 ± 0.50	0.00 - 1.71
Geomorphology					
Mean bank angle	R.M.BnkAng	degrees	ln(x)	42.04 ± 17.56	8.05 - 101.95
Mean elevation of reach	R.M.Elev	m	x ^{1/2}	1,431.32 ± 784.55	95.00 - 3,660.00
Mean specific stream power at site (S*A ^{0.4})	R.M.OutSSP	km ^{0.8}	arcsin(x)	0.08 ± 0.10	0.00 - 0.95
Mean vertical profile area of residual pools ^a	R.M.RPArea	m ² /pool	-1/x	2.05 ± 4.25	0.04 - 35.65
Channel sinuosity ^a	R.M.Sinu	m/m	-1/x ⁸	1.14 ± 0.16	1.00 - 2.53
Mean slope of reach	R.M.Slp	%	-1/x ^{1/8}	5.14 ± 5.23	0.00 - 34.92
Mean width/depth ratio of reach	R.M.WD	m/m	-1/x ^{1/4}	20.08 ± 10.76	2.73 - 125.99
Mean width*depth product	R.M.WxD	m ²	-1/x ^{1/2}	2.67 ± 3.57	0.01 - 25.04

Description	Label	Unit	Tran.	Mean \pm SD	Range
Riparian					
Prop. of reach with coniferous riparian canopy	R.R.Con	proportion	None	0.28 \pm 0.37	0.00 - 1.00
Mean riparian vegetation ground cover	R.R.Grnd	Comp. prop.	None	0.55 \pm 0.23	0.02 - 1.02
Prop. of reach with mid- and herb. ground layers	R.R.RchMGH	proportion	arcsin(x)	0.62 \pm 0.36	0.00 - 1.00
Prop. of reach with mid-, woody ground layers	R.R.RchMGW	proportion	arcsin(x)	0.90 \pm 0.20	0.00 - 1.00
Prop. of reach w 3 layers: ground, mid, canopy	R.R.RchVeg	proportion	arcsin(x)	0.74 \pm 0.33	0.00 - 1.00
Substrate					
Prop. of substrate that is bedrock	R.S.BdRk	proportion	arcsin(x)	0.06 \pm 0.12	0.00 - 0.74
Mean bed surface particle diameter	R.S.Dgm	mm	ln(x)	123.28 \pm 240.60	0.01 - 2,702.60
StDev of mean bed surface particle diameter	R.S.Dgm_SD	mm	-1/x ^{1/4}	26.89 \pm 50.97	2.99 - 668.11
Relative bed stability (no bedrock/hardpan)	R.S.RBS_R_No	mm/mm	-1/x ⁴	0.32 \pm 0.52	0.00 - 4.55
LWD vol. in bankfull channel - all sizes	R.S.WAllSq	m ³ /m ²	arcsin(x)	0.02 \pm 0.04	0.00 - 0.37
Temperature (stream) ^a	R.T.Temp	degrees C	x ^{1/4}	13.08 \pm 4.61	3.00 - 29.00

^a Variables absent for some sites. Number of sites missing for each variable is: V.M.Dist_1 (98), V.M.MArea_1 (98), R.H.Flow (82), R.M.Sinu (13),

R.M.RPArea (13), and R.T.Temp (24)

Trait data

At each site, the WEMAP crews collected a biological sample from each of the 11 transects and composited them into a single sample for the site. In the lab, up to 500 (± 50) individuals were identified to the lowest feasible taxonomic level (usually genus) using a fixed count procedure (Stoddard et al. 2005a), producing a dataset with abundance and richness data. For this paper, we transformed taxonomic richness into trait relative richness by summing the number of taxa at a site exhibiting a specific trait state (i.e., category) and dividing that number by that site's total number of taxa, a technique similar to Poff and Allan (1995). We computed richness for genus-level taxa designations with the exception of Chironomidae, which was computed at the tribe level. We used a modified version of the trait database described in Poff et al. (2006), with some additional taxa added to the database since publication. The database consists of 20 traits with six life history traits, five mobility traits, five morphology traits, and four ecology traits (Table 2.2). Each trait consists of 2-5 nominal categories (hereafter referred to as states) for a total of 58 states, with each taxon belonging to only one state per trait.

Table 2.2: Traits and states sorted according to four general categories, adapted from Poff et al. (2006).

Trait	State and label
<i><u>Life History Traits</u></i>	
Adult exiting ability	Absent (not including emergence) – Exit.Absnt Present - Exit.Prsnt
Adult life span	Very short (< 1 week) – Life.VShrt Short (< 1 month) – Life.Shrt Long (> 1 month) – Life.Long
Desiccation resistance	Absent (i.e., cannot survive desiccation) – Desi.Absnt

	Present – Desi.Prsnt
Development	Fast seasonal – Devl.Fast
	Slow seasonal – Devl.Slow
	Non-seasonal (all stages present at all times) – Devl.Non
Synchronization of emergence	Poorly synchronized (over weeks) – Sync.Poor
	Well synchronized (over days) – Sync.Well
Voltinism	Semivoltine (< 1 reproductive generation/year) – Volt.Semi
	Univoltine (1 reproductive generation/year) – Volt.Uni
	Bi- or multivoltine (> 1 rep. generation/year) – Volt.Multi

Mobility Traits

Adult flying strength	Weak flyer (e.g., cannot fly into light breeze) – Flgt.Weak
	Strong flyer – Flgt.Strng
Female dispersal	Low (< 1 km flight before laying eggs) – Disp.Low
	High (> 1 km flight before laying eggs) – Disp.High
Maximum crawling rate	Very low (< 10 cm/hr) – Crwl.VLow
	Low (< 100 cm/hr) – Crwl.Low
	High (> 100 cm/hr) – Crwl.High
Occurrence in drift	Rare (Catastrophic only) – Drft.Rare
	Common (Typically observed) – Drft.Cmmn
	Abundant (Dominant in drift samples) – Drft.Abun
Swimming ability	None – Swim.None
	Weak – Swim.Weak
	Strong – Swim.Strng

Morphology Traits

Armoring	None (soft-bodied forms) – Armr.None
	Poor (heavily sclerotized) – Armr.Poor
	Good (e.g., snails, some cased caddisflies) – Armr.Good
Attachment	None (free-ranging) – Atch.Free

	Some (sessile, sedentary) – Atch.Sed
	Both – Atch.Both
Respiration	Tegument – Resp.Teg
	Gills – Resp.Gill
	Air (via plastron, spiracle, etc.) – Resp.Air
Shape	Streamlined (flat, fusiform) – Shpe.Strm
	Not streamlined (cylindrical, round or bluff) – Shpe.NtStrm
Size at maturity	Small (<9mm) – Size.Small
	Medium (9-16 mm) – Size.Med
	Large (>16 mm) – Size.Large

Ecology Traits

Functional feeding group	Collector-gatherer – Trop.CGath
	Collector-filterer – Trop.CFilt
	Herbivore (scraper, piercer, and shredder) – Trop.Herb
	Predator (piercer and engulfer) – Trop.Pred
	Shredder (detritivore) – Trop.Shrd
Functional habit	Burrow – Habt.Brrw
	Climb – Habt.Clmb
	Sprawl – Habt.Sprwl
	Cling – Habt.Clng
	Swim – Habt.Swim
Rheophily	Depositional only – Rheo.Depo
	Depositional and erosional – Rheo.Both
	Erosional – Rheo.Eros
Thermal tolerance	Cold stenothermal or Cool eurythermal – Ther.Cold
	Cool/warm eurythermal – Ther.CIWm
	Warm eurythermal – Ther.Warm

Statistical analyses

A traits-based response to an environmental change can be assessed using at least three approaches. The first approach would be to determine which of the 58 individual trait states are correlated with any of the 81 single environmental variables. This approach determines which traits may be adequate as stand-alone tools in bioassessment, but it does not necessarily detect shifts in community composition between trait states nor does it incorporate the relationship between multiple traits and multiple environmental variables. If a trait has more than two states, a steady increase in one trait state may not result in a distinct decrease of another state, but may be mitigated through multiple states. A second approach would be to detect community composition shifts between multiple states of single trait to address the question of whether the increase in a trait state (e.g., multivoltine) across an environmental gradient (e.g., temperature) is associated with a corresponding decrease in another state of the trait (e.g., semivoltine). If so, that would be a strong indication of a community-wide, trait-level response to a change in environmental conditions. A complication in these analyses is the fact that traits do not act independently of each other; many traits are correlated and particular combinations of trait states are incompatible (Townsend and Hildrew 1994, Poff et al. 2006, Verberk et al. 2013). Environmental variables are also frequently correlated with each other. A third approach to address this issue would be to use a multivariate method to detect the relationships between multiple trait states and multiple environmental variables. This latter approach is of interest, although it is more difficult to interpret and include in bioassessment tools. Therefore, we used all three approaches to provide insights by separately measuring 1) the univariate responses of single trait states to single environmental variables, 2) the shifts in multiple state distributions

within a single trait to single environmental variables, and 3) correlations between multiple trait states and multiple environmental variables.

1. Detecting responses of single trait states. – The occurrence of trait states within a community is described by their relative richness, with values between 0 and 1; therefore, we used a logistic regression analysis to model relationships between single traits and a single environmental variable. Logistic regressions were performed using the *lrm* function in the *rms* package (Harrell 2011) in the R statistical program (version 2.15.2; R Core Team 2012). The resulting R^2 value from this analysis is the Nagelkerke R^2 index, which is a measure of improvement over the null model, with a fully fitted model equaling 1 (Nagelkerke 1991). While this pseudo- R^2 is not a true measure of variance explained by the model, we found that the Nagelkerke R^2 values in our logistic regression models were very close to R^2 values in linear regression models built from the same data (results not shown, but the mean Nagelkerke R^2 s for values ≥ 0.20 were within 8% of the mean calculated R^2 from linear regressions). Another more commonly used measure of model fit is the area under the Receiver Operating Characteristic curve (AUC) which is a measure of model classification strength (Hosmer and Lemeshow 2000). An AUC value of 0.7 or greater indicates that a model adequately discriminates between true positives and false positives. We compared the Nagelkerke R^2 and AUC values using a quadratic regression analysis and found them highly correlated, with an R^2 of 0.969 using values for all but two traits states. The two remaining trait states, warm eurytherms and air breathers, had results that diverged from the remaining traits states. These two states were not found at most sites and had relatively low proportions of taxa at the sites where the trait state was present and these two states tended to be present only on one end of many environmental gradients. This tendency to be on one end of the environmental gradient increased classification strength even if

the model improvement over the null model was poor, represented by the Nagelkerke R^2 . We decided to use the Nagelkerke R^2 because of this discrepancy. We also discovered that the logistic regression models were very sensitive in detecting even a minor change in slope, given the size of our dataset. A relationship between a trait state and an environmental variable would be found to be statistically significant even if the R^2 was only 0.02. Such relationships were not insightful or ecologically meaningful. Since the strongest relationship had an $R^2 = 0.53$, we decided to assess relationships only for environmental variables with an $R^2 \geq 0.20$ for at least one trait state (roughly equivalent to an AUC of 0.66), a value we consider to usefully explain variation in the data and to provide some ecological meaning.

2. *Detecting shifts in multiple state distributions within a single trait.* – We used a multinomial regression model to determine if an increase or decrease in a trait state distribution results in a corresponding decrease or increase in another state of the same trait. Since all the relative richness of all states within a single trait sum to 1, a multinomial regression is the most appropriate way to model these relationships (Qian et al. 2012). The multinomial regression sets one trait state as a baseline and models the probability ratios (log odd ratios) of the remaining trait states over the baseline state. If the regression coefficient for the environmental variable is significantly different from zero, then the ratio of that state over the baseline state can be inferred to increase (or decrease) along the environmental gradient (i.e., one state becomes more dominant in the community while the other state becomes less so). We performed the multinomial regression using the *multinom* function in the *nnet* package (Venables and Ripley 2002) in R. The *multinom* function fits a multinomial model using neural networks and requires that the explanatory variables be scaled between 0 and 1 to avoid convergence problems. We determined that a model coefficient was significant if the 95% confidence interval did not

include 0. We plotted the estimated relative richness curves and the 95% credible intervals for select trait-environment relationships, generally those with the strongest relationships. We derived credible intervals using a Monte Carlo simulation that drew 10,000 random samples for each coefficient from a multinomial distribution. Methods and code to derive the estimated values and credible intervals are found in the appendix of Qian et al. (2012).

3. *Detecting correlations between multiple traits and multiple environmental variables.* – We used redundancy analysis (RDA) to determine which individual or groups of trait states had the strongest relationships with environmental variables accounting for all other trait states and environmental variables. Redundancy analysis models the relationships between two matrices of data using a combination of linear regression and ordination (i.e., principle components analysis) and has commonly been used in aquatic trait studies using nominal traits (Feld and Hering 2007, Heino et al. 2007, Weigel and Robertson 2007, Poff et al. 2010). This RDA used a forward stepwise model selection criterion that selected for environmental variables that maximized the adjusted R^2 . We used the *rda* function for the RDA and *ordiR2step* function for the stepwise selection procedure in the *vegan* package (Oksanen et al. 2011) in R.

A priori predictions and literature review

Townsend and Hildrew (1994) advocated a rigorous *a priori* approach to traits-based analyses, by hypothesizing theoretical, niche-based relationships between trait distributions and environmental gradients and then testing these hypotheses. Many studies, however, have taken a less restrictive approach, describing relationships between all available traits and environmental variables. We believe both approaches can be informative. The less restrictive approach provides a more complete picture of the trait-environment dynamics in stream systems, but these

patterns may lack an adequate ecological explanation. An *a priori* approach provides the theoretical underpinnings for each relationship, but by focusing only on published, *a priori* relationships we may inadvertently exclude important, yet poorly understood relationships. We therefore incorporated both approaches, analyzing all possible relationships, but focusing on relationships supported by niche theory.

Niche theory posits that an organism's traits should provide an adaptive advantage (or disadvantage) in a given environmental condition. At the level of the individual and along evolutionary time scales, this translates into natural selection, where traits in a population can evolve according to environmental constraints. At the level of the community and along ecological time scales, this translates into species sorting, where the environment selects (or "filters") for species possessing a given trait or suite of traits (Webb et al. 2010, Verberk et al. 2013). Many publications in stream ecology have applied phenotypic plasticity, natural selection, or species sorting reasoning to explain or predict the distribution of particular trait states in aquatic macroinvertebrate communities. These explanations were commonly based on experiments on individual taxa, expert knowledge of taxa or stream systems, or reviews of previous studies.

We reviewed the literature (108 papers and books, see Table 2.3) and extracted *a priori* trait-environment hypotheses advanced by the authors. We found two common lines of thought in describing *a priori* predictions of trait distributions of aquatic insects in streams. These generally follow the reasoning of species sorting along environmental gradients (Webb et al. 2010). First, a trait state may be constrained by normal (non-extreme) environmental conditions. For example, organisms that are multivoltine require a minimum level of energy for growth to achieve the fast development needed for multiple generations per year. Thus, multivoltinism

should not occur abundantly in streams with inadequate degree-day accumulation and/or nutrient levels (Hynes 1970b, Resh and Rosenberg 1984, Giller and Malmqvist 1998, Thorp and Covich 2010a, and many other references in Table 2.3). Second, specific trait states may exhibit resistance or resilience to extreme environmental conditions. For example, with the ability to complete life cycles between disturbances, multivoltine taxa may be more common in streams with frequent hydrologic disturbances (Ward 1992, Poff 1997, McCafferty 1998, Merritt et al. 2008). Some of these trait states may be energetically expensive (e.g., multivoltinism, fast development, desiccation resistance) and only occur in conditions where the advantage against disturbance mortality risk outweighs the energetic cost. In some instances, local selection for these traits has been demonstrated or inferred (Lytle 2002, Lytle et al. 2008). Regardless of the reasoning behind authors' *a priori* predictions, we have extrapolated these predictions as community-level responses to specific environmental variables based on niche concepts. For the 20 traits used in this analysis, we identified 516 *a priori* trait-environment relationships with 129 environmental variables in 108 publications. These relationships were not derived from the results of studies, but from predictions and trait descriptions the authors developed using ecological theory. We used our data to develop empirical relationships to test these literature-based, theoretical predictions. For this analysis, we restricted our testing of *a priori* predictions to those environmental variables we had with predictions across many traits and were found in multiple publications. That reduced our 129 *a priori* variables down to 11 general variables. About half of these *a priori* variables are hydrological, with flow or runoff (represented in the dataset by variable C.H.MAR), flow predictability (C.H.CV, C.H.SpFl, C.H.SuFaFl), flood frequency (C.H.Fldfree, C.H.HCnt), low flow frequency (C.H.LCnt), low flow duration (C.H.LDurY), and stream flashiness (C.H.CV, C.H.HCnt). The other predictions relate to a

variety of stream conditions, such as elevation or latitude (C.M.Elev, S.L.Lat), temperature (C.T.JulT), stream size (R.M.WxD, C.M.Area), substrate size (R.S.Dgm, R.Ha.Fast), and nutrients (R.C.Cond, R.C.DOC, R.C.TN, R.C.TP). The *a priori* predictions, with references, are found in Table 2.3.

Table 2.3: *A priori* predictions of trait distributions along environmental gradients. General environmental variables are represented by variables from this dataset (in parentheses). Source references are located below the table. The symbol “U” represents a unimodal relationship, “N” no expected change, and “+/-” or “+U” contradictory predictions. The trait and trait state abbreviations are in Table 2.2.

Trait	Altitude or Latitude	Stream Size	Temperature	Substrate Size	Stream Nutrients	Flow or Runoff	Flow Predictability	Flood Frequency	Low Flow Frequency	Low Flow Duration	Stream Flashiness	Sources
Armr												
Good						+	+/-	+/-	+/-	+/-	+/-	12, 15, 32, 36, 39, 76, 79
None						-	+/-	+/-	+/-	+/-	+/-	12, 15, 32, 36, 39, 76, 79
Poor												No <i>a priori</i> predictions
Atch												
Both				+		+						2, 16, 43, 50, 65, 68, 72, 77
Free						-	+	+	+			2, 15, 18, 43
Sed				+		+	-	-	-	-	-	1, 15, 18, 20, 50, 72
Crwl												

Trait	Altitude or Latitude	Stream Size	Temperature	Substrate Size	Stream Nutrients	Flow or Runoff	Flow Predictability	Flood Frequency	Low Flow Frequency	Low Flow Duration	Stream Flashiness	Sources
High								+	+	+	+	66, 71, 76
Low												No <i>a priori</i> predictions
VLow								-	-	-	-	66, 71, 76
Desi												
Prsnt ^a			+/-						+	+		2, 5-6, 11, 20, 26, 32, 43, 45, 56, 59, 64, 66, 72, 76
Devl												
Fast	-		+	+				+	+	+	+	2-3, 8, 16-17, 26, 32, 38, 42-43, 54, 59, 75
Non							-		+		+	11, 26, 32, 35, 59
Slow	+		-	-	-	+	-	-	-	-	-	2, 8, 17, 26, 32, 38, 42-43, 54, 57, 72
Disp												
High ^a								+	+	+	+	5, 11, 26, 32, 48, 63-64
Drft												
Abun	+		+	+	-	+/-	-	+	+/-	+/-	+	2, 16, 30, 32, 40, 43, 57, 59, 72-73, 78
Cmmn												No <i>a priori</i> predictions

Trait	Altitude or Latitude	Stream Size	Temperature	Substrate Size	Stream Nutrients	Flow or Runoff	Flow Predictability	Flood Frequency	Low Flow Frequency	Low Flow Duration	Stream Flashiness	Sources
Rare			-		+	+/-	+		+/-	+/-		2, 31, 59, 72-73, 79
Exit												
Prsnt ^a								+	+	+	+	11, 79
Flgt												
Strng ^a								+	+	+	+	14, 20, 79
Habt												
Brrw				-		-		+	+	+		2, 7, 13, 16-17, 32-33, 40, 43-45, 47, 50, 52, 59, 60, 63, 65, 68, 72-73, 76, 78, 80-81
Clmb				-		-						7, 33
Clng				+		+		-			-	7, 34, 44, 47, 52, 59, 72, 75, 80
Sprwl				-								7, 44, 47, 59, 73
Swim				+		-	-		+	+	+	2, 7, 32, 50, 56, 65, 72, 77-78
Life												
Long	-		+				+		-	+		16, 26, 57, 70
Shrt	+		U						U			16, 26, 33
VShrt	+		-						+	-		16, 26, 33, 70

Trait	Altitude or Latitude	Stream Size	Temperature	Substrate Size	Stream Nutrients	Flow or Runoff	Flow Predictability	Flood Frequency	Low Flow Frequency	Low Flow Duration	Stream Flashiness	Sources
Resp												
Air			+			-	+	+	+			2, 16, 32, 53, 56, 59, 72-73, 78-79
Gill			U	+					U	U		31, 56, 72
Teg			-			+			-	-		2, 32, 53, 72-73, 77, 79
Rheo												
Both												No <i>a priori</i> predictions
Depo				-		-			+	+		2, 16, 24, 76, 79
Eros				+		+			-	-		2, 16, 51, 70, 79
Shpe												
Strm ^a				+/-		+/-	+	+/-	+/-	+		2, 16-17, 20, 24, 28, 30, 32, 40, 42-43, 49-51, 59, 61, 65, 70, 72-73
Size												
Large			-	+		-	+	-	-	-	-	2, 11, 20, 32, 43, 50, 54, 56, 65, 70, 72, 77
Med					-	+/-		-	-		-	56, 68, 72
Small			+/ U	-		+	-	+	+	+		2, 11, 16, 32, 35, 43, 50, 53-54, 56-57, 61, 63, 65, 68, 70, 72-73, 76-78
Swim												

Trait	Altitude or Latitude	Stream Size	Temperature	Substrate Size	Stream Nutrients	Flow or Runoff	Flow Predictability	Flood Frequency	Low Flow Frequency	Low Flow Duration	Stream Flashiness	Sources
None				+		+	+	-	-	-	-	2, 7, 10, 32, 50, 56, 65, 72, 77, 78-79
Strng				-		-	-	+	+	+	+	2, 7, 10, 32, 50, 56, 65, 72, 77, 78-79
Weak				+								10
Sync												
Well ^a	+/-		+/-	+			+	-	-	-	-	11, 17, 35, 59, 66, 70
Ther												
CIWm												No <i>a priori</i> predictions
Cold	+	-	-			+						2, 17, 32, 43, 67, 73
Warm	-	+	+			-						2, 17, 32, 43, 73
Trop												
CFilt		+		+	+	+	+/-	+/-	-	-	+/-	2, 4, 10, 12, 17, 18-19, 22-23, 25, 27, 29, 31, 34, 37, 41, 46, 54-55, 68, 70, 72-73, 77
CGath		+	+	+/-		-	+/-	+/-	+	+	+/-	4, 12-13, 17, 19, 22-23, 25, 27, 29, 34, 37, 41, 46, 50, 54-55, 63, 70, 78
Herb		-/U	+	+	+		+/-	+/-	-	-	+/-	2, 4, 10, 19, 21-23, 25, 29, 34, 37, 41, 46, 63, 68, 70, 81
Pred		N	+			-	+/-	+/-	+/-	+	+/-	4, 19, 22-23, 29, 34, 37, 41, 63, 69,

Trait	Altitude or Latitude	Stream Size	Temperature	Substrate Size	Stream Nutrients	Flow or Runoff	Flow Predictability	Flood Frequency	Low Flow Frequency	Low Flow Duration	Stream Flashiness	Sources
												72, 77
Shrd	-	+/-	-				+/-	+/-	+/-	+/-	+/-	4, 12, 18, 19, 22-23, 25, 29, 34, 37, 40-41, 46, 62-63, 74
Volt												
Multi	-		+	-	+		+	+	+	+	+	2, 6, 8-9, 16-17, 21, 28, 32-35, 38, 40, 42-43, 50, 58-59, 64, 68, 70, 73, 78
Semi	+		-		-	-	-	-	-	-	-	2, 6, 8, 16-17, 20-21, 32, 35, 40, 42-43, 56, 59, 70, 72-73, 77
Uni		U				-		-	-	-	-	16-17, 20, 34, 40, 42-43, 73, 77

Sources: 1 - Cordone and Kelley 1961, 2 - Hynes 1970a, 3 - Macan 1974, 4 - Vannote et al. 1980, 5 - Dudley and Anderson 1982, 6 - Ward and Stanford 1982, 7 - Cummins et al. 1984, 8 - Resh and Rosenberg 1984, 9 - Wolda 1988, 10- Plafkin et al. 1989, 11 - Poff and Ward 1989, 12 - Jeffries and Mills 1990, 13 - Barnes and Mann 1991, 14 - Mackay 1992, 15 - Power 1992, 16 - Ward 1992, 17 - Williams and Feltnate 1992, 18 - Scarsbrook and Townsend 1993, 19 - Kerans and Karr 1994, 20 - Townsend and Hildrew 1994, 21 - Cushing et al. 1995, 22 - Barbour et al. 1996, 23 - Fore et al. 1996, 24 - Koehl 1996, 25 - Wallace and Webster 1996, 26 - Williams 1996, 27 - Lorenz et al. 1997, 28 - Poff 1997, 29 - Smith and Voshell Jr 1997, 30 - Townsend et al. 1997, 31 - Wood and Armitage 1997, 32 - Giller and Malmqvist 1998, 33 - McCafferty 1998, 34 - Barbour et al. 1999, 35 - Dudgeon 1999, 36 - Gasith and Resh 1999, 37 - Harrington and Born 1999, 38 - Collier and Winterbourn 2000, 39 - Huryn and Wallace 2000, 40 - Cushing and Allan 2001, 41 - Royer et al. 2001, 42 - Wetzel 2001, 43 - Angelier 2003, 44 - Johnson et al. 2003, 45 - Dodds et al. 2004, 46 - Ofenböck et al. 2004, 47 - Heino 2005a, 48 - Heino 2005b, 49 - Robson et al. 2005, 50 - Statzner et al. 2005, 51 - Lancaster and Belyea 2006, 52 - Lepori and Hjerdt 2006, 53 - Zigliio et al. 2006, 54 - Allan and Castillo 2007, 55 - Battle et al. 2007, 56 - Bonada et al. 2007a, 57 - Dobson and Frid 2008, 58 - Dudgeon 2008, 59 - Merritt et al. 2008, 60 - Polunin 2008, 61 - Statzner 2008, 62 - Heino et al. 2009, 63 - Thompson et al. 2009, 64 - Clarke et al. 2010, 65 - Dolédec and Statzner 2010, 66 - Elosegi et al. 2010, 67 - Hamilton et al. 2010a, 68 - Larsen and Ormerod 2010, 69 - Miller et al. 2010, 70 - Řezníčková et al. 2010, 71 - Robertson and Wood 2010, 72 - Statzner and Bêche 2010, 73 - Thorp and Covich 2010b, 74 - Boyero et al. 2011, 75 - Culp et al. 2011, 76 - Walters 2011, 77 - Demars et al. 2012, 78 - Feio and Dolédec 2012, 79 - U.S. Environmental Protection Agency 2012, 80 - Yoshimura 2012, 81 - Mondy and Usseglio-Polatera 2013

A This trait has two states; the distribution of the second state is a compliment of the first. Thus the second state is not shown.

Results

1. Detecting response of single trait states

Using the traditional criterion of $p \leq 0.05$, all trait states were found to have significant relationships with some environmental variables, with semivoltinism having the fewest number of relationships with environmental variables (11) and cool/warm eurytherms having the most (67). The use of a traditional $p \leq 0.05$, as opposed to $p \leq 0.005$ or $p \leq 0.001$, has recently been called into question (Johnson 2013) and our analysis demonstrates the futility of this criterion. Of the possible 4756 relationships, 2667 were significant at $p \leq 0.05$, but most had very low Nagelkerke R^2 values, indicating limited ecological meaning. For example, 1931 of the 2667 significant relationships (72%) had a Nagelkerke $R^2 \leq 0.10$. Using our criterion of Nagelkerke $R^2 \geq 0.20$, 17 of the 20 traits exhibited at least one “strong” relationship (all but attachment, desiccation resistance, and shape). Conversely, the strongest univariate relationship was between the distribution of cold stenotherms and mean annual runoff ($R^2 = 0.54$). Of the remaining 17 traits, a total of 30 states (out of a possible 58) had strong relationships, with cold stenotherms having the most at 22 followed by warm eurytherms (20), weak swimmers (18), small size (17), and cool/warm eurytherms (17) (Figure 2.2a). Among environmental variables, 28 were involved in strong relationships (which we defined as Nagelkerke $R^2 \geq 0.20$), with mean annual runoff having the most (22 relationships) followed by conductivity (21), annual precipitation (19), and mean July air temperature (17) (Figure 2.2b).

We also found that for many traits with three states (e.g., voltinism, armoring, life span, swimming ability), two of those states had consistently strong relationships with environmental variables while the third state consistently had weak relationships. This may reflect, in part, the method of trait state designations, as discussed below. If this was the case, we determined if the

relative relationships between the two remaining states matched *a priori* expectations (see footnotes in Tables 2.4 and 2.6). For example, since the semivoltine trait state had consistently weak (Nagelkerke $R^2 < 0.20$) relationships, we assessed if the relationship between multivoltinism and univoltinism matched *a priori* expectations.

A priori variables included hydrological variables and an assortment of geographic, climatic, chemistry, and substrate variables. Hydrological variables included variables describing mean annual stream runoff (C.H.MAR), variance in stream flow (C.H.CV), frequency

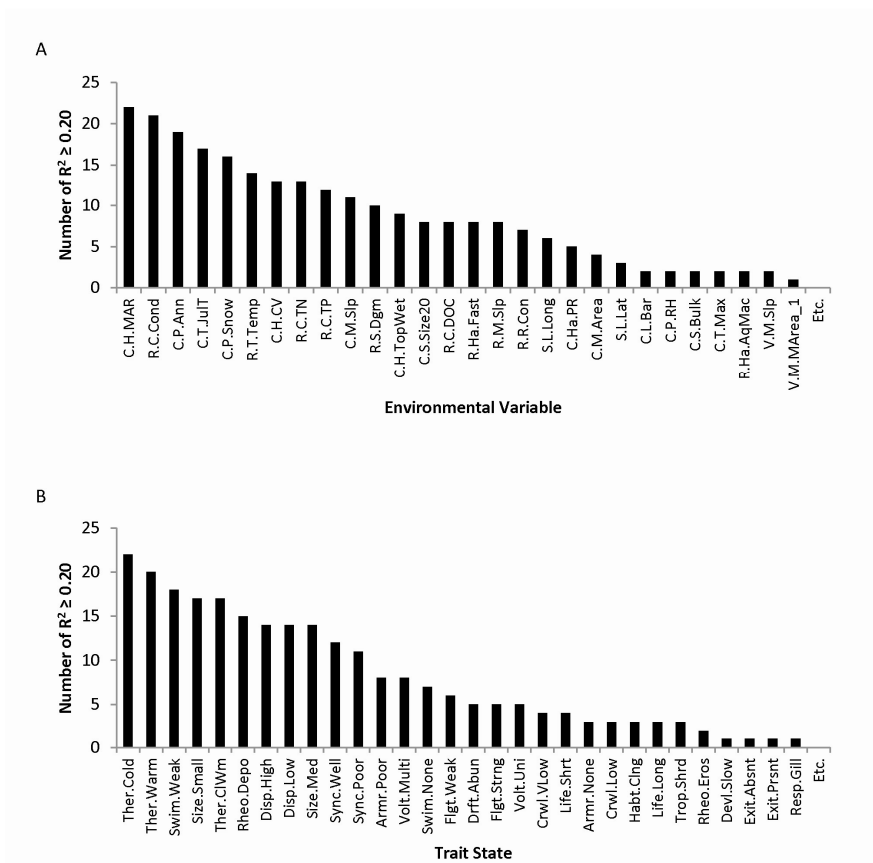


Figure 2.2: Number of univariate logistic regression relationships with a Nagelkerke R^2 index ≥ 0.20 for each A) environmental variable and B) trait state. Only variables and states with at least one relationship with $R^2 \geq 0.20$ are shown. All other variables are represented by the term “Etc.”.

(C.H.LCnt) and duration (C.H.LDurY) of low flows, frequency (C.H.HCnt) of high flows and time between (C.H.FldFree) floods, and measures of seasonality in flow (C.H.SprFl, C.H.SuFaFl). Only two of these variables, mean annual runoff (C.H.MAR) and Median annual coefficient of variation of daily flows (C.H.CV), exhibited relationships with $R^2 \geq 0.20$ (Table 2.4). All other measures of hydrological timing, duration, extreme conditions had only very weak relationships. The relative community composition of high female dispersal, small size, medium size, and multivoltinism matched *a priori* predictions for variance in stream flow. Low crawling ability and weak swimming ability contradicted *a priori* expectations for their relationship with variance in stream flow, while poor armor both matched and contradicted some *a priori* expectations. Low crawling rate, very low crawling rate, depositional preference, and thermal tolerance matched *a priori* expectations for mean annual runoff, but voltinism, swimming ability, size, and armoring did not. Mean annual precipitation was highly correlated with mean annual stream runoff (Spearman $r = 0.977$) and exhibited similar relationships with traits.

Other *a priori* environmental variables included measures of elevation (C.H.Elev) and latitude (S.L.Lat), stream size (C.H.Area, V.M.MArea_1), air and stream temperature in the summer months (C.T.JulT, C.T.Max, R.T.Temp), stream nutrients (R.C.Cond, R.C.DOC, R.C.TN, R.C.TP), and substrate size (R.Ha.Fast, R.S.Dgm). Each of these variables exhibited relationships with $R^2 \geq 0.20$, except elevation. The three measures of temperature all exhibited the same relationships with traits, but the strength of those relationships varied, with one (mean July air temperature) having the strongest relationships. The same was true for the four measures of stream nutrients, two measures of substrate size, and two measures of stream size, each set of variables exhibiting the same relationships, but with one variable having stronger relationships

Table 2.4: Results of logistic regression between insect traits and hydrological variables described in the *a priori* section above. The number is the Nagelkerke R^2 index from the univariate logistic regression analysis and the sign in the parentheses represents the direction of the relationship. The superscript indicates if the result matches *a priori* predictions (see footnotes). Only traits with an $R^2 \geq 0.20$ with at least one hydrological variable are included in the table. Relationships with $R^2 \geq 0.20$ are in bold. The abbreviations for the environmental variables names (i.e., column names) are described in Table 2.1. The abbreviations for the trait state names (i.e., row names) are described in Table 2.2.

	C.H.CV	C.H.MAR	S.L.Lat	C.M.Area	C.T.JulT	R.C.Cond	R.C.TN	R.S.Dgm
Armr.None	0.10 (-)	0.11 (+)	0.04 (+)	0.07 (-)	0.26 (-)	0.20 (-)	0.04 (-)	0.04 (+)
Armr.Poor	0.21 (+)^a	0.26 (-)	0.14 (-)	0.06 (+)	0.34 (+)	0.35 (+)	0.09 (+)	0.11 (-)
Crwl.Low	0.25 (-)	0.27 (+)^c	0.11 (+)	0.03 (-)	0.18 (-)	0.20 (-)	0.15 (-)	0.10 (+)
Crwl.VLow	0.20 (+)^b	0.32 (-)^a	0.11 (-)	0.05 (+)	0.14 (+)	0.20 (+)	0.19 (+)	0.13 (-)
Devl.Slow	0.07 (-)	0.19 (+)	0.02 (+)		0.04 (-)	0.09 (-)	0.19 (-)	0.21 (+)
Disp.High	0.23 (+)^a	0.39 (-)	0.11 (-)	0.13 (+)	0.26 (+)	0.33 (+)	0.23 (+)	0.17 (-)
Drft.Abun	0.09 (+)	0.28 (-)^a	0.02 (-)	0.08 (+)	0.03 (+)	0.14 (+)	0.21 (+)^b	0.22 (-)^b
Flgt.Strng	0.18 (+)	0.23 (-)	0.12 (-)	0.09 (+)	0.28 (+)	0.21 (+)	0.15 (+)	0.06 (-)
Habt.Clng	0.17 (-)	0.17 (+)	0.03 (+)		0.10 (-)	0.21 (-)	0.10 (-)	0.22 (+)^a
Life.Long	0.08 (+)	0.22 (-)	0.06 (-)	0.05 (+)	0.22 (+)^a	0.21 (+)	0.13 (+)	0.13 (-)
Life.Shrt	0.11 (-)	0.31 (+)	0.06 (+)	0.08 (-)	0.08 (-)	0.15 (-)	0.22 (-)	0.26 (+)
Resp.Gill	0.11 (-)	0.18 (+)	0.09 (+)		0.13 (-)	0.20 (-)	0.06 (-)	0.11 (+)

Rheo.Depo	0.30 (+)	0.34 (-)^a	0.08 (-)	0.18 (+)	0.25 (+)	0.42 (+)	0.24 (+)	0.22 (-)
Rheo.Eros	0.05 (-)	0.12 (+)			0.03 (-)	0.10 (-)	0.09 (-)	0.24 (+)
Size.Med	0.25 (-)^a	0.40 (+)^b	0.10 (+)	0.07 (-)	0.25 (-)^c	0.32 (-)	0.25 (-)	0.24 (+)^c
Size.Small	0.29 (+)^a	0.49 (-)^b	0.13 (-)	0.10 (+)	0.26 (+)^a	0.33 (+)	0.33 (+)	0.27 (-)^a
Swim.None	0.17 (+)	0.40 (-)^b	0.16 (-)	0.17 (+)	0.29 (+)	0.34 (+)	0.17 (+)	0.13 (-)
Swim.Weak	0.22 (-)^b	0.48 (+)	0.23 (+)	0.21 (-)	0.31 (-)	0.36 (-)	0.24 (-)	0.17 (+)
Sync.Well	0.16 (-)	0.32 (+)	0.17 (+)	0.12 (-)	0.36 (-)^a	0.34 (-)	0.17 (-)	0.18 (+)
Ther.CIWm	0.26 (+)	0.49 (-)	0.24 (-)	0.16 (+)	0.43 (+)^a	0.44 (+)	0.26 (+)	0.22 (-)
Ther.Cold	0.33 (-)	0.53 (+)^a	0.24 (+)^a	0.20 (-)^a	0.48 (-)^a	0.49 (-)	0.31 (-)	0.26 (+)
Ther.Warm	0.40 (+)	0.41 (-)^a	0.06 (-)	0.25 (+)^a	0.40 (+)^a	0.43 (+)	0.24 (+)	0.16 (-)
Trop.Shrd	0.08 (-)	0.14(+)		0.30 (-)^a	0.03 (-)	0.06 (-)	0.14 (-)	0.05 (+)
Volt.Multi	0.25 (+)^a	0.38 (-)	0.15 (-)	0.17 (+)	0.12 (+)	0.21 (+)^a	0.28 (+)^a	0.19 (-)
Volt.Uni	0.14 (-)	0.33 (+)^b	0.09 (+)	0.10 (-)	0.16 (-)	0.17 (-)	0.25 (-)^c	0.19 (+)

A The result matches at least some *a priori* predictions

B The result contradicts *a priori* predictions

C The result matches *a priori* predictions if substituted for an ineffective state (e.g., medium size used in lieu large size)

with traits (conductivity, mean substrate size and catchment area, respectively). The correlations for the variables with the strongest relationships are in Table 2.4. Thermal tolerance matched *a priori* predictions with latitude, catchment area, and temperature; long adult life span for July air temperature; size for July air temperature and substrate size; voltinism for stream nutrients; shredder functional feeding group for catchment area; and clinger habit for measures of substrate size. The abundant-in-drift trait state contradicted *a priori* expectations for fast water habitat and total nitrogen (representative of stream enrichment). The remaining $R^2 \geq 0.20$ relationships had no *a priori* predictions.

Several environmental variables lacking *a priori* expectations exhibited strong relationships with traits. Proportion of barren lands in the catchment and silica had strong positive and negative relationships, respectively, with the trait state of high emergence synchronization. Eleven other variables had strong relationships with at least two traits (Table 2.5), including topographic wetness (C.H.TopWet), proportion of riffle-pool sequences in the catchment (C.Ha.PR), slope (C.M.Slp), proportion of fine soils in the catchment (C.S.Size20), bulk soil density (C.S.Bulk), aquatic macrophytes (R.Ha.AqMac), proportion of reach with coniferous riparian canopy (R.R.Con), and longitude (S.L.Long).

2. *Detecting shifts in multiple state distributions within a single trait*

Nine of the 20 traits had significant multinomial regression models using the 32 environmental variables (Table 2.6) as explanatory variables. One example of a multinomial regression is given for each of the nine traits in Figure 2.3. Seven traits (armoring, adult life span, voltinism, female dispersal, synchronization of emergence, swimming ability, and size at maturity) had significant relationships for one log odds ratio, indicating that only two states exhibited a strong response along the environmental gradient. The two remaining traits, thermal

Table 2.5: Results of logistic regression between insect traits and environmental variables not described in the *a priori* section above, but have relationships of $R^2 \geq 0.20$ with at least two trait states. Valley and reach slope had relationships to traits similar to catchment slope, but the relationships were weaker. They were not included in the table. See Table 2.4 for the description of table symbols.

	C.H.TopWet	C.Ha.PR	C.M.Slp	C.P.RH	C.S.Bulk	C.S.Size20	R.Ha.AqMac	R.R.Con	S.L.Long
Armr.Poor	0.10 (+)	0.08 (+)	0.14 (-)	0.11 (-)	0.13 (+)	0.12 (+)	0.12 (+)	0.14 (-)U	0.02 (+)
Crwl.VLow	0.12 (+)	0.12 (+)	0.17 (-)	0.20 (-)	0.14 (+)	0.13 (+)	0.15 (+)	0.06 (-)	0.15 (+)
Disp.High	0.25 (+)	0.22 (+)	0.27 (-)	0.13 (-)	0.10 (+)	0.26 (+)	0.16 (+)	0.12 (-)U	0.15 (+)
Drft.Abun	0.14 (+)	0.17 (+)	0.14 (-)	0.11 (-)	0.05 (+)	0.11 (+)	0.15 (+)	0.02 (-)U	0.34 (+)
Exit.Prsnt	0.04 (+)	0.09 (+)	0.07 (-)	0.04 (-)		0.08 (+)	0.11 (+)		0.21 (+)
Flgt.Strng	0.14 (+)	0.08 (+)	0.10 (-)	0.08 (-)	0.08 (+)	0.20 (+)	0.07 (+)	0.16 (-)U	0.03 (+)
Rheo.Depo	0.25 (+)	0.17 (+)	0.25 (-)	0.08 (-)	0.09 (+)	0.27 (+)	0.13 (+)	0.16 (-)U	0.14 (+)
Size.Med	0.16 (-)	0.16 (-)	0.26 (+)	0.17 (+)	0.20 (-)	0.19 (-)	0.24 (-)	0.12 (+)	0.18 (-)
Size.Small	0.19 (+)	0.19 (+)	0.29 (-)	0.21 (-)	0.23 (+)	0.21 (+)	0.26 (+)	0.14 (-)	0.23 (+)
Swim.None	0.17 (+)	0.15 (+)	0.18 (-)	0.18 (-)	0.15 (+)	0.16 (+)	0.12 (+)	0.21 (-)	0.08 (+)
Swim.Weak	0.24 (-)	0.20 (-)	0.23 (+)	0.24 (+)	0.18 (-)	0.19 (-)	0.12 (-)	0.25 (+)	0.13 (-)
Sync.Well	0.19 (-)	0.13 (-)	0.22 (+)	0.10 (+)	0.14 (-)	0.18 (-)	0.06 (-)	0.25 (+)	0.03 (-)
Ther.CIWm	0.23 (+)	0.20 (+)	0.26 (-)	0.19 (-)	0.18 (+)	0.29 (+)	0.13 (+)	0.28 (-)	0.08 (+)
Ther.Cold	0.29 (-)	0.24 (-)	0.32 (+)	0.20 (+)	0.18 (-)	0.35 (-)	0.17 (-)	0.28 (+)	0.12 (-)
Ther.Warm	0.31 (+)	0.26 (+)	0.27 (-)	0.07 (-)	0.07 (+)	0.35 (+)	0.12 (+)	0.22 (-)U	0.21 (+)

Trop.Shrd	0.24 (-)	0.16 (-)	0.09 (+)	0.02 (+)		0.07 (-)	0.06 (-)	0.02 (+)	0.18 (-)
Volt.Multi	0.23 (+)	0.17 (+)	0.17 (-)	0.19 (-)	0.17 (+)	0.18 (+)	0.17 (+)	0.12 (-)	0.26 (+)
Volt.Uni	0.19 (-)	0.17 (-)	0.20 (+)	0.12 (+)	0.14 (-)	0.16 (-)	0.14 (-)	0.14 (+)	0.13 (-)

Table 2.6: The coefficients of the statistically significant ($p < 0.05$) multinomial regression models. Trait labels are in the first row and the ratio of two trait states from each model are labeled in the second row. The superscript indicates if the result matches *a priori* predictions (see footnotes). If the model was not significant, then the cell was left blank.

	Armor	Female Disp.	Adult Lifespan	Rheophily		Size at Maturity	Swim. Ability	Sync. of Emerg.	Thermal Tolerance			Voltinism
	Poor/ None	Low/ High	Long/ Short	Both/ Depo.	Ero./ Depo.	Med./ Small	Weak/ None	Poor/ Well	Cold/ CIWm	Warm/ CIWm	Warm/ Cold	Uni./ Multi
C.H.CV				-2.26	-2.61	-1.44 ^c			-2.16		7.56	
C.H.MAR		1.34	-1.86	2.02	2.48 ^a	1.39 ^b	1.51	-1.23	1.94		-10.13 ^a	1.51 ^b
C.H.TopWet				-2.77	-3.13	-1.37	-1.46		-2.03	7.04	9.07	
C.Ha.PR					-1.80				-1.22		6.13	
C.L.Bar									1.19			
C.L.Ever					1.97				1.16			
C.M.Area				-2.17					-1.58		7.10 ^a	
C.M.Slp		1.35		2.16	2.73	1.35	1.24	-1.24	1.81		-7.52	

	Armor	Female Disp.	Adult Lifespan	Rheophily		Size at Maturity	Swim. Ability	Sync. of Emerg.	Thermal Tolerance			Voltinism
	Poor/ None	Low/ High	Long/ Short	Both/ Depo.	Ero./ Depo.	Med./ Small	Weak/ None	Poor/ Well	Cold/ CIWm	Warm/ CIWm	Warm/ Cold	Uni./ Multi
C.P.Ann		1.43	-2.02	2.14	2.70	1.55	1.64	-1.27	2.02		-7.75	1.68
C.P.RH							1.42		1.59			
C.P.Snow				1.70	1.91	1.06	1.17	-1.28	1.80			
C.S.Bulk									-1.54			
C.S.Size20		-1.61		-2.65	-3.12				-2.29		9.18	
C.T.JulT	1.36	-1.32		-2.27	-2.46	-1.28 ^a	-1.52	1.59 ^a	-2.28		9.67 ^a	
C.T.Max									-1.12			
R.C.Cond	1.26	-1.41		-2.50	-2.93	-1.38	-1.53	1.45	-2.18		9.14	
R.C.DOC				-2.45	-3.00	-1.43			-1.71		8.48	
R.C.pH									-1.58			
R.C.TN				-2.63	-3.28	-1.72	-1.52		-2.14		8.50	-2.01 ^c
R.C.TP					-2.33	-1.32	-1.39	1.41	-1.91		6.98	
R.C.TSS					-1.99				-1.21			
R.Ha.AqMac					-2.49	-1.72			-1.80			
R.Ha.Fast				2.21	3.06 ^a			-1.28 ^a	1.77		-6.76	

	Armor	Female Disp.	Adult Lifespan	Rheophily		Size at Maturity	Swim. Ability	Sync. of Emerg.	Thermal Tolerance			Voltinism
	Poor/ None	Low/ High	Long/ Short	Both/ Depo.	Ero./ Depo.	Med./ Small	Weak/ None	Poor/ Well	Cold/ CIWm	Warm/ CIWm	Warm/ Cold	Uni./ Multi
R.M.Slp				2.35	2.84				1.76		-7.24	
R.R.Con							0.76	-0.86	0.98			
R.R.RchVeg					1.59							
R.S.Dgm				1.99	3.00 ^a	1.44 ^c			1.74		-5.93	
R.S.WallSq									1.78			
R.T.Temp							-1.73	1.94 ^a	-2.73		9.04 ^a	
S.L.Lat									1.25			
S.L.Long					-2.09	-1.15						
V.M.Slp									1.71			

A The result matches at least some *a priori* predictions

B The result contradicts *a priori* predictions

C The result matches *a priori* predictions if substituted for an ineffective state (e.g., medium size used in lieu large size)

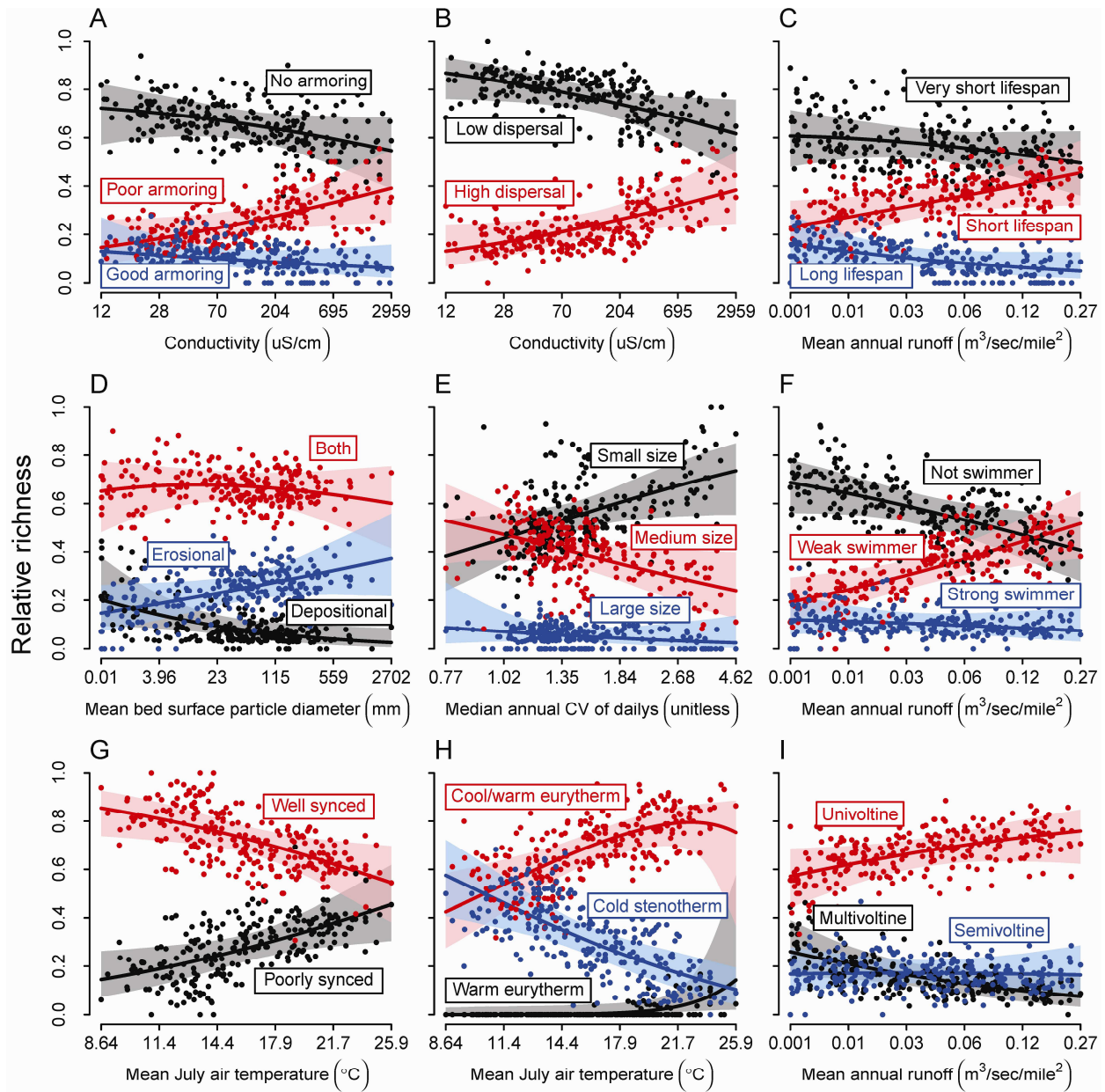


Figure 2.3: Predicted and actual relative richness values from the multinomial regression models for A) armoring and conductivity, B) female dispersal and conductivity, C) adult lifespan and mean annual runoff, D) rheophily and mean bed surface particle diameter, E) size at maturity and median annual coefficient of variation of daily flows, F) swimming ability and mean annual runoff, G) synchronization of emergence and mean July air temperature, H) thermal tolerance and mean July air temperature, and I) voltinism and mean annual runoff. The lines represent the model predictions, the shaded areas the 95% credible intervals for those predictions, and the points the actual data. Note that the scale of the x-axis is not linear. The x-values are transformed, but the actual un-transformed values are listed on the x-axis.

tolerance and rheophily, had significant relationships for more than one log odds ratio, indicating a strong interaction effect between all states. Rheophily had two significant ratios, Erosional obligate over depositional obligate and both erosional and depositional over depositional obligate. Both ratios shared the same coefficient sign, indicating that the depositional state is negatively associated with the other two states for environmental variables such as mean annual runoff and fast water habitat. The thermal tolerance trait had at least one significant relationship for all three possible ratios. The two ratios with the warm eurythermal trait as the numerator shared the same coefficient sign, indicating that warm eurytherms were negatively associated with the two other states for one environmental variable: topographic wetness (an index of slope and catchment area). The other two ratios, warm eurythermal over cold stenothermal and cold stenothermal over cool/warm eurythermal had 18 and 30 significant relationships, respectively.

3. Detecting correlations between multiple traits and multiple environmental variables.

All 77 environmental variables in the RDA accounted for 62.7% of the total variation in the trait data. The stepwise selection procedure selected 17 environmental variables that accounted for 47.5% of the total variation in the trait data. For the stepwise selection analysis, the first RDA axis accounted for 71.9% of explained variation (34.2% of total variation) and the second RDA axis accounted for 13.4% of explained variation (6.4% of total variation). The first RDA axis appears to represent a gradient of stream habitat conditions consisting of a combination of flow, temperature, and physical habitat variables (Figure 2.4a). Mean annual runoff and mean July air temperature had the strongest relationships with the first axis, followed by mean bed surface particle diameter, median annual coefficient of variation of daily flows, and proportion fine soils in the catchment. Trait states strongly associated with the first RDA axis

included short adult lifespan (Figure 2.4b), well synchronized emergence (Figure 2.4b), weak and no swimming ability (Figure 2.4c), high female dispersal (Figure 2.4c), small and medium size (Figure 2.4d), cold stenothermal and cool/warm eurythermal thermal tolerance (Figure 2.4e),

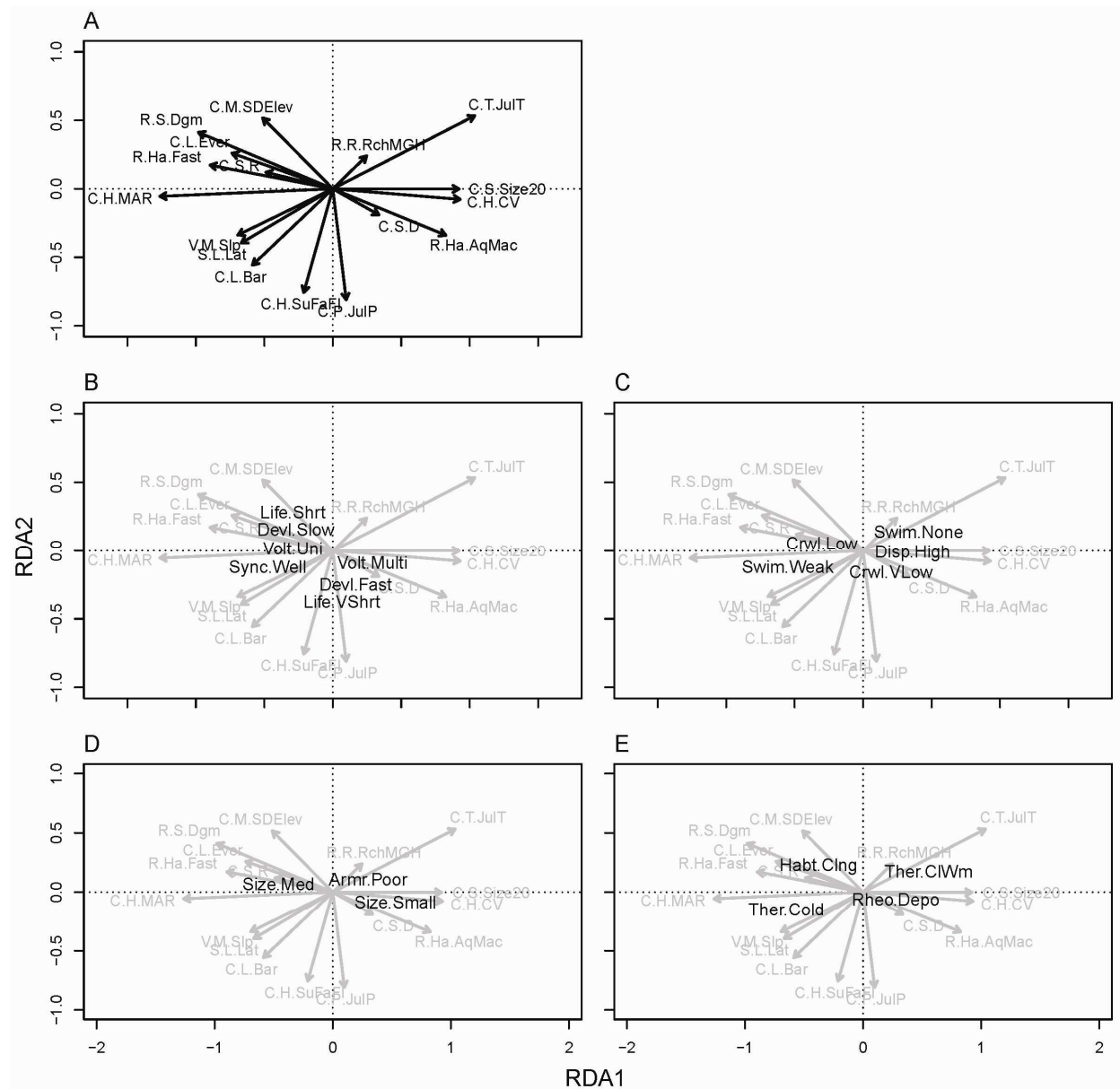


Figure 2.4: A) Location of the 17 environmental along the first two RDA axes superimposed with the location of the prominent traits from the B) life history, C) mobility, D) morphology, and E) ecology categories.

and clinging habit (Figure 2.4e). The second RDA axis represents a gradient of catchment climate and geomorphology. Mean July precipitation and proportion of mean of daily flows from July-October were strongly associated with the second RDA axis, followed by proportion of the catchment with barren land use, mean July air temperature, and standard deviation of catchment elevation. Trait states strongly associated with the second RDA axis were fast seasonal development (Figure 2.4a), very short adult lifespan (Figure 2.4a), and clinger habit (Figure 2.4d).

Discussion

We had mixed results concerning our *a priori* predictions. Nineteen of the 58 states had 36 strong univariate relationships ($R^2 \geq 0.20$) with variables with *a priori* predictions, but of those relationships 28 matched *a priori* predictions while only eight contradicted predictions. Environmental variables that had consistently strong relationships with traits in our 253 “reference” streams reflected general stream conditions instead of measures of hydrological extremes, valley configuration, land use, or riparian condition. Mean annual runoff, catchment precipitation, conductivity, mean July air temperature of catchment, total nitrogen and phosphorus, substrate size, slope, and coefficient of variation in daily flows had the strongest relationships, overall, with trait states. Other measures of stream hydrological disturbance (e.g., flood frequency, low flows) or natural land use did not have strong relationships, at least at the large scale. Some previous studies have found strong relationships between traits and measures of low flow. Miller et al. (2010), Brooks (2011), and Walters (2011) found traits such as exiting ability, life spans, crawling rate, armoring were correlated with stream diversions. Bêche et al. (2006) found that lifespans and desiccation resistance were correlated with low seasonal flows,

but only if intermittent streams were included in the dataset. Conversely, Feld et al. (2014) evaluated trait diversity across a wide range of hydrological disturbance ranging from least impacted to straightened, stagnant, and/or unshaded (but, not desiccated) streams in Germany, Poland, and the Netherlands. They found that there was minimal change in trait diversity across these hydrological gradients and if some species were reduced or lost, they were replaced by taxa with similar traits. They suggested that one reason for this result is that their traits only indirectly respond to hydrological disturbance. Our analysis, however, did incorporate traits that should have directly responded to hydrological disturbance (e.g., rheophily, development time), but we still found that, at a broad regional scale encompassing many climatic zones and hydrological conditions, traits did respond to the magnitude (C.H.MAR) and flashiness (C.H.CV) of flow, but did not respond to other measures of natural hydrological variation in perennial reference-condition streams. The positive response of traits in the previous studies involving intermittency and diversions, but lack of response to the same variables in our study, which only includes perennial streams, indicates that a large-scale, traits-based approach may not be effective in detecting some levels of disturbance in perennial streams, such as anthropogenically induced low flows that fall well within the range of natural flow regimes. Traits in our analysis did respond strongly to changes in the general condition of streams (e.g., stream chemistry, runoff, temperature) and it may be necessary to account for variation in these variables before using traits to detect some anthropogenic disturbances. For example, runoff and substrate variation between sites would need to be minimized in order to use a traits-based approach to detect changes in agricultural land uses or flood frequency.

One of the more remarkable results of this study was the lack of strong relationships with elevation. Most of the variables with the strongest relationships across all analyses, including

mean July air temperature, mean annual runoff, and conductivity, had a high correlation with elevation, which is often considered as a general surrogate for these metrics (e.g., Finn and Poff 2005, Tomanova et al. 2007). Some previous studies found that traits were correlated with elevation (Finn and Poff 2005, Cabecinha et al. 2007, Tomanova et al. 2007, Šporka et al. 2009), while others did not or had mixed results (Marchant et al. 1985, Ward 1986, Statzner et al. 2004). Our results suggest that elevation is not an appropriate surrogate for important climatic and geomorphic variables in large-scale studies that include a diverse array of climatic regions and land forms. Hawkins et al. (1997) has similar conclusions in the Sierra Nevadas, where aquatic insect assemblages tracked temperatures, but temperatures were unrelated to elevation.

Traits exhibiting robust relationships with environmental variables provide a baseline understanding about how stream communities respond to natural variation and possibly provide good indicators of anthropogenic changes to the stream system. Thermal tolerance, size, swimming strength, rheophily, voltinism, armoring, synchronization of emergence, and female dispersal all exhibited strong multivariate and univariate responses to our environmental data. Thermal tolerance, size at maturity, rheophily, armoring, and voltinism are also evolutionarily labile (Poff et al. 2006). Because these traits are relatively unconstrained according to phylogenetic groups, they may robustly respond to environmental changes across large scales, since traits restricted to specific phylogenetic groups will also be constrained according to evolutionary history and zoogeography. While swimming strength, emergence synchronization, and female dispersal are not as evolutionarily labile, their strong responses to environmental conditions signify a taxonomic preference for specific stream conditions. The lack of lability across taxa may complicate the use of these traits in bioassessment if the associated taxonomic groups are not present in the regional pool of taxa, resulting in an unpredictable trait response to

anthropogenic induced changes to the stream system. Other traits, such as maximum crawling rate, occurrence in drift, adult life span, and development were less responsive to natural gradients in streams, and thus of limited assessment value. Other traits, including adult exiting ability, shape, respiration, functional feeding group, functional habit, and attachment were largely responsive.

A priori hypotheses suggest that well synchronized emergence patterns would be advantageous if ideal conditions for reproduction are temporally limited, which may occur if temperatures are too low or high for the majority of the growing season (Williams and Feltmate 1992, Malmqvist 2002, Merritt et al. 2008). Mean July air temperature was negatively correlated with well synchronized emergence, supporting Merritt et al.'s (2008) argument that this trait would be advantageous at sites with very low temperatures most of the year. Infrequent, predictable disturbances should also promote well synchronized emergence, allowing all adults to emerge between disturbances (Poff and Ward 1989, Dudgeon 1999, Elosegi et al. 2010), but poorly synchronized emergence would be advantageous in frequent, unpredictable disturbance, allowing at least some adults to be present between disturbances (Yule 1996, Merritt et al. 2008). In our analysis, the lack of strong relationships with any measure of hydrological disturbance indicated that temperature may override hydrologic disturbance at large scales. This result may also be due to the fact that thermal gradients are fairly consistent across the western U.S.A. (e.g., warm or hot summer, cool or cold winter) while hydrological gradients vary greatly according to stream type (e.g., snowmelt streams, rainfall streams, intermittent streams). It may be more appropriate to detect emergence synchronization responses to hydrological variation within specific hydrological regimes.

Our results matched *a priori* predictions concerning the positive influence of temperature and nutrients on the occurrence of multivoltine taxa. Following *a priori* reasoning, the increase of energy through temperature or nutrients would allow taxa to grow and develop at a rate fast enough to complete multiple life cycles in a year, resulting in an evolutionary advantage (Ward 1992, Thorp and Covich 2010a). The positive relationships between multivoltinism and temperature and nutrient levels did not concur with previous studies of voltinism and stream nutrient and climatic conditions (Griswold et al. 2008, Lawrence et al. 2010), but those studies were spatially limited, encountering a limited range of climatic and stream conditions. No state had any strong relationships with frequency or duration of low or high flows, but multivoltinism was positively associated with flow variation (C.H.CV). Some studies have found that multivoltinism is more common in disturbed streams (Usseglio-Polatera and Beisel 2002, Mendez 2007, Tullos et al. 2009), but these studies encompassed human-caused disturbance and may have included more extreme conditions. Multivoltine relative richness increases with stream flashiness, but not necessarily with characteristics associated with natural high and low flows. But, that may change if the extremes of human disturbance are incorporated. Most *a priori* sources proposed an inverse relationship between the distributions of multivoltinism and semivoltinism, but the distribution of semivoltine taxa was not strongly associated with multivoltinism or any environmental variable. The univoltine state did have an inverse relationship with multivoltinism.

There has been much speculation as to how armoring may increase the fitness of organisms in streams. The presence of some form of body armoring could convey resistance to increased flows (Jeffries and Mills 1990, Giller and Malmqvist 1998), but also may be important in low flow areas as a defense against predation (Huryn and Wallace 2000). We found that

armoring was negatively correlated with stream runoff, a relationship also found in Walters (2011), which may support an anti-predator role. An *a priori* understanding of the relationship between armoring and disturbance is based on two conflicting concepts. Armoring may reduce injuries and mortality from scouring and moving substrate associated with disturbance (Huryn and Wallace 2000), but armoring may also reduce mobility and increase the time of growth, increasing the risk of desiccation or injury from scour (Gasith and Resh 1999). Our results did not support either presupposition for most measures of hydrological disturbance, but some level of armoring was positively correlated with variation in flows, indicating that a moderate amount of armoring may have an advantage in flashy streams, supporting the former *a priori* reasoning. These results are somewhat speculative: however, given the rather general classification of armoring we use and should serve as hypotheses for future research.

High female dispersal was strongly correlated with variables associated with slow-moving, highly eutrophic streams, such as high conductivity, low runoff, and high nitrogen. This state should be selected for in streams with a limited distribution of sites ideal for reproduction and development and was positively correlated with stream flashiness (as expected), but showed only weak correlation with other measures of hydrological disturbance, contradictory to *a priori* expectations. Previous research (Dolédec et al. 1999, Dolédec et al. 2006, Magbanua et al. 2010), did not find consistent relationships between high dispersal and anthropogenic disturbance, but Vieira et al. (2004) found that strong dispersal ability was positively associated with wildfire disturbance and Fisher and Gray (1981) found that some high dispersers recovered quickly after desert flash floods. These latter results may be due to the fact that high dispersers can colonize a stream from nearby streams after localized, intense disturbances, but not be very effective for long-term events, like low flow duration.

The rarity of the strong swimming trait state indicates it may not be suitable for lotic systems. With that said, however, our results still contradicted *a priori* predictions concerning swimming ability distributions along runoff and variance of flow gradients. Many authors in the *a priori* literature we reviewed argued that an organism swimming in high flow or runoff would be swept downstream and be selected against (Hynes 1970a, Giller and Malmqvist 1998, Feio and Dolédec 2012). We found, however, that the distribution of weak swimmers was positively correlated with mean annual runoff. Organisms may be swept downstream if they entered the water column in high flows, but the ability to move along the benthos would be advantageous. We found that some swimming ability was positively correlated with variation in daily flows, but had no relationship with low flows. Tullos et al. (2009) and Miller et al. (2010) did find that strong swimming ability was positively correlated with channel reconfiguration and increased variability, but also found that it was negatively associated with water withdrawals. Localized, short disturbance may facilitate dispersal via swimming ability, but our dataset only included perennial streams and we cannot determine if desiccation selects against swimming ability or for it.

Size at maturity exhibited strong relationships with multiple environmental variables. Communities dominated by small-sized individuals are found in warm, eutrophic streams, with small sediment size, low slope, low runoff, and/or flashy streams. These results concur with *a priori* expectations, except predictions for runoff, which indicated that smaller size would allow organisms to avoid flow by residing between substrates (Hynes 1970a, Angelier 2003, Dobson and Frid 2008). We saw a decrease in proportion of taxa with small size as runoff increased. It is difficult to compare our results to other studies that use various classifications of size. Some studies found that large taxa are negatively impacted by disturbance frequency (Scarsbrook and

Townsend 1993) and sandy and smaller sediment (Richards et al. 1997), which concur with our results, but most studies have found no consistent relationships between size and environmental variables, often only having one or two specific states (e.g., 2.5-5 mm, 5-10 mm, etc.) correlated with an environmental variable (Lamouroux et al. 2004, Bonada et al. 2007b, Tomanova and Usseglio-Polatera 2007, Lawrence et al. 2010).

Rheophily and thermal tolerance had the strongest relationships in the dataset. Both traits matched the *a priori* predictions concerning substrate size/habitat type and temperature respectively. Depositional preference was positively correlated with environmental variables associated with low gradient, slow moving streams and erosional preference with steep, fast moving streams. These relationships have been substantiated by other studies (Richards et al. 1996, Richards et al. 1997, Hutchens et al. 2009). All three thermal tolerance states had strong relationships with environmental variables. These strong relationships have also been found in other studies (Chessman 2009, 2012), although some studies have found a regional or site effect, with some sites having a strong relationship temperature and some having no relationship (Hamilton et al. 2010b, Stamp et al. 2010).

Traits with weak ($R^2 < 20$) correlations in our analysis may still be effective in detecting anthropogenic change. Our dataset only deals with perennial, reference condition streams and traits that lacked variation in natural stream state may become vital for survival when environmental conditions are pushed beyond natural limits. For example, we found no strong relationships for desiccation resistance in our analysis, but this result is not surprising given the perennial nature of our streams. If perennial streams become more intermittent due to climate change or withdrawals, this trait is predicted to become more vital for survival (Giller and Malmqvist 1998, Bêche et al. 2006). The same can be inferred for the respiration trait. While

we could not confirm any *a priori* predictions concerning respiration, the ability to breathe air is likely to become vital for taxa as oxygen or flow are reduced (Ziglio et al. 2006, Thorp and Covich 2010a). Tests of these *a priori* presuppositions, however, have met with mixed results. Effective use of traits requires both a reasonable understanding of trait distribution under natural conditions and effective application of trait to an appropriate scale or question.

Trait categorization

The effective use of traits in bioassessment also depends on how traits are categorized. We discovered an interesting trend concerning multinomial traits, particularly traits with three states. Most *a priori* predictions contrasted two dichotomous states, based on the assumption that intermediate trait states are moderate enough to allow organisms to survive in most environmental conditions and not track environmental variation. Some of our results supported this expectation. For example, common occurrence in drift, intermediate between rare and abundant occurrences in drift, had no strong correlations with any environmental variables in our dataset. But, for most other trichotomous traits we found a different trend, with one extreme state lacking strong relationships with environmental variables. There are at least four possible explanations for this trend. First, the categorical trait designation may not reflect natural sorting in the environment. For example, size at maturation is a continuous trait, but was separated into three categories in our trait dataset. In this analysis, we found that large and medium sizes had similar univariate responses, with medium having much stronger relationships. The similar relationships may indicate that these two states could be combined. A second possible explanation is lack of non-insects in our dataset. The strongest armoring state did not perform well, possibly due to the lack of gastropods in the dataset. A third possible explanation for the

poor results of this particular state is the amount of energy required to create strong armor. Extreme trait states may be too energetically expensive to be a viable state for most organisms and will be too underrepresented to strongly track environmental conditions. Good armoring, semivoltinism, high maximum crawling rate, and very short adult life span require a large investment of energy and resources as well as possible specialized adaptations. A final possible explanation would be the lack of environmental conditions outside of the reference lotic environment. The strong swimming state may be more correlated with environmental conditions if lentic habitats were included in the dataset.

Scales of traits-based bioassessment

A scale and climate specific application of traits to bioassessment contradicts the conclusions made by many Europe-based assessments of aquatic macroinvertebrate trait distributions in natural or semi-natural streams. Charvet et al. (2000) found there was little correlation between stream size, elevation, or slope and trait distributions in France and Europe. Statzner et al. (2001, 2005) argued that traits-based changes along a stream continuum were gradual and minimal, and trait distributions in Europe's semi-natural streams were fairly consistent. Statzner and Bêche (2010) expanded this argument using data from both the United States and Europe. A relatively consistent trait distribution across streams with natural conditions would mean a general traits-based bioassessment technique could be developed for the entire temperate region. Our results and other studies, however, indicate a different trait paradigm in the United States and elsewhere. Poff et al. (2010) found three distinct traits-based communities in the western United States, strongly associated with general ecoregions: humid regions, desert mountains, and plains. A regional, traits-based differentiation was also found by

Zuellig and Schmidt (2012) when they examined traits across the entire contiguous United States. They differentiated traits-based communities according to three general regions: western mountains, plains and lowlands, and eastern highlands. They also found that the use of traits to differentiate between land uses also required an ecoregional context. Schmera et al. (2013) also found that traits-based communities were dissimilar in three catchments spread across northern Finland. Our analysis indicated that large-scale environmental conditions change gradually, but those changes will result in very different traits-based community types perhaps in conjunction with ecoregional or climatic regions. One possible explanation for the discrepancy between our and European results is the fact that western streams experience greater shifts in climatic variables as they leave relatively humid mountains and enter the desert or plains. Zuellig and Schmidt (2012) argued that the greater inclusion of such streams in their dataset allowed them to detect trait community differences, while Statzner and Bêche (2010), which included data mostly from humid regions, could not. We argue that a single traits-based bioassessment reference-condition would not work for the western United States, but needs to be geographically constrained, perhaps by climatic or ecoregion regionalization, an approach advocated in a recent review of trait research in streams (Heino et al. 2013)

This study establishes a baseline understanding of how the distributions of traits change along environmental gradients in the heterogeneous and geographically large western U.S. Our results demonstrate that understanding and accounting for the climate and structure of stream systems is important for stream traits-based bioassessments. For large-scale analyses of anthropogenic disturbance, it will be important to detect anthropogenically-induced deviance from natural trait-environment relationships and for some disturbances, such as anthropogenic alteration of flood and low flood frequency or duration, it may be necessary to use small-scale

studies controlling for stream climate and geomorphology. We also believe that scale, stream structure, and climate are important in defining our understanding of how streams shape macroinvertebrate communities.

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CHAPTER 3: MODELING THE RESPONSE OF CLIMATE-SENSITIVE, AQUATIC INSECT TRAITS TO MULTIPLE ENVIRONMENTAL FACTORS IN THE WESTERN UNITED STATES USING A BAYESIAN PATH MODEL

Summary

Trait groups, where each species is grouped according to a trait classification, have been used in stream systems research for decades. Recently, two trait groups, cold stenotherms (taxa found only in cold water) and erosional obligates (taxa found only in habitat with fast flowing water) have been used to assess the effect of climate change on macroinvertebrate communities in streams. These studies, however, have mostly ignored the regional variation in trait responses to current climate conditions and the relative contribution of non-climatic variables (e.g., habitat, stream size) on climate-sensitive trait distributions. We developed a Bayesian path model for 251 sites in the western United States to determine how the distributions of cold stenotherms and erosional obligates are influenced by climatic and non-climatic variables in eight different climatic ecoregions. The models accounted for 40-85% of variation in cold stenotherm distributions in most ecoregions, but only accounted for 10-20% of the variation in erosional obligate distributions. The distribution of cold stenotherms was driven by different variables according to ecoregion, with temperature and runoff driving distributions in the three temperate ecoregions while other non-climatic variables drive cold stenotherm distributions in some warmer ecoregions. Our results indicate that in more temperate ecoregions, we may see a slight shift on cold stenotherm richness, but cold stenotherms are at their thermal limits in warmer ecoregions and are selecting non-climatic stream conditions that mitigate the effect of high temperatures.

Introduction

A major goal in climate change research is to understand how organisms respond to current climate conditions and predict how they may respond to increased temperatures due to climate change. The two most common approaches to assess organismal sensitivity to temperature are to use thermal ramping experiments to assess thermal thresholds (Cowles and Bogert 1944, Lutterschmidt and Hutchison 1997) and use environmental niche modeling to extrapolate potential habitat contractions and expansions from a species current distribution (Pearson and Dawson 2003). Both approaches assess climate vulnerability at the organismal level with the former requiring a significant investment of time and equipment for each species and the latter lacking the mechanistic link between and organism and the environment (Pearson et al. 2014). A third approach is to assess the response of organisms to their environment using species traits – life history, morphological, physiological, or ecological characteristics that provide a mechanistic link between the organism and its environment (McGill et al. 2006). This approach is appealing because it can be applied to an entire community and provides the theoretical justification for species sorting across a given environment (Webb et al. 2010). Traits have been used to describe community responses to climate change in multiple animal and plant systems (Foden et al. 2013, Frenette-Dussault et al. 2013, Pearson et al. 2014).

Community-level trait groups (i.e., grouping taxa in a community according to a nominal trait classification and using a community-level metric, such as richness or abundance) have been commonly used in aquatic ecosystems. Trait groups have been incorporated in stream ecosystem theory (Vannote et al. 1980) and used to assess the effect of various anthropogenic influences on stream ecosystems (Townsend and Hildrew 1994), such as hydrological alteration (Statzner et al. 2001, Carlisle et al. 2011), land use (Townsend et al. 1997, Zuellig and Schmidt 2012), and

stream eutrophication (Morais et al. 2009, Feio and Dolédec 2012). Climate change is expected to alter thermal and flow regimes in streams (Palmer et al. 2009, Poff et al. 2010, Filipe et al. 2013), which in turn should influence two ecological traits that can be considered “climate sensitive”, thermal preference and flow habitat preference (i.e., rheophily), since both traits were derived directly using taxa preference for temperature and flow. Thermal preference has been used to evaluate community responses to stream chemistry (Usseglio-Polatera and Beisel 2002, Horrigan and Baird 2008), hydrological alteration (Miller et al. 2010, Brooks et al. 2011), glaciation (Füreder 2007, Brown and Milner 2012), and stream size (Usseglio-Polatera et al. 2000, Usseglio-Polatera and Beisel 2002). Flow habitat preference has been used to evaluate community responses to flow and water velocity (Hughes et al. 2009, Steuer et al. 2009, Walters 2011), habitat type (Brabec et al. 2004), and stream geomorphology (Richards et al. 1996).

Thermal preference and flow habitat traits have recently been used specifically to address the effects of climate change in streams, with mixed success. Chessman (2009, 2012) found that the distribution of taxa that prefer cold water (hereafter referred to as cold stenotherms) and taxa associated with high flow habitats (hereafter referred to as erosional obligates) were being negatively influenced by increased temperatures and reduced flows in southeastern Australia, but attributed weak correlations between the climate-sensitive traits and climate over a 13-year period to both the influence of non-climatic and non-hydraulic environmental variables, as well as regional variability in climate. Poff et al. (2010) found that the current distribution of cold stenotherms and erosional obligates were associated with air temperature, precipitation, and runoff, but also found that some non-climatic variables, such as turbidity, had a strong influence. Hamilton et al. (2010) and Stamp et al. (2010) found that cold stenotherms were negatively associated with warmer air temperatures for some sites, but no relationships for others. These

analyses covered large geographic extents and assumed that these traits should respond in a similar fashion across the entire study area. It has been argued that the distributions of aquatic insect traits in natural or near-natural stream conditions should be similar across large temperate regions (Statzner and Bêche 2010), but other studies have found regional differences in trait groups (Poff et al. 2010, Zuellig and Schmidt 2012). Additionally, several studies have found that while thermal preference and rheophily traits were correlated with temperature and flow habitat respectively, they were also correlated with other associated variables, such as water quality, dissolved oxygen, and stream velocity (Usseglio-Polatera and Beisel 2002, Horrigan and Baird 2008, Poff et al. 2010). The influence of non-climatic variables appears to confound the relationship between these climate-sensitive traits and climatic variables, possibly due to regional variation in climate.

Predicting community response to climate change requires a 1) quantification of regional variation in trait responses to current climate conditions and specification of the sensitivity of species to climate variables across the region and 2) determination of the relative contribution of non-climatic variables (e.g., habitat, stream size) on trait distributions. These two issues have never been addressed together in stream ecosystems. Our aim here is to develop predictive models for aquatic insect traits in the western United States using both a regional context and incorporating variables, both climatic and non-climatic, described in the literature as drivers of cold stenotherm and erosional obligate distributions. The western United States is climatically variable, ranging from hot desert to temperate rainforest climates, and we hypothesize that the distributions of cold stenotherms and erosional obligates are more closely tied to temperature and hydrology in the more temperate regions, but since the distribution of these traits would already be constrained in more climatically harsh environments (e.g., the Great Plains, Mediterranean

California), other factors would mitigate the effect of high temperatures or low flows and would therefore be more important in describing trait distributions. Our reasoning is that the cold stenotherm and erosional obligate traits are explicitly defined according to climate sensitivity and if organisms with these traits are found in marginal nearly unsuitable habitat, then they are already at their thermal or flow limits and must compensate by inhabiting portions of the stream that buffer or insulate against such conditions. If this reasoning is correct, then the distributions of cold stenotherms or erosional obligates should gradually change with temperature or fast water habitat well within their thermal or flow limits, but once they near their limits (i.e., approach a threshold), those relationships break down and non-climatic relationships begin to emerge. To test this hypothesis, we developed a Bayesian path regression model for natural or near-natural streams in eight different climatic regions (i.e., ecoregions) in the western United States, incorporating an *a priori* understanding of how environmental factors drive the distribution of cold stenotherms and erosional obligates. The goal of our analysis not to make specific quantitative predictions concerning community responses to climate change, but instead gain a greater understanding of how traits currently respond to their environment and infer how those relationships may change due to climate change. Other methods, such as niche modeling, are more conducive to such predications and will be utilized in Chapter 4.

Methods

We selected 251 reference, or least-impacted, sites from the U.S. Environmental Protection Agency's (USEPA) Environmental Monitoring and Assessment Program – Western Pilot Study (WEMAP). In the WEMAP study, stream sites were selected in 12 western U.S. states using a stratified random design (Stoddard et al. 2005a), being stratified according to state, Strahler order (Strahler 1957) and ecoregion (Omernik 1987). Thirteen hundred and forty sites

were sampled from 2000 to 2004, mostly during summer months (with some May and October), with biological, chemical, and physical habitat data collected at each site following the procedures in Peck et al. (2006). The reference condition of each site was assessed at the reach-scale (Stoddard et al. 2005a) using phosphorus, nitrogen, chloride, sulfate, pH, turbidity, a riparian disturbance index, % fine substrates, and canopy density. Reference condition was also assessed at the catchment-scale (Chapter 2) using dams and reservoirs, pipes/conduits and canals/ditches, roads, land use, population density, and National Pollutant Discharge Elimination System pollutants. Specific criteria for reference condition are found in Stoddard et al. (2005a) for the reach-scale and Chapter 2 for the catchment-scale. We only included sites that met reference criteria at both reach and catchment scales. We also eliminated some sites found in the same stream network of another site. If two sites were found in the same stream network and were ≤ 6 km apart, we randomly eliminated one of the sites to reduce the effect of spatial autocorrelation between sites. Full details on the lack of independence between sites and our rationalization for eliminating sites ≤ 6 km apart are found in Chapter 2. Finally we removed sites with ambiguous placement in our Geographic Information System (GIS), poorly defined watersheds, without biological samples, or without environmental variables used in this analysis.

We further separated the 251 sites into ecoregions. The goal of this analysis is to understand how organisms restricted to low stream temperatures and fast flowing habitat respond to their environment, but we would not expect these organisms to respond in a similar fashion across different climatic regions. We separated our sites according to eight ecoregions that we modified from Omernik's level-I ecoregions (Omernik 1987) in way that we felt best reflected temperature and flow regimes in the western U.S. We kept Omernik's desert, Mediterranean, and plains ecoregion designations, but modified the remaining five ecoregions. We combined

Omernik's Southern Semi-arid Highlands and Temperate Sierras ecoregions in Arizona into a single ecoregion, our Southern Dry Highlands ecoregion, which had drier climatic conditions than other mountainous regions to the north. We combined the western and northern Cascade Mountains with Omernik's Marine West Coast Forest ecoregion into our Northwestern Wet Forests, a region which experienced some of the highest precipitation in the 48 states and markedly different hydrological and thermal regimes than other, drier mountainous areas in the western United States. We broke the remaining portions of Omernik's Northern Forested Mountains ecoregion into three ecoregions. Our Klamath Mountains ecoregion in northern California and southern Oregon contained mountainous flora and fauna, but had very dry, warm summers. We divided the remaining mountains according to latitude with the Middle Temperate Mountains ecoregion (consisting of the Sierra Nevadas, Wasatch and Uinta Mountains, and the southern Rockies of Colorado) being lower in latitude with warmer summers. The Northern Temperate Mountains ecoregion (consisting of the northern and middle Rockies, eastern Cascades, and Blue Mountains) had generally shorter, cooler summers. Our resulting dataset included 251 sites across eight ecoregions in 12 western U.S. states (Figure 3.1).

We selected two traits, thermal preference and rheophily, to assess how stream insect communities respond to the complex interaction of environmental variables in streams. The two traits are taken from a modified version of the Poff et al. (2006) database and are nominal, with three categories each. We focused our analysis on one category for each trait, using cold stenothermal/cool eurythermal (i.e., prefers 0-15 °C), hereafter referred to as cold stenotherm, for temperature preference and erosional obligate for flow habitat preference. We transformed the WEMAP biological richness data into a trait metric by summing the number of taxa at a site assigned to that trait category and dividing by the total richness. Richness was recorded at the

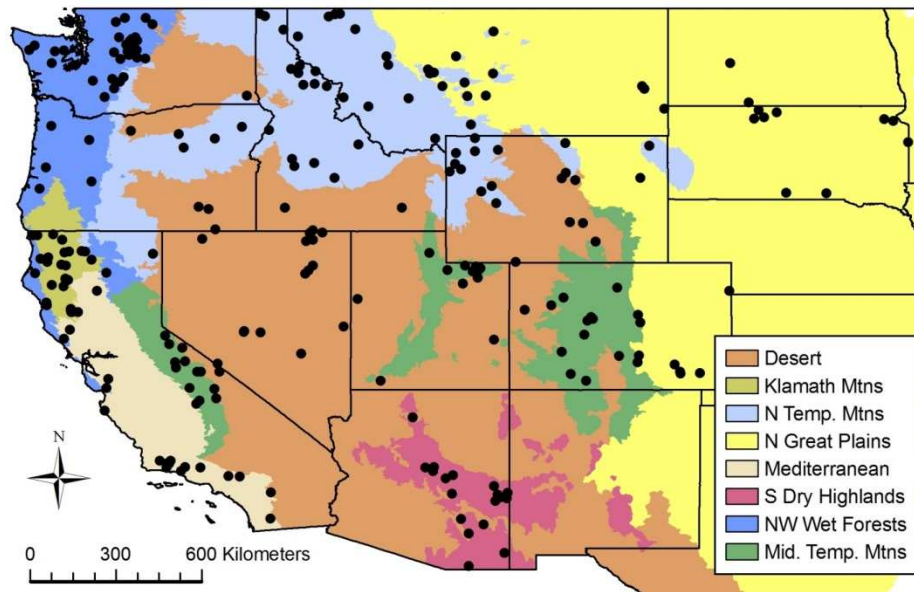


Figure 3.1: The distribution of WEMAP sites across modified ecoregions used in this paper.

genus-level for most taxa except Chironomidae, which was recorded at the sub-family level. The WEMAP biological data was collected from 11 transects at each site and were composited into a single sample for the site and up to 500 (± 50) individuals were identified to the lowest feasible taxonomic levels (usually genus) using a fixed count procedure (Stoddard et al. 2005a).

We included environmental variables in our models that have a theoretical connection to the distribution of cold stenotherms and erosional obligates at the catchment, valley, or reach scale. The theoretical justifications for the selection of our environmental variables are further elaborated in the model justification sections in the methods. The reach-scale variables were collected at each EMAP site (Stoddard et al. 2005a, Stoddard et al. 2005b) using the procedures from Peck et al. (2006), Kaufmann et al. (1999), and Kaufmann et al. (2008) and are: 1) mean width/depth ratio of reach, 2) mean mid-channel canopy density, and 3) proportion of the reach that is fast water habitat (e.g., riffle, run). The valley-scale geomorphology variables, valley slope and valley entrenchment, were derived by the Brian Bledsoe lab at Colorado State

University using the techniques found in Cuhaciyar (2006) and the National Elevation Dataset 30-meter resolution Digital Elevation Models (Gesch 2007) in a GIS. The watershed-scale climatic variables, mean July air temperature and mean annual precipitation, were derived from the 800-m-resolution Parameter-elevation Regressions on Independent Slopes Model (PRISM) database (30-y period of record from 1971–2000; PRISM Climate Group, Oregon State University, Corvallis, Oregon; <http://www.prismclimate.org>). Finally, the three watershed-scale hydrological variables were developed by the Daren Carlisle lab at the USGS using the random-forest methods found in Carlisle et al. (2010) and are: 1) mean annual runoff (mean annual flow standardized according to watershed), 2) proportion of flow attributed to baseflow (hereafter referred to as baseflow), and 3) mean total low flow pulse duration per year. We partitioned the data according to ecoregion, transformed the environmental variables approximate normal distributions, and standardized the environmental data.

Path diagrams - relationships between variables

The relationships between environmental variables and traits are complex with multiple possible pathways of influence. To adequately understand these relationships, we developed path diagrams using current theory about stream structure and stream ecology to outline the causative relationships between environmental variables and their influence on trait distributions. These path diagrams include direct causal relationships and indirect relationships through an intermediary environmental variable. We will first describe the relationships between trait groups and the environmental variables and then describe the inter-relationships between environmental variables.

Cold stenotherm model justification – The ultimate factor regulating cold stenotherm distribution is water temperature, but a single measure of stream temperature at the time of

collection is not adequate in predicting the distribution of these organisms. A single measure would not capture the spatial and temporal variations that test thermal limits of cold stenotherms as well as provide thermal refuges. Poole and Berman (2001) describe three general categories of environmental variables that influence and mediate stream water temperature: drivers, buffers, and insulators. Drivers are independent of stream structure and provide the temperature template by adding or removing heat from the stream system (e.g., climate). Buffers and insulators are components of the stream system and floodplain that influence stream temperature. Buffers modulate heat transfer between components of the stream system (e.g., stream geomorphology), resulting in temperature variation. Insulators mitigate the addition or removal of heat into the stream system (e.g., canopy cover). Only by including the effect of drivers, buffers, and insulators can we attempt to determine how cold stenotherms use the temporal and spatial variations in stream temperature to avoid crossing thermal thresholds and how increases in temperature due to climate change may affect these organisms.

We selected drivers, buffers, and insulators available in our dataset that we felt most influenced the distribution of cold stenotherms (Table 3.1). Cold stenotherms are influenced by the seasonal means, extremes, and variance in stream temperature as well as the availability of thermal refuges, but recent research also indicated that thermal preference was influenced by physiological constraints, particularly sensitivity to the amount of dissolved oxygen available (Verberk and Calosi 2012, Verberk and Bilton 2013). We selected the variables in Table 1 using reasoning found in Hynes (1970), Poff et al. (1997), Giller and Malmqvist (1998), Poole and Berman (2001), Allan and Castillo (2007), Rolls et al. (2012), and Verberk and Bilton (2013).

Table 3.1: The drivers, buffers, and insulators influencing the distribution of cold stenotherms in streams with descriptions of the theoretical relationships. The +, -, or +/- signs at the end of the description indicate positive, negative, or variable theoretical relationships with the trait distribution, respectively.

Environmental		
Influence	Variable	Relationship with stream temperature
Drivers	Mean July air temperature of the catchment (°C; Temp)	The atmosphere conducts heat into or out of stream water and is a surrogate for solar radiation. This variable is a measure of potential thermal maximum, since our data consists of mean monthly temperatures and July had the highest temperature for most sites. (-)
	Mean annual runoff (ft ³ /sec/mile ² ; MAR)	The speed and volume of water movement in a stream system mitigates the influence of atmospheric heat exchange (i.e., thermal inertia), provides dissolved oxygen, and indicates the relative influence of upstream thermal and chemistry conditions. (+)
	Baseflow (total baseflow/total flow)	A higher proportion of baseflow potentially receives more thermally stable water from subsurface pathways, minimizing the influence of atmospheric temperature fluctuations year-round and minimizing extreme air temperatures during the summer months. (+)
Buffers	Proportion of reach with fast water habitat (Fast)	Fast water habitats may provide a habitat for oxyconformers, providing faster oxygen replenishment. Some fast water habitats, such as riffles, also have higher substrate complexity and larger open spaces between

		substrate, providing physical refuges from surface temperatures and close contact to thermally stable hyporheic effluent where it occurs. (+)
Mean width/depth ratio of reach (m/m; WD)		The relative depth of stream describes the proportion of stream available to atmospheric convection and solar radiation as well as how effectively heat is transferred throughout the stream. (-)
Mean valley entrenchment - width based (Entrench)		A measure of valley morphology; influencing topographic shading of the stream (i.e., shading from the hillslope landmass), the potential size of the floodplain aquifer, and potential hyporheic inflow. (+/-)
Mean total low flow pulse duration per year (proportion; LowDurY)		A long period of reduced water volume, with corresponding increases in surface air to volume ratio; decreases the ability of streams to buffer against variation and extremes in air temperature. (-)
Insulators	Mean mid-channel canopy density (proportion; MidCan)	Canopy cover reduces insolation and radiant heating. (+)
	Mean slope of the valley above the site (unitless; Slope)	Greater slope increases stream turbulence and flow rate, factors that can increase dissolved oxygen availability. (+)

These relationships are shown in the path diagram in Figure 3.2. Precipitation does not have a direct causal relationship with cold stenotherms, but does have indirect effects through hydrology, riparian, and stream habitat variables. Although, other variables, such as geology, also have indirect effects on cold stenotherms through hydrology and habitat, they were not included since the focus of this analysis is on climatic variables.

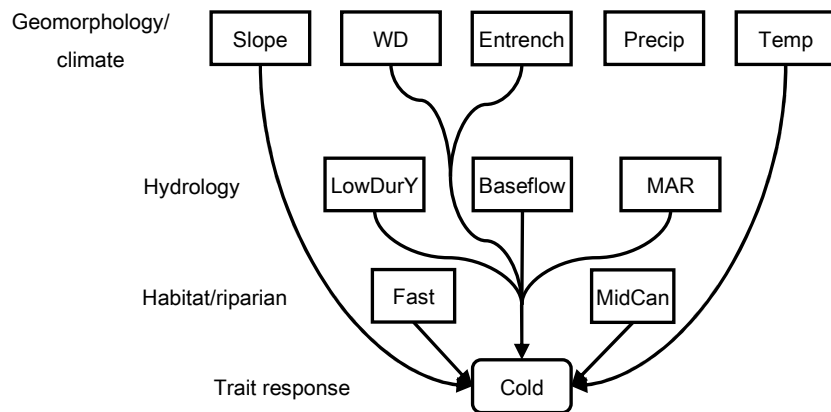


Figure 3.2: The path diagram of the direct causal relationships between cold stenotherms with climate, geomorphology, hydrology, riparian, and stream habitat variables. Abbreviations are listed in Table 3.1

Erosional obligate model justification – The erosional obligate model is more straightforward than the cold stenotherm model with the proportion of fast-water habitat being the ultimate driver of erosional obligate distribution. Erosional obligates need high flow conditions to provide oxygen and food while a large substrate size provides refugia and traps for organic matter. Both conditions are typified in fast-water habitat (Hynes 1970, Ward 1992, Lancaster and Belyea 2006). Stream size, lithology (including sediment size), valley confinement, stream flow, and slope are the main factors in developing fast water habitat types (Brussock et al. 1985, Montgomery and Buffington 1993, Montgomery and Buffington 1997, Church 2002, Wohl and Merritt 2005). Changes in slope and stream flow can also compensate

for a lack of ideal fast water habitat for erosional obligates. For example, erosional obligates typically do not inhabit pools, but some pools in high slope streams, such as plunge pools or step pools, experience significant water velocity or turbulence (Wilcox and Wohl 2007) and could provide conditions suitable for erosional obligates. Additionally, low flows can disrupt favorable conditions in fast water habitat. Temperature, although an important component of climate change, was not included in this model because it has no mechanistic link to habitat preference and the correlation between cold stenotherm and erosional obligate distributions is low (Spearman r : 0.176). We selected the variables that act as drivers, compensator, or disrupters of erosional obligates (Table 3.2) using reasoning found in Brussock et al. (1985), Hawkins et al. (1993), Wilcox and Wohl (2007).

Table 3.2: The drivers, compensators, and disrupters influencing the distribution of erosional obligates in streams with descriptions of the theoretical relationships. The +, -, or +/- signs at the end of the description indicate positive, negative, or variable theoretical relationships with the trait distribution, respectively.

Environmental		
Influence	Variable	Relationship with stream temperature
Driver	Proportion of reach with fast water habitat (Fast)	Erosional obligates require habitat with constant flowing water and coarse sediment typified by fast flowing water habitat. (+)
Compensate	Mean slope of the valley above the site (Slope)	Typically depositional habitat in streams sections with high slope experience high water velocities and turbulence that can provide suitable habitat for erosional obligates. (+)

	Mean annual runoff (MAR)	High runoff carries greater oxygen and food and may provide suitable conditions in some portions of depositional habitat for erosional obligates. (+)
Disrupt	Mean total low flow pulse duration per year (LowDurY)	During long periods of reduced water volume, sections of the reach that are typically defined as fast water habitat can experience decreased flows and sediment accumulation making it inhospitable for erosional obligates. (-)

These relationships are shown in the path diagram in Figure 3.3. Temperature has no effect on erosional obligates, but precipitation has indirect effects through hydrology and stream habitat variables.

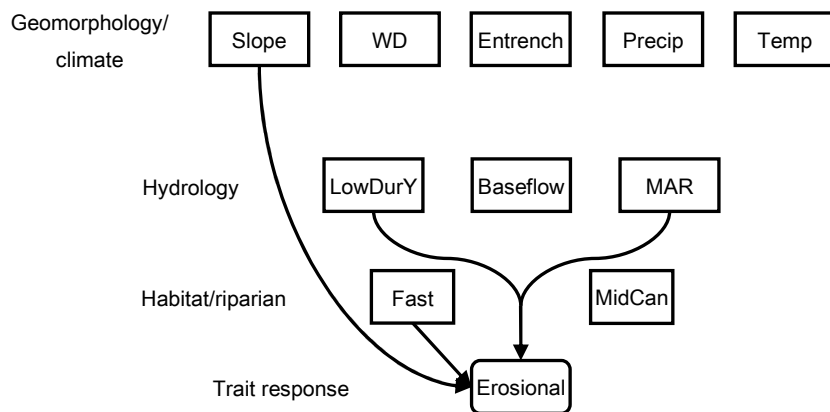


Figure 3.3: The path diagram of the direct causal relationships between geomorphology, hydrology, and stream habitat variables with erosional obligates

Environmental model justification – Five of the ten environmental variables used in this analysis are also influenced by other variables in the model. Mean annual runoff, baseflow, and

low flow duration are influenced by the amount of precipitation in the watershed and the geomorphology of the reach and valley. The proportion of fast-water habitat in the reach is influenced by hydrological and geomorphic factors. Canopy cover is influenced by climate, hydrology, and geomorphology. These relationships are described in Table 3.3. Other stream and watershed characteristics with only an indirect influence on cold stenotherm or erosional obligate distributions were not included in the model. For example, catchment geology, soil configuration, and upland vegetation are all significant drivers of baseflow (Price 2011), but they do not directly influence the distribution of cold stenotherms, rather indirectly through hydrologic flow paths. The one exception to this exclusion of strictly indirect factors is mean annual precipitation (Precip). Because this study aims to determine how climate change influences stream communities, it is important to know how tightly linked precipitation is to the environmental variables directly linked to cold stenotherm and erosional obligate distributions.

Table 3.3: The relationships between environmental variables in the Bayesian path regression model. The +, -, or +/- signs at the end of the description indicate positive, negative, or variable theoretical relationships with the trait distribution, respectively.

Variable	Relationships with other environmental variables
Mean annual runoff (MAR)	<ul style="list-style-type: none"> - Mean annual precipitation for the catchment (Precip) provides the maximum volume of water available to the stream system. (+) - A greater mean slope of the valley above the site (Slope) increases the velocity of stream water. (+) - Mean width/depth ratio of reach (WD), a measure of stream cross-section during sampling time (approaching baseflow conditions), describes the dimensions of stream movement and the relative

	influence of bed friction on velocity. (-)
Baseflow	<ul style="list-style-type: none"> - The amount of annual precipitation for the catchment (Precip), interacting with multiple variables, such as geology, provides the major source of groundwater into the watershed. (+) - Mean slope of the valley above the site (Slope) reduces the rate of water infiltration and retention in the soil and, ultimately, the inclusion that water as a component of baseflow. (-) - Mean valley entrenchment (Entrench) is an indicator of the amount of alluvial plain and valley storage available for subsurface water. (-)
Mean total low flow pulse duration per year (LowDurY)	<ul style="list-style-type: none"> - Mean annual precipitation for the catchment (Precip) provides the maximum volume of water available to the stream system. (-) - Greater channel incision (WD) and mean valley entrenchment (Entrench) reduces the surrounding water table, leading to longer low flow durations during the dry season. (-) - Greater mean valley entrenchment (Entrench) reduces the surrounding water table and soil infiltration rates (+) - Mean slope of the valley above the site (Slope) reduces precipitation infiltration and storage, reducing the available groundwater during dry seasons. (+)
Proportion of reach with fast water habitat (Fast)	<ul style="list-style-type: none"> - Streamflow, represented by total runoff (MAR) and proportion of relatively stable flow (Baseflow), mean valley entrenchment (Entrench), a measure of channel confinement, and mean slope of the valley above the site (Slope) influence the transport capacity in a

- stream and what habitats result from substrate transport. (+)
- Some fast water habitats, such as riffles, form only under specific range of mean width/depth ratios of the reach (WD). (+)
- Mean mid-channel canopy density (MidCan)
- Mean annual precipitation for the catchment (Precip) provides the volume of water available for plant growth. (+)
 - High mean July air temperature of the catchment (Temp) places additional stress on plants due to high transpiration and reduce overall water volume available for plants. (-)
 - Lengthy periods of low-flow (LowDurY), would not provide adequate water for some riparian vegetation. (-)
 - Mean slope of the valley above the site (Slope) influences stream power, which influences bank degradation and the establishment of riparian vegetation. Slope also effects water retention in the soil available for plant use. (-)
 - Mean valley entrenchment (Entrench) can limit the amount of suitable riparian corridor available for riparian vegetation and can affect valley storage available for water, which may limit plant growth. (-)

References for relationships – **Mean annual runoff**: Giller and Malmqvist (1998), Knighton (1998), and Allan and Castillo (2007); **Baseflow**: Singh (1968) and Price (2011); **Low-flow duration**: Vogel and Kroll (1992), Marston (1994), and Smakhtin (2001); **Fast-water habitat**: Montgomery and Buffington (1993), Montgomery and Buffington (1997), Church (2002), and Buffington et al. (2003); **Mean mid-channel canopy density**: Naiman and Décamps (1998), Smakhtin (2001), and Naiman et al. (2005).

Based on the reasoning above, we developed the environmental path diagram shown in Figure 3.4. The solid lines represent the causal relationships between variables and the dashed

lines represent non-directional, correlative relationships between variables. The non-directional correlations between the variables in the model account for confounding factors between variables, such as elevation or watershed area. Correlations are shown in Figure 3.4a, causal relationships between hydrologic metrics and geomorphology and precipitation shown in Figure 3.4b, causal relationships between fast water habitat/canopy cover and hydrology, geomorphology and climate shown in Figure 3.4c. All these relationships, plus the relationships with the traits, are combined into one path analysis each for the two trait variables, shown in figure 3.5, with Figure 3.5a showing the full model for cold stenotherms and Figure 3.5b showing the full model for erosional obligates.

Model Development

Our data consist of multiple environmental variables at multiple scales that have complex relationships with both direct influences on the trait data and indirect influences through an intermediary variable (i.e., mediation; Warner 2013). Path regression analysis is an ideal approach to evaluate the validity of theoretical direct and indirect relationships between variables in complex ecological systems (McCune and Grace 2002). Path regression analysis performs simultaneous regression analyses and allows for multiple *a priori* causal pathways in the model as well as correlation between independent variables, allowing for a measure of both direct and indirect effects. The strength of each direct causal relationship is represented by the regression coefficient and the indirect effects are the product of coefficients. For example, if annual precipitation has a significant direct influence on mean annual runoff with a coefficient of 0.75

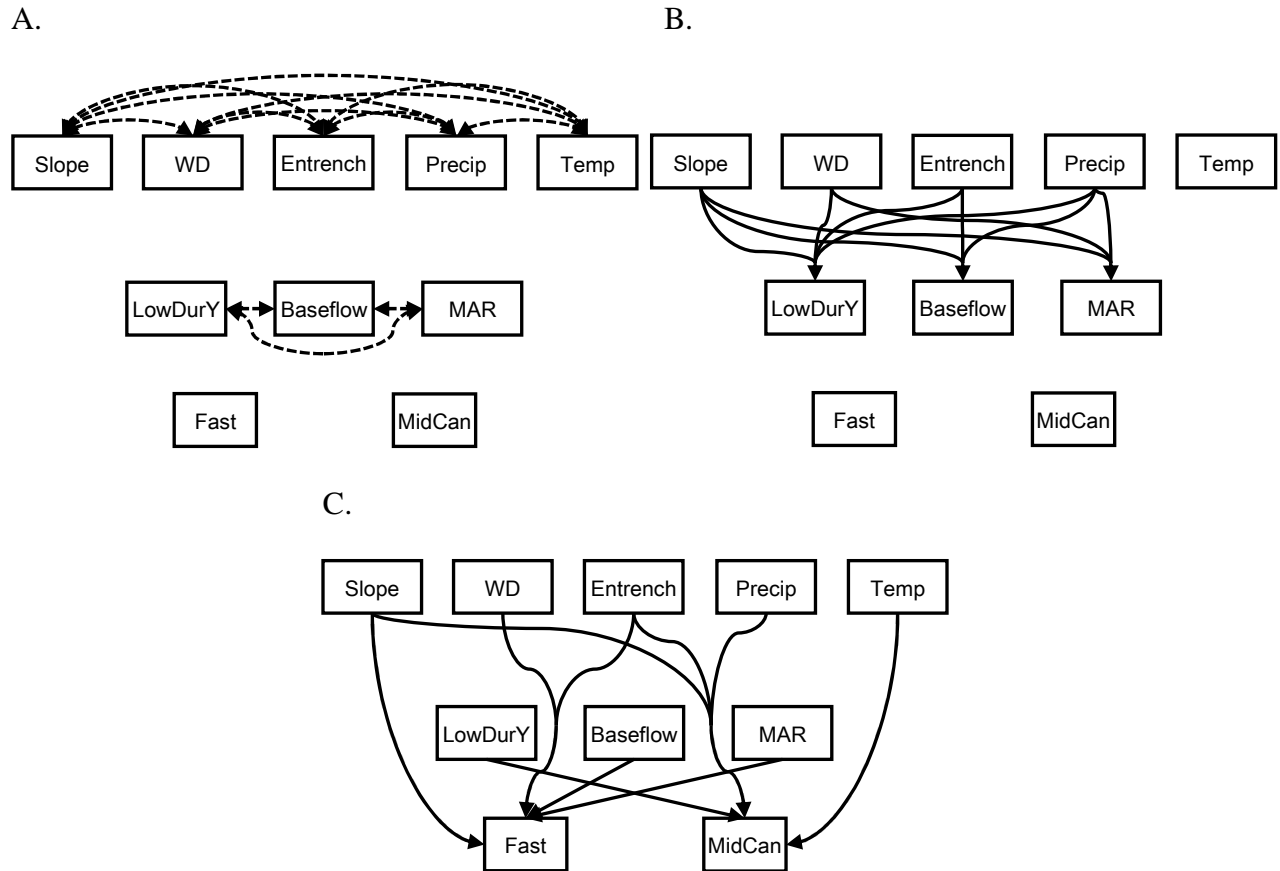


Figure 3.4: The environmental components of the path regressions models showing the correlations between environmental variables (A), direct causal relationships for hydrology variables (B), and direct causal relationships for the habitat/riparian variables (C)

and mean annual runoff has a significant direct influence on the distribution of cold stenotherms with a coefficient of 0.4, then the indirect causal effect of precipitation on the distribution of cold stenotherms would be $0.75 \times 0.4 = 0.3$. In order to compare the strength of relationships (i.e., coefficients), the environmental variables were transformed to approximate normal distributions and standardized with a mean of 0 and a standard deviation of 1. Finally, the use of the term *causal relationship* is somewhat of a misnomer in these models. The models do not determine causality such as in an experiment, but instead test the validity of an *a priori* hypothesis or hypotheses.

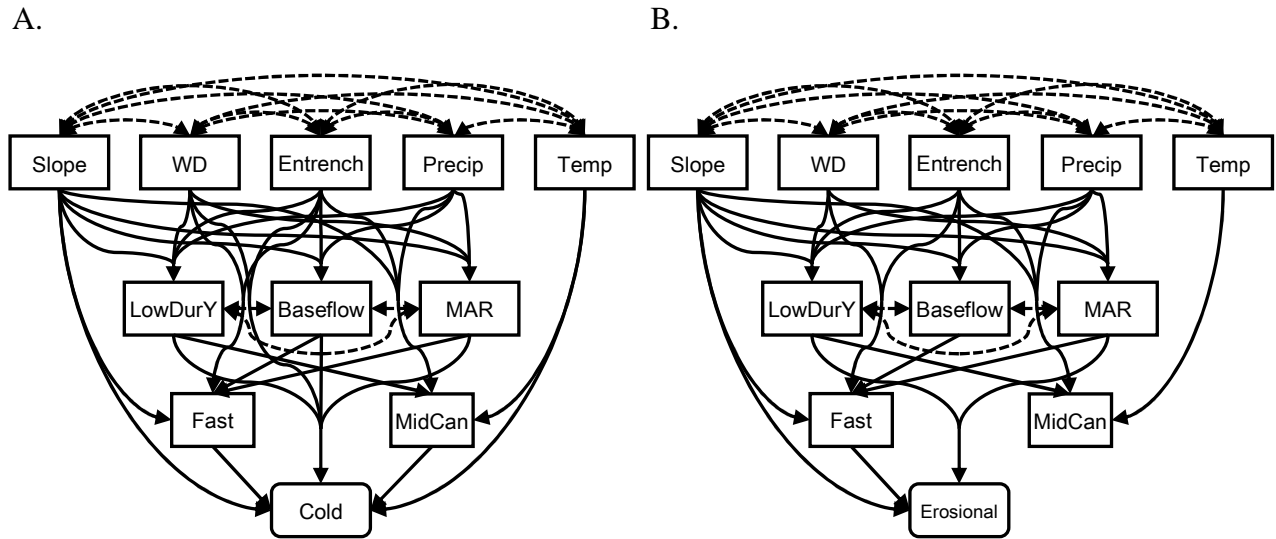


Figure 3.5: The full path models for cold stenotherms (A) and erosional obligates (B).

Most path regressions analyses have been conducted using a frequentist statistical framework with the assumption of normal distributions, but the cold stenotherm and erosional obligate data are nominal variables with a binomial distribution, each trait having two possible designations for taxa: being a cold stenotherm/erosional obligate or not. To account for this data structure, we developed a Bayesian path regression model. The Bayesian model was also desirable in this analysis due to some ecoregions having a limited number of sites and the Bayesian model allowed us perform a sensitivity analysis, evaluating if the parameter estimates were being driven by the data instead of the prior distributions. The binomial trait variable (either cold stenotherm or erosional obligate) was represented by $T = (t_{r,s}; r = 1,2)$, where r represents the two possible states for each state (e.g., cold stenotherm and non-cold stenotherm) and s represents the number of sites in the ecoregion. There were three groups of environmental variables: 1) habitat/riparian variables represented by $X = (x_{i,s}; i = 1,2)$, where i represents the number of variables and s represents the number of sites in the ecoregion; 2) hydrology variables

represented by $Y = (y_{j,s}; j = 1, \dots, 3)$, where j represents the number of variables and s represents the number of sites in the ecoregion; and 3) geomorphology/climate variables represented by $Z = (z_{k,s}; k = 1, \dots, 5)$, where k represents the number of variables and s represents the number of sites in the ecoregion. Each trait state (cold stenotherm and erosional obligate) was distributed as

$$T \sim \text{Binomial}(P, N)$$

$$N = \sum_r t_r$$

with P representing the probability of a taxon being a cold stenotherm or erosional obligate and N representing the total number of taxa. The probability of trait state membership is a response to habitat/riparian, hydrology, and geomorphology/climate variables and, thus, all sets of environmental variables are included as predictors in the following logistic regression, which is the appropriate link function for probability data

$$\text{Logit}(P) = \beta_0 + \sum_{i=1}^2 \beta_{ia}X + \sum_{j=1}^3 \beta_{jb}Y + \sum_{k=1}^5 \beta_{kc}Z$$

where β_0 represents the intercept and β_{ia} , β_{jb} , and β_{kc} represent the regression coefficients for the habitat/riparian, hydrology, and geomorphology/climate variables respectively.

All of the environmental data were transformed to approximate normal distributions and were centered with a mean of 0 and scaled with a standard deviation of 1. The habitat and

riparian variables were not expected to be correlated with each other based on *a priori* reasoning (which they were not, with a Spearman correlation of 0.06), so they were each assigned separate normal distributions

$$X \sim \text{Normal}(\mu_i, \tau_i)$$

where μ_i represents the mean for variable i and τ_i represents the variance for variable i . Fast water habitat and canopy cover are influenced by stream hydrology, geomorphology, and climatic conditions. To account for these influences, the mean from the habitat/riparian normal distributions were included as response variables in regression equations including hydrology and geomorphology/climate as the predictor variables

$$\mu_i = \gamma_0 + \sum_{j=1}^3 \gamma_{jb} Y + \sum_{k=1}^5 \gamma_{kc} Z$$

where γ_0 represents the intercept and γ_{jb} and γ_{kc} represent the regression coefficients for the hydrology and geomorphology/climate variables respectively. The hydrology variables had normal distributions, but also were expected to be correlated with each other (they had Spearman correlations of -0.30, -0.21, and 0.22). We wanted to determine the correlation, so we assigned the three variables to a multivariate normal distribution

$$Y \sim \text{Multivariate Normal}(\nu_j, \Sigma_Y)$$

where ν_j represents the model mean mean for variable j and Σ_Y represents the model covariance matrix. The hydrology variables were influenced by geomorphology and climatic variables, which was represented in the following regression equations with the multivariate normal means as the response variables

$$\nu_j = \delta_0 + \sum_{k=1}^5 \delta_{kc} Z$$

Where δ_0 represents the intercept and δ_{kc} represents the regression coefficients for the geomorphology/climate variables. Finally, we assumed the geomorphology/climate variables were correlated (due to the effect of elevation, latitude, and catchment area) and were assigned multivariate normal distribution

$$Z_s \sim \text{Multivariate Normal}(0, \Sigma_z).$$

where Σ_z represents the covariance matrix. The variance in the normal distribution was assigned the traditional vague gamma for linear regression

$$\tau_i \sim \text{Gamma}(0.1, 0.1)$$

which has a mean of 1 and a variance of 10, adequate for standardized variables. The intercepts and coefficients were assigned minimally informative priors centered on zero due to the standardization of the environmental data

$$(\beta_0, \gamma_0, \delta_0) \sim \text{Normal}(0, 0.01)$$

$$(\beta_{1a\dots ma}, \beta_{1b\dots nb}, \beta_{1c\dots pc}) \sim \text{Normal}(0, 0.1)$$

$$(\gamma_{1b\dots nb}, \gamma_{1c\dots pc}) \sim \text{Normal}(0, 0.1)$$

$$\delta_{1c\dots pc} \sim \text{Normal}(0, 0.1)$$

and prior for each covariance matrix had a Wishart distribution, which is a generalized, noninformative, multi-dimension gamma distribution, the standard prior to use with multivariate normal distributions

$$\Sigma_Y \sim \text{Wishart}(I_3, 3)$$

$$\Sigma_Z \sim \text{Wishart}(I_5, 5)$$

where I_3 was an identity matrix with three rows and columns and I_5 was an identity matrix with five rows and columns.

One potential problem with this type of model is overfitting; if the model was overly complex even nonsensical data could explain the most of the variation in the response variables (Kline 2011), although this is a greater problem for frequentist models than Bayesian models. This is of particular concern with the cold stenotherm model with nine possible direct drivers of cold stenotherm distribution and some ecoregions having a low number of sites, such as the Southern Dry Highlands (15 sites) or Mediterranean California (18 sites). A common technique using path models is to reduce explanatory variables in the model to only those relationships with the largest coefficient values by comparing a model fit metric, such as AIC or DIC, between

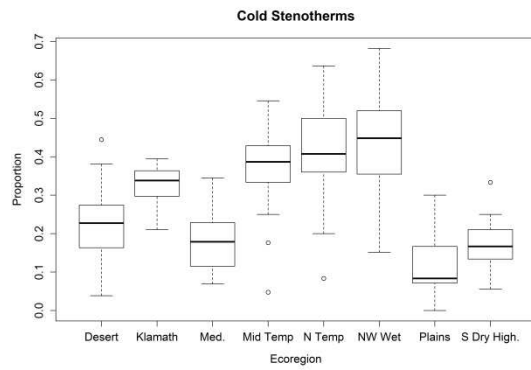
possible models (McCune and Grace 2002, Kline 2011). We used the deviance information criterion (DIC), a Bayesian-based selection criterion, to compare the reduced models and the full model and selected the model with the lowest DIC score. We also calculated an R^2 for the trait, fast water habitat, canopy cover, and hydrology variables using the fraction of unexplained variance method described in Gelman and Hill (2007). The regression coefficients were considered significant if their 95% credible interval did not include 0 and marginally significant if their 90% credible interval did not include 0. We interpreted significant or marginally significant regression coefficients as direct effects and multiplied these direct effects to get indirect effects. Each model was run using three Markov chains with 100,000 iterations each (burn-in of 10,000) in the WinBUGS 14 program (© WinBugs, 2007, Imperial College and MRC, UK), using the R2WinBugs interface package (Sturtz et al. 2005) in R (version 2.15.2; R Core Team 2012). We initially ran each model with regression coefficients having priors with normal distributions and a variance of 0.1 and then performed the sensitivity analysis by changing the variances of the coefficient priors to 0.01 and 0.001. We compared the coefficients of the three model variants and looked for significant changes in coefficient values, which would indicate that results are being driven by the priors and not the data.

Results

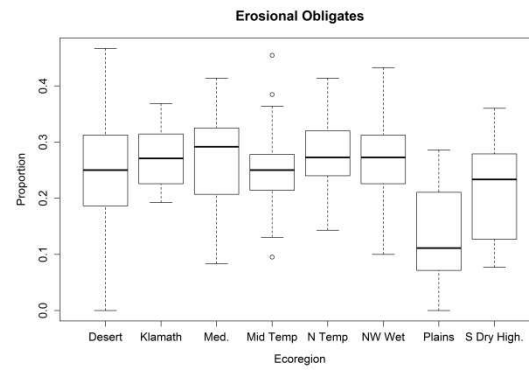
Our dataset consisted of eight unique ecoregions. The variations in the environmental and trait metrics between ecoregions are shown in (Figure 3.6). The Northwestern Wet Forests ecoregion was wet, cold and geomorphically variable with high and variable precipitation and mean annual runoff, low temperatures, and a wide range of slopes. The two temperate mountain ecoregions also had lower temperatures, were drier with lower runoff, and had the highest

median baseflow, indicating fairly stable streams. The Northern Temperate Mountains also had wide range of width/depth ratios. The Klamath Mountains had a combination of very high precipitation and runoff, similar to the NW Wet Forests ecoregion to the north, and very high temperatures, similar to the Mediterranean ecoregion to the south. The Klamath ecoregion also had very high canopy density. The Mediterranean ecoregion had high temperatures and long low flow duration, with low precipitation, runoff, and baseflows, indicating hydraulically unstable streams. The Southern Dry highlands had the unusual combination of high temperatures, low precipitation, low flows, and low slopes with high proportions of fast water habitat and canopy cover density. The Desert ecoregion exhibited a wide range of temperature values, had low flows and mean annual runoff, but a high proportion of baseflow, indicating small, stable streams. The plains ecoregion should be the most hostile to cold stenotherms and erosional obligates with high temperatures and low flow durations while having low precipitation, runoff, baseflow, fast water habitat, and canopy cover. Plains also had high entrenchment reflecting the highly incised channels of many plains streams. Cold stenotherm distributions varied according to ecoregion, but could be generalized into two groups (Figure 3.6a). The Northwestern Wet Forests, Mid- and Northern Temperate Mountains, and Klamath ecoregions had higher median proportions of cold stenotherms, with values between 0.30-0.50. The Desert, Plains, Mediterranean, and Southern Dry Highlands had lower median proportions between 0.05-0.25. The distribution of erosional obligates was very similar across ecoregions (Figure 3.6b), with median values near 0.25, with the sole exception of the Plains, which had a median value near 0.10.

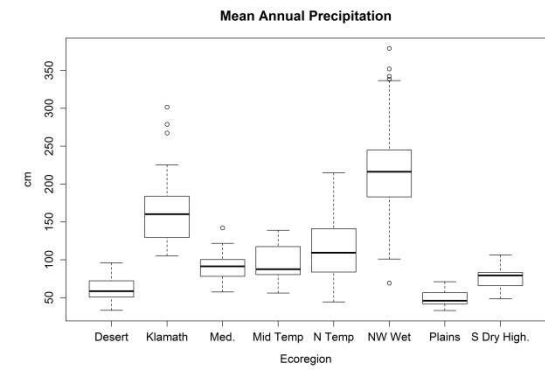
A



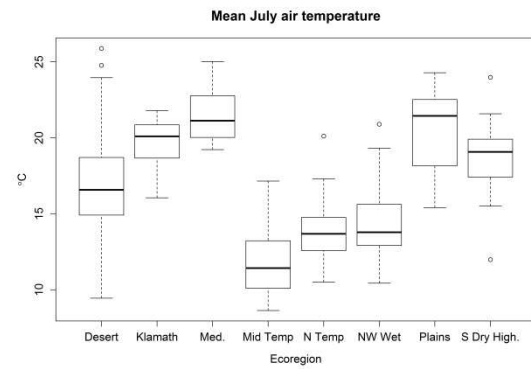
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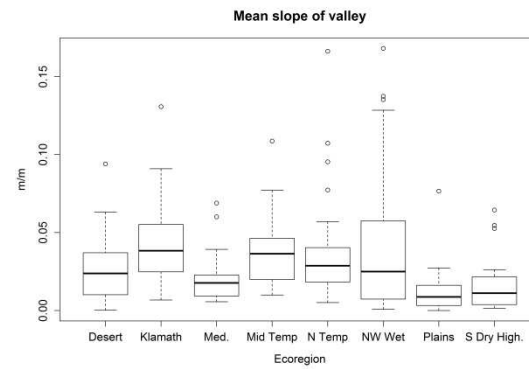
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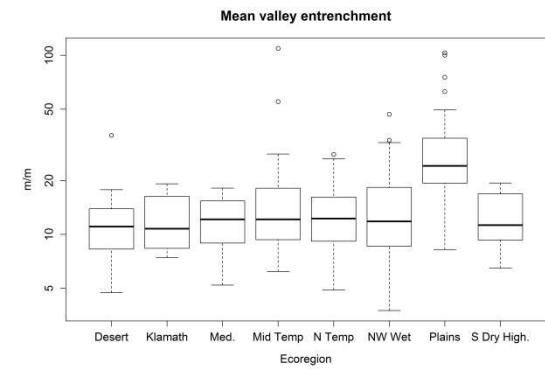
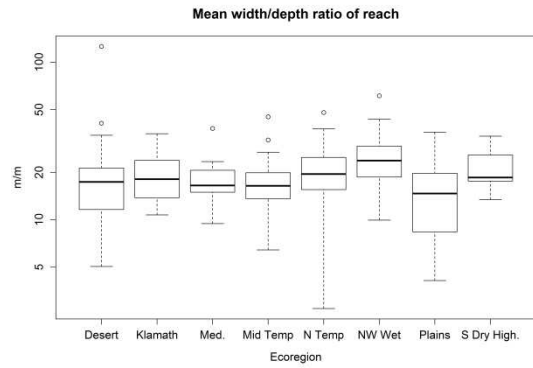
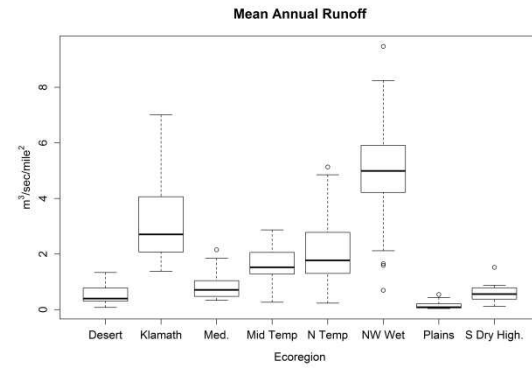


Figure 3.6: Boxplots of each trait and environmental variable separated according to ecoregion.

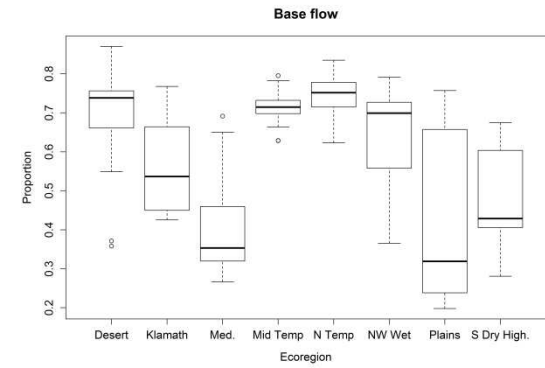
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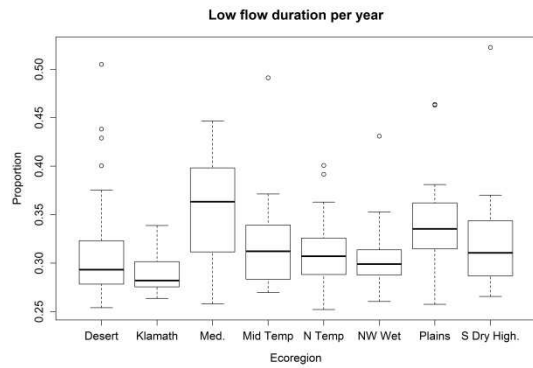
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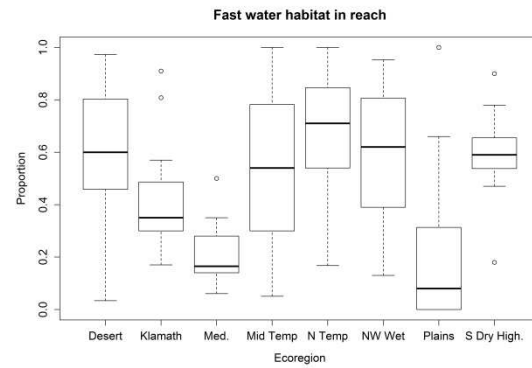
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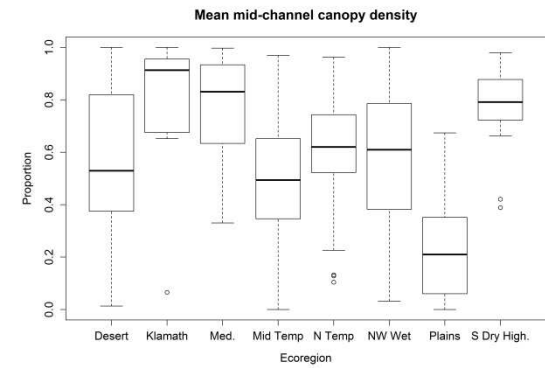


Figure 6 continued.

The model reduction procedure for each ecoregion produced different sets of significant parameters for the cold stenotherm and erosional obligate models, shown in Tables 3.4-3.11.

The sensitivity analyses revealed little variation in parameter estimates as priors were adjusted, indicating that the priors had a minimal impact on model results, even for the ecoregions with few sites.

Table 3.4: The model reduction process for the cold stenotherm and erosional obligate traits in the Desert ecoregion, starting with the full model and subsequent removal of single predictor variables based on coefficient size. The DIC values are listed for each iteration of the model with a single variable removed.

Cold stenotherm model			Erosional obligate model		
Response variable	Predictor variable removed	DIC	Response variable	Predictor variable removed	DIC
Full model		1343.15	Full model		1342.17
Fast	Slope	1340.73	LowDurY	Entrench	1339.90
MidCan	Entrench	1338.87	MidCan	Entrench	1337.72
LowDurY	Entrench	1336.75	Fast	Slope	1335.21
Cold	Slope	1334.22	MidCan	LowDurY	1333.24
Cold	LowDurY	1332.34	Eros	MAR	1332.71
MidCan	LowDurY	1330.34	Eros	LowDurY	1329.75
Cold	Baseflow	1328.67	MAR	Slope	1328.97
Cold	WD	1325.82	Fast	Baseflow	1327.13
Cold	MidCan	1324.71	Fast	WD	1325.18
MAR	Slope	1323.99	LowDurY	WD	1323.43
Fast	Baseflow	1322.05	MidCan	Precip	1322.07
Fast	WD	1320.17	Fast	Entrench	1320.76
LowDurY	WD	1318.38	Baseflow	Slope	1320.27
MidCan	Precip	1317.03	Baseflow	Entrench	1319.86
Cold	Entrench	1316.81			
Fast	Entrench	1315.67			
Baseflow	Slope	1315.28			
Baseflow	Entrench	1315.02			

Table 3.5: The model reduction process for the cold stenotherm and erosional obligate trait models in the Klamath Mountains ecoregion, starting with the full model and subsequent removal of single predictor variables based on coefficient size. The DIC values are listed for each iteration of the model with a single variable removed.

Cold stenotherm model			Erosional obligate model		
Response variable	Predictor variable removed	DIC	Response variable	Predictor variable removed	DIC
Full model		663.18	Full model		651.40
Cold	Slope	662.21	LowDurY	WD	648.98
Cold	Entrench	660.12	MAR	WD	646.40
Cold	LowDurY	658.59	Eros	LowDurY	644.07
LowDurY	WD	655.88	Baseflow	Entrench	641.75
Cold	MAR	652.72	LowDurY	Entrench	639.40
MAR	WD	650.32	Baseflow	Slope	637.17
Baseflow	Entrench	648.02	MAR	Slope	635.19
LowDurY	Entrench	645.58	MidCan	Entrench	633.17
Cold	Temp	644.55	Fast	WD	630.76
Baseflow	Slope	642.27	Eros	Slope	629.31
MAR	Slope	640.23	Eros	Fast	628.98
MidCan	Entrench	637.48	Fast	Slope	627.71
Cold	MidCan	636.86	Fast	MAR	625.65
Cold	Baseflow	635.81	MidCan	Precip	623.88
Fast	WD	632.03	MidCan	Temp	622.31
Fast	Slope	631.94	MidCan	Slope	621.73
Cold	Fast	629.94			
Fast	MAR	628.89			
MidCan	Precip	626.51			
MidCan	Temp	625.72			
MidCan	Slope	624.36			

Table 3.6: The model reduction process for the cold stenotherm and erosional obligate trait models in the Mediterranean ecoregion, starting with the full model and subsequent removal of single predictor variables based on coefficient size. The DIC values are listed for each iteration of the model with a single variable removed.

Cold stenotherm model			Erosional obligate model		
Response variable	Predictor variable removed	DIC	Response variable	Predictor variable removed	DIC
Full model		581.04	Full model		582.41
MidCan	Slope	578.17	MidCan	Slope	579.82
Fast	Baseflow	576.01	Fast	Baseflow	577.44
Cold	Baseflow	572.82	Eros	Fast	575.24

Cold	WD	570.55	Baseflow	Slope	573.06
Fast	MAR	568.19	Fast	MAR	570.45
Baseflow	Slope	565.91	Fast	Entrench	568.13
Cold	Fast	564.10	Eros	Slope	565.71
Fast	Entrench	563.04	Fast	WD	563.61
Fast	WD	559.94	Eros	LowDurY	563.01
Cold	MidCan	557.41	Eros	MAR	560.97
Cold	Slope	556.72	MidCan	Entrench	559.29
Cold	Entrench	555.10	LowDurY	Slope	557.74
Cold	LowDurY	554.79	LowDurY	WD	555.96
MidCan	Entrench	553.21	Baseflow	Entrench	554.51
LowDurY	Slope	551.70	LowDurY	Entrench	553.19
LowDurY	WD	549.77			
Baseflow	Entrench	548.21			
LowDurY	Entrench	547.01			

Table 3.7: The model reduction process for the cold stenotherm and erosional obligate trait models in the Middle Temperate Mountains ecoregion, starting with the full model and subsequent removal of single predictor variables based on coefficient size. The DIC values are listed for each iteration of the model with a single variable removed.

Cold stenotherm model			Erosional obligate model		
Response variable	Predictor variable removed	DIC	Response variable	Predictor variable removed	DIC
Full model		959.03	Full model		943.72
Cold	WD	958.23	Eros	LowDurY	941.60
MAR	Slope	955.77	MAR	Slope	939.24
MidCan	Entrench	953.81	MAR	WD	937.26
MAR	WD	951.77	Eros	Slope	935.83
Cold	Slope	948.53	MidCan	Entrench	933.70
Cold	MidCan	948.37	Fast	Slope	931.93
Cold	LowDurY	945.73	MidCan	Temp	929.55
Fast	Slope	943.68	Fast	Entrench	927.37
Cold	Fast	941.70	Fast	WD	925.14
Fast	Entrench	940.46	LowDurY	Slope	923.41
Fast	WD	937.37	LowDurY	WD	921.87
MidCan	Temp	936.20	LowDurY	Precip	920.46
Cold	Baseflow	933.60	MidCan	Precip	919.72
LowDurY	Slope	931.89	MidCan	LowDurY	918.89
LowDurY	WD	930.67	Baseflow	Entrench	917.72
LowDurY	Precip	929.13	Baseflow	Precip	916.37
MidCan	Precip	928.20	Baseflow	Slope	916.02
MidCan	LowDurY	927.06	LowDurY	Entrench	915.79
Baseflow	Entrench	926.24			

Baseflow	Precip	925.02
Baseflow	Slope	924.41
LowDurY	Entrench	924.13

Table 3.8: The model reduction process for the cold stenotherm and erosional obligate trait models in the Northern Temperate Mountains ecoregion, starting with the full model and subsequent removal of single predictor variables based on coefficient size. The DIC values are listed for each iteration of the model with a single variable removed.

Cold stenotherm model			Erosional obligate model		
Response variable	Predictor variable removed	DIC	Response variable	Predictor variable removed	DIC
Full model		1459.86	Full model		1439.22
LowDurY	WD	1457.66	LowDurY	WD	1436.97
Cold	Entrench	1454.62	Eros	Slope	1435.09
Cold	Baseflow	1454.05	Eros	MAR	1432.77
Cold	LowDurY	1451.23	Eros	LowDurY	1431.72
MAR	Slope	1451.00	MAR	Slope	1431.66
Cold	WD	1450.38	MidCan	Precip	1429.88
Cold	MidCan	1449.00	MidCan	Entrench	1428.37
MidCan	Precip	1447.14	LowDurY	Precip	1426.87
MidCan	Entrench	1445.61	Fast	MAR	1425.31
LowDurY	Precip	1444.00	Fast	WD	1423.57
Fast	MAR	1442.49	MidCan	LowDurY	1422.73
Fast	WD	1440.78	Baseflow	Slope	1421.76
MidCan	LowDurY	1439.66	Fast	Slope	1421.41
Baseflow	Slope	1438.69	LowDurY	Slope	1420.65
Fast	Slope	1438.35			
LowDurY	Slope	1437.59			

Table 3.9: The model reduction process for the cold stenotherm and erosional obligate trait models in the Northwestern Wet Forests ecoregion, starting with the full model and subsequent removal of single predictor variables based on coefficient size. The DIC values are listed for each iteration of the model with a single variable removed.

Cold stenotherm model			Erosional obligate model		
Response variable	Predictor variable removed	DIC	Response variable	Predictor variable removed	DIC
Full model		1287.78	Full model		1275.24
Cold	WD	1284.59	MidCan	LowDurY	1272.83
MAR	WD	1282.00	MAR	WD	1270.62
MidCan	LowDurY	1279.86	Eros	Slope	1267.55

Cold	LowDurY	1278.65	LowDurY	WD	1265.50
Cold	MidCan	1276.97	MAR	Slope	1264.80
LowDurY	WD	1274.99	LowDurY	Entrench	1263.05
MAR	Slope	1274.20	Eros	MAR	1262.94
Cold	Baseflow	1272.14	Eros	LowDurY	1260.47
LowDurY	Entrench	1270.41	Fast	Entrench	1258.73
Cold	Fast	1269.31	MidCan	Entrench	1257.60
Fast	Entrench	1267.52	Baseflow	Entrench	1257.28
MidCan	Entrench	1266.34	Fast	WD	1256.53
Baseflow	Entrench	1265.84			
Fast	WD	1265.37			

Table 3.10: The model reduction process for the cold stenotherm and erosional obligate trait models in the Great Plains ecoregion, starting with the full model and subsequent removal of single predictor variables based on coefficient size. The DIC values are listed for each iteration of the model with a single variable removed.

Cold stenotherm model			Erosional obligate model		
Response variable	Predictor variable removed	DIC	Response variable	Predictor variable removed	DIC
Full model		837.25	Full model		841.12
Cold	Fast	835.08	Baseflow	Entrench	838.96
Baseflow	Entrench	832.81	Eros	LowDurY	835.71
Cold	Slope	829.60	Eros	MAR	834.61
Cold	WD	829.07	LowDurY	Entrench	832.97
Cold	MAR	825.49	MAR	WD	832.59
LowDurY	Entrench	823.72	Fast	Slope	831.23
MAR	WD	823.45	Fast	Baseflow	829.63
Cold	Entrench	823.11	MidCan	Slope	828.10
Cold	Baseflow	820.82	Eros	Slope	826.81
Fast	Slope	819.28	LowDurY	Slope	826.17
Fast	Baseflow	817.95			
MidCan	Slope	816.29			
Cold	Temp	816.14			
LowDurY	Slope	815.40			

Table 3.11: The model reduction process for the cold stenotherm and erosional obligate trait models in the Southern Dry Highlands ecoregion, starting with the full model and subsequent removal of single predictor variables based on coefficient size. The DIC values are listed for each iteration of the model with a single variable removed.

Cold stenotherm model			Erosional obligate model		
Response variable	Predictor variable removed	DIC	Response variable	Predictor variable removed	DIC
Full model		483.94	Full model		482.44
Baseflow	Slope	481.33	Baseflow	Slope	479.84
Cold	WD	478.44	MAR	Slope	476.79
MAR	Slope	475.54	MAR	WD	473.73
MAR	WD	472.86	LowDurY	Entrench	471.51
LowDurY	Entrench	470.48	Baseflow	Entrench	469.24
Baseflow	Entrench	468.06	Eros	Slope	468.65
Cold	MAR	466.33	Fast	Baseflow	466.39
LowDurY	WD	464.39	LowDurY	WD	464.36
LowDurY	Precip	462.29	LowDurY	Precip	462.05
Cold	MidCan	459.81	MidCan	LowDurY	459.97
Cold	LowDurY	458.01	Baseflow	Precip	458.41
Cold	Baseflow	457.25	Eros	MAR	456.93
Cold	Temp	454.89	Fast	Slope	455.13
Fast	Baseflow	452.37	Fast	WD	452.73
Baseflow	Precip	450.82	MidCan	Entrench	451.46
MidCan	LowDurY	448.62	Fast	Entrench	450.63
Fast	WD	446.72	Fast	MAR	449.45
Fast	Slope	444.29	MidCan	Precip	449.07
MidCan	Entrench	443.18			
Fast	Entrench	442.46			
Fast	MAR	441.28			
MidCan	Precip	441.05			

Cold stenotherm and erosional obligate traits

The models performed fairly well accounting for cold stenotherm distributions, with R^2 values between 0.40-0.85, except for the Klamath Mountains ecoregion model, which had no significant drivers of cold stenotherm distribution and a R^2 of only 0.18. The total effects (direct + indirect effects) of environmental variables on the distribution of cold stenotherms indicated two general groups of ecoregions, one consisting of ecoregions with temperature and mean

annual runoff as the main direct drivers of cold stenotherm distribution, with precipitation having a strong indirect effect through mean annual flow. These ecoregions are the Northwestern Wet Forests (Table 3.12), Northern Temperate Mountains (Table 3.13), Middle Temperate Mountains (Table 3.14) and Mediterranean California (Table 3.15). The second group, consisting of the Klamath Mountains (Table 3.16), Southern Dry Highlands (Table 3.17), Desert (Table 3.18), and Great Plains ecoregions (Table 3.19), lacked significant coefficients from temperature and mean annual runoff, instead having low flow, geomorphology, canopy cover, and fast water habitat acting as the main drivers of cold stenotherm distribution or no significant drivers of cold stenotherm distribution, in the case of the Klamath Mountains. Precipitation had a moderate indirect impact on cold stenotherms through hydrology and canopy cover variables in all the ecoregions except the Southern Dry Highlands and Klamath Mountains. The erosional obligate model performed poorly, only accounting for about 10-20% of the variation in the distribution of erosional obligates (Tables 3.20-3.27). Most significant direct effects were the fast water habitat variable, the theoretical main driver of erosional obligate distribution. The exception was the Southern Dry Highlands, where mean low flow duration was the dominant driver of erosional obligate distribution.

Environmental variables

The models performed fairly well for canopy cover, accounting between roughly 20-60% of the variation, with precipitation having a significant positive direct effect in the Northwestern Wet Forests, Mediterranean, and Great Plains. Temperature had a significant or marginally significant positive direct effect on canopy cover in the Northwestern Wet Forests, Southern Dry Highlands, and Desert ecoregions, while having a negative effect in the Mediterranean and

Table 3.12: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the cold stenotherm trait state in the Northwestern Wet Forests ecoregion. Values in bold had direct effects with significant 95% credible intervals, underlined values had direct effects with significant 90% credible intervals, and blanks mean the variable was not in the reduced model with the lowest DIC. Values with asterisks indicate only indirect effects.

	N	R ²	Precip	Temp	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast	MidCan
NW Wet Forests	45	0.718	0.197*	-0.209	0.201			-0.161	-0.218			

Table 3.13: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the cold stenotherm trait state in the Northern Temperate Mountains ecoregion. See Table 3.12 for descriptions of significance.

	N	R ²	Precip	Temp	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast	MidCan
N. Temp. Mtns	49	0.495	0.139*	-0.174	0.137	0.035*		-0.038*	0.136	0.011*	0.136	

Table 3.14: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the cold stenotherm trait state in the Middle Temperate Mountains ecoregion. See Table 3.12 for descriptions of significance.

	N	R ²	Precip	Temp	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast	MidCan
Mid. Temp. Mtns	30	0.544	0.195*	-0.343	0.207			<u>-0.169</u>				

Table 3.15: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the cold stenotherm trait state in the Mediterranean ecoregion. . See Table 3.12 for descriptions of significance.

	N	R ²	Precip	Temp	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast	MidCan
Mediterranean	18	0.579	0.236*	-0.244	0.250							

Table 3.16: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the cold stenotherm trait state in the Klamath Mountains ecoregion. Values in bold had direct effects with significant 95% credible intervals, underlined values had direct effects with significant 90% credible intervals, and values with asterisks indicate only indirect effects. Blanks mean the variable was not in the reduced model with the lowest DIC.

	N	R ²	Precip	Temp	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast	MidCan
Klamath Mtns	22	0.180								-0.106		

Table 3.17: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the cold stenotherm trait state in the Southern Dry Highlands ecoregion. See Table 3.16 for descriptions of significance.

	N	R ²	Precip	Temp	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast	MidCan
S. Dry Highlands	15	0.814						0.404	<u>0.259</u>		0.310	

Table 3.18: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the cold stenotherm trait state in the Desert ecoregion. See Table 3.16 for descriptions of significance.

	N	R ²	Precip	Temp	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast	MidCan
Desert	43	0.413	0.170*	<u>-0.188</u>	0.196					0.026*	0.221	

Table 3.19: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the cold stenotherm trait state in the Great Plains ecoregion. See Table 3.16 for descriptions of significance.

	N	R ²	Precip	Temp	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast	MidCan
Great Plains	29	0.416	0.352*	-0.135*			-0.237	-0.074*		0.083*		0.361

Table 3.20: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the erosional obligate trait state in the Northwestern Wet Forests ecoregion. Values in bold had direct effects with significant 95% credible intervals, underlined values had direct effects with significant 90% credible intervals, and values with asterisks indicate only indirect effects. Blanks mean the variable was not in the reduced model with the lowest DIC.

	R ²	Precip	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast
NW Wet Forests	0.191	0.01*	0.035*	0.061*			0.07*		0.141

Table 3.21: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the erosional obligate trait state in the Northern Temperate Mountains ecoregion. See Table 3.20 for descriptions of significance.

	R ²	Precip	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast
N. Temp. Mtns	0.127								<u>0.106</u>

Table 3.22: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the erosional obligate trait state in the Middle Temperate Mountains ecoregion. See Table 3.20 for descriptions of significance.

	R ²	Precip	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast
Mid. Temp. Mtns	0.260	0.073*	0.141						0.216

Table 3.23: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the erosional obligate trait state in the Klamath Mountains ecoregion. See Table 3.20 for descriptions of significance.

	R ²	Precip	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast
Klamath Mtns	0.190		0.118						

Table 3.24: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the erosional obligate trait state in the Mediterranean ecoregion. Values in bold had direct effects with significant 95% credible intervals, underlined values had direct effects with significant 90% credible intervals, and values with asterisks indicate only indirect effects. Blanks mean the variable was not in the reduced model with the lowest DIC.

	R ²	Precip	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast
Mediterranean	0.000								

Table 3.25: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the erosional obligate trait state in the Southern Dry Highlands ecoregion. . See Table 3.24 for descriptions of significance.

	R ²	Precip	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast
S. Dry Highlands	0.419				-0.348		-0.164*		0.147

Table 3.26: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the erosional obligate trait state in the Desert ecoregion. . See Table 3.24 for descriptions of significance.

	R ²	Precip	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast
Desert	0.203	0.028*	0.033*				<u>-0.133</u>	0.004*	<u>0.138</u>

Table 3.27: The total effects (direct effect + indirect effect) of environmental variables on the distribution of the erosional obligate trait state in the Great Plains ecoregion. . See Table 3.24 for descriptions of significance.

	R ²	Precip	MAR	Baseflow	LowDurY	Entrench	Slope	WD	Fast
Great Plains	0.280	0.218*	0.316*			-0.080*	0.113*	0.176*	0.427

Great Plains. Slope had a positive significant or marginally significant direct effect on canopy cover in the Northwestern Wet Forests, Northern and Middle Temperate Mountains, Southern Dry Highlands, and Desert ecoregions. Low flow duration had, surprisingly, a significantly positive direct effect on canopy cover for the Klamath Mountains and Mediterranean ecoregions. Most of the significant or marginally significant effects for temperature, slope and low flow duration on canopy cover contradicted our *a priori* expectations, which predicted that they would have negative relationships.

Most models only explained a small amount of variation (5-15%) in the distribution of fast water habitat for most ecoregions except for Northwestern Wet Forests, Klamath Mountains, and the Great Plains, which explained 40-70% of the variation. The model did not include important predictors of fast water habitat, such as lithology, so the high R^2 values for those ecoregions were somewhat surprising. The significant parameters did match *a priori* expectations in most cases, but each ecoregion had different array of significant or marginally significant drivers of fast water habitat, with mean annual runoff having a positive direct effect in the Northwestern Wet Forests and Great Plains, while having a negative effect in the Middle Temperate Mountains. Baseflow had positive direct effects on fast water habitat in the Northwestern Wet Forests, Northern Temperate Mountains, and Middle Temperate Mountains. Entrenchment had a negative direct effect on fast water habitat in the Northern Temperate Mountains and a positive direct effect in the Klamath Mountains, while slope had a positive effect in the Northwestern Wet Forests, and width-depth ratio had a positive effect in the Great Plains.

Precipitation explained the majority of variation (70-95%) for mean annual runoff in all ecoregions, according to *a priori* expectations, with some minor positive direct effects from

slope and width-depth ratios in the Northern Temperate Mountains, Desert, and Great Plains. Baseflow had higher R^2 s (36-57%) in the Northwestern Wet Forest, Klamath Mountains, and Plains ecoregions (35-60%), but low R^2 s in the remaining ecoregions. Precipitation had a negative direct effect on baseflow in Northwestern Wet Forests and Klamath ecoregions and a positive effect in the Great Plains, while slope had a positive direct effect on baseflow in the Northwestern Wet Forests and Great Plains ecoregions. Low flow duration had a moderate amount of variation explained by the models for most ecoregions (20-40%) except the Middle and North Temperate Mountains (0-5%). Precipitation had a positive direct effect on low flow duration in the Mediterranean, Desert, and Great Plains ecoregions, according to *a priori* expectations, but a negative effect in the Northwestern Wet Forest and Klamath Mountain ecoregions. Slope also had a positive effect on low flow durations in Southern Dry Highlands and Desert ecoregions and width-depth ratio had a negative effect in the Great Plains. It is interesting to note that in the two wettest ecoregions, the influence of precipitation on baseflow and low flow duration showed responses contradicting *a priori* expectations, while expectations were met in drier ecoregions. Finally, the correlation analyses showed that baseflow and low flow duration were negatively correlated and mean annual runoff and baseflow were positively correlated for some ecoregions. The correlations between geomorphology and climate variables were inconsistent between ecoregions, but the relationships that were significant matched *a priori* expectations in most cases, indicating that elevation, latitude or catchment size are characteristics possibly influencing these variables.

Discussion

We hypothesized that the distribution of organisms with climate-sensitive traits would be influenced by climate and climate-driven variables in ecoregions with mild climatic conditions, namely low temperatures and higher runoff, while these distributions would be disconnected from climatic variables in ecoregions with more extreme climatic conditions, namely higher temperatures and low precipitation/runoff. Our reasoning for this hypothesis was that if organisms with thermophilic and rheophilic tendencies are currently found in regions with high temperatures and low runoff, they are compensating by living in stream conditions that buffer or insulate against warm temperatures and compensate for the lack of typical erosional conditions. In the context of our models, this would mean that in warm ecoregions geomorphology, baseflow and low flows, riparian, and habitat features would drive the distribution of cold stenotherms. In regions with little fast water habitat or low precipitation, geomorphology and hydrology would drive the distribution of erosional obligates.

Our results mostly matched the hypothesis concerning cold stenotherms but did not match our hypothesis concerning erosional obligates. The distribution of cold stenotherms was driven by temperature and runoff in the three ecoregions with low temperatures, the NW Wet Forest and two temperate mountain ecoregions, as well as in the Desert ecoregion, which has a wide range of temperature values. Precipitation also had a large indirect effect in these regions due to its significant relationship with mean annual runoff. The Plains, Klamath Mountains, and Southern Dry Highlands ecoregions also matched our hypothesis with little or no effect from temperature or runoff on the distribution of cold stenotherms. Instead cold stenotherm distribution was driven by low flows, entrenchment, canopy cover, and fast water habitat, or in the case of the Klamath Mountains, nothing at all (at least significantly). It is interesting to note that

precipitation had a large indirect effect in the Plains ecoregion, but that effect was mediated through low flows and canopy cover, not runoff. The sole exception to our hypothesis for cold stenotherms was the Mediterranean ecoregion. We would have expected this ecoregion to have results similar to the other warm ecoregions. The distribution of erosional obligates was driven mainly by fast water habitat across a wide range of ecoregions (e.g., NW Wet Forest, Plains), contrary to our hypothesis. The sole exception was the Southern Dry Highlands ecoregion, where erosional obligates avoided stream sites with long low flow durations, regardless of fast water habitat in the reach. Based on these results, it is important to understand the current climatic setting in which cold stenotherms are distributed, but not necessarily for erosional obligate distribution. The erosional obligate trait did not perform well in this analysis, but our dataset consisted of natural or near-natural perennial streams, found mostly in hilly or mountains regions in the western U.S. If we had included intermittent and/or disturbed streams, erosional obligate distribution likely would have more closely tracked variation on runoff and the distribution of fast water habitat.

Some relationships between environmental variables consistently contradicted our *a priori* expectations, suggesting different dynamics than we thought. The influence of precipitation on low flow duration per year met our expectations of a negative relationship in the dry ecoregions (Desert, Mediterranean, and Plains), but we saw a positive relationship in the Klamath Mountains and Northwestern Wet Forest ecoregions. This suggests that the low flow metric encapsulated a different phenomenon in wet versus dry ecoregions. In dry ecoregions low flow represents extreme periods of very low precipitation where streams begin to dry out. In wet ecoregions with areas of extremely high precipitation, the low flow metric may merely be describing the normal stream state, with the extreme events being high precipitation events. Our

a priori expectations were also inadequate in explaining the canopy cover. Canopy cover was positively correlated with temperature the NW Wet Forests, Southern Dry Highlands, and Desert ecoregions. For the Northwestern Wet Forests, warmer areas may reflect a greater intensity in temperate rainforest as opposed to cooler locations. For the dry ecoregions, our dataset included only perennial streams and the streams may become smaller as they enter warmer climate, yet still maintain a riparian corridor. Canopy cover was also positively related to slope in the NW Wet Forest, temperate mountains, and desert ecoregions, contrary to our expectations. This again may be due to the fact that slope may be a surrogate for stream size along mostly forested ecoregions. Finally, canopy cover was positively correlated with low flows for Mediterranean and Klamath Mountains ecoregions. For the Mediterranean, this may reflect the size of the stream, but for the Klamath Mountains, low flows are positively associated with high precipitation, which is usually positively associated with vegetation density.

The potential effects of climate change

Previous studies have shown that in temperate ecoregions cold stenotherm distributions were driven by temperature and flow (Hamilton et al. 2010, Stamp et al. 2010, Chessman 2012). Thermal preference of taxa in Europe and Canada shifted along gradients related to stream size, such as flow, temperature, as well as other correlated variables such as dissolved oxygen, and turbidity, with cold water adapted species preferring small, clear, oxygen-saturated streams (Usseglio-Polatera et al. 2000, Usseglio-Polatera and Beisel 2002, Horrigan and Baird 2008). Other studies also found that cold adapted taxa are more dominant in glaciated watersheds (Füreder 2007, Brown and Milner 2012). These results, as well as our own, suggest that the distribution of cold stenotherms in temperate regions may contract as temperatures rise and

runoff falls, but the resulting impact may be minimal. For example, according to our model in the Northern Temperate Mountains, a 2 °C increase in temperature would result in a 6.3% reduction in cold stenotherms. For a mountain stream consisting of 25 taxa, this change would translate into a loss of 1-2 taxa.

The potential impact of climate change on cold stenotherms residing in warmer ecoregions, such as our Southern Dry Highlands, Plains, Mediterranean, and Klamath Mountains, presents a more intriguing dilemma. Except for the Mediterranean ecoregion, which we will discuss below, the models for these ecoregions recorded no significant relationship between temperature and runoff with cold stenotherms. We speculate that this may be due to the fact that cold stenotherms are at their thermal limits and compensate by inhabiting stream sections or habitats that buffer or insulate against thermal extremes. If this is true, then any increase in temperature may eliminate the remaining suitable habitat for these organisms and push them beyond their thermal limits (see Chapter 4). Most sites in the Plains and Southern Dry Highlands ecoregions have low proportions of cold stenotherms, so the overall community impact may be small. The same is not true for the Klamath Mountains ecoregion, which has high proportions of cold stenotherms and may be heavily impacted by climate change. The climatic oddity of the Klamath, with high temperatures, yet with high runoff and a high proportion of cold stenotherms provide the perfect ingredients for a high potential for species loss. The environmental variables in our model for the Klamath Mountains did not account for any significant variation in cold stenotherms, implying missing variables, undetected scales, or a random distribution. Cold stenotherms in this region may be utilizing a microhabitat characteristic to avoid extreme temperatures. The Mediterranean ecoregion also presents a potential problem. Unlike the other warm ecoregions, the model for the Mediterranean

ecoregion includes temperature and runoff as significant drivers of cold stenotherm distribution and if temperature were changed 2 °C in the model, the resulting loss would only be about a 4% loss of cold stenotherm taxa. The concern for this ecoregion is that although the cold stenotherm distribution does change along the temperature gradient, the gradient is fairly narrow and temperatures are already near the upper limit in our dataset. Both facts indicate a potential threshold, where increases in temperature may push most cold stenotherms past their thermal limits in Mediterranean California, which has moderate to high proportions of cold stenotherms.

A few other studies have evaluated potential climate change effects on aquatic macroinvertebrates in an ecoregional context, particularly comparing arid with temperate ecoregions. Bonada et al. (2007) compared multiple biological trait distributions (but not including thermal preference) between temperate and Mediterranean Europe and found that traits considered resistant and resilient to drought were more common in the Mediterranean. Hering et al. (2009), Tierno de Figueroa (2010), and Conti et al. (2014) classified the climate vulnerability Ephemeroptera, Trichoptera, and Plecoptera (EPT) taxa using a set of traits they defined as being climate sensitive (including thermal preference) and compared climate vulnerability across the major European ecoregions. They found that EPT in general, and Trichoptera taxa specifically, were more vulnerable in the Mediterranean climates with a gradual northward decrease in vulnerability, while Plecoptera species were vulnerable across Europe. This contradicted Bonada et al. (2007), but supports our results. Hamilton et al. (2010) and Stamp et al. (2010) compared cold stenotherms to 7-22 year temperature data for 6-11 sites in three ecoregions in the United States and found that cold stenotherms in some semi-arid sites in Utah had more consistent relationships with temperature than sites in more temperate ecoregions.

Defining vulnerable taxa through categorical traits (Bonada et al. 2007, Chessman 2012, Conti et al. 2014) or niche models (Chapter 4) provide a valuable tool in projecting community responses to climate change scenarios. Comparing trait distributions to historical climate records (Chessman 2009, Hamilton et al. 2010) can provide valuable insight into current trait distribution trajectories. But, our approach incorporating a hierarchical model using multiple climatic and non-climatic variables provides two valuable insights into climate change research using traits. First, we can determine which traits may good indicators of vulnerability to climate change in at least some ecoregions and assess the potential drivers of that trait. This has been apparent with cold stenotherms, but we have paid scant attention to the erosional obligate trait in our discussion. With the trait having R^2 values only near 0.20 for most ecoregions, we feel that it is not particularly sensitive to the potential effects of climate change (at least using perennial streams), although this may be reflect the variables we selected for this analysis. Second, we can identify and evaluate possible environmental characteristics that can be used to mitigate the effect of climate change. For example, if the distribution of cold stenotherms in the Plains ecoregion streams is driven mostly by canopy cover and short low flow durations, then efforts to maintain such conditions may provide suitable habitat these taxa, which were defined as climate-sensitive *a priori*. By linking trait distributions to the theoretical constructs of stream ecology, we can make informed decisions concerning the biological integrity of streams in the light of climate change and anthropogenic disturbance. The disconnect between “climate-sensitive” traits and climatic variables in climatically extreme ecoregions could mean one of two things: 1) climate change won’t affect these taxa in these ecoregions and the model is appropriate, or 2) climate sensitive taxa are at their thermal limits in these ecoregions and this model would not be appropriate for quantitatively projecting community change according to climate change

scenarios. If the latter is true, which we argue that it is, then other methods, such as niche modeling, would be more appropriate to capture taxa response to climate change, as is demonstrated in Chapter 4.

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CHAPTER 4: VULNERABILITY OF WESTERN UNITED STATES STREAM INSECT COMMUNITIES TO TEMPERATURE AND HYDROLOGIC CHANGE PROJECTED UNDER GLOBAL WARMING

Summary

Stream insect species vary in their sensitivities to temperature and runoff conditions and thus should respond differentially to climate change across their geographic ranges. We used General Additive Models to classify sensitivity of two responses to 1) increased temperature and 2) change in runoff for 88 insect taxa at 252 least-impacted sites in the western US. We used a cumulative percentile technique to calculate thermal and runoff thresholds for sensitive taxa. Climate change at each site was simulated by co-varying temperature (0 to 4 °C increase) and runoff (up to +/- 80% change in mean runoff). We calculated percent change in community composition from potential loss of taxa due to projected site temperatures and runoff crossing taxa threshold values. Sixty-two taxa were sensitive to temperature increases, 59 to runoff decreases and 23 to runoff increases. Most mountain communities were relatively invulnerable to the range of climate change exposures, whereas species and communities in southern and northern California were significantly modified. This is the first study to predict how simultaneous changes in temperature and runoff interact to regulate insect species distributions and community structure and function in streams across multiple biomes.

Introduction

Species may be introduced to new climatic and hydrological conditions under anthropogenically induced climate change, so knowledge of species tolerances to climatic

variables is vital in order to predict how species may respond. Commonly used approaches to determine species tolerances are to record the physiological responses of a species while performing thermal ramping experiments (Calosi et al. 2008, Cottin et al. 2012) or using detailed information on population growth (Deutsch et al. 2008). These approaches require a significant amount of effort per species and are usually restricted to a few species considered economically or culturally important, such as commercially fished marine invertebrates (Paschke et al. 2013), salmonoids (Underwood et al. 2012, Zeigler et al. 2013), pollinating insects (Jevanandam et al. 2013), invasive species (Coccia et al. 2013, Hill et al. 2013), and declining taxonomic groups (Pandolfo et al. 2010, Scheffers et al. 2013). If we want to estimate the response of an entire large and complex community to climate change, these approaches have limited use. Alternative approaches include using expert judgment (Segurado et al. 2011) or using biological inference models that estimate tolerances from species distributions across environmental gradients using various statistical approaches (highlighted in Yuan 2006, Segurado et al. 2011).

Biological inference models are most commonly used to estimate species tolerances to temperature, but in aquatic ecosystems climate change is not the mere rising of temperatures. For example, in marine systems climate change is expected to affect ocean temperatures, circulation, stratification, nutrients, and pH (Doney et al. 2012). Stream ecosystems may be particularly vulnerable to climate change due its effect on hydrologic processes (Fenoglio et al. 2010, Wenger et al. 2011, Chessman 2012). Changes in factors such as flow and water quality may have a greater effect on the distribution of aquatic organisms than changes in temperature in some types of stream systems (Durance and Ormerod 2009). Studies have recommended including factors other than temperature in making species distribution predictions in light of climate change (Filipe et al. 2013), but this has seldom been done. Most studies of climate

change in freshwater ecosystems have only looked at temperature (Eaton and Scheller 1996, Hamilton et al. 2010) or have looked at the overall effects of climate change without quantifying temperature or flow (Chessman 2009, 2012, Li et al. 2013). A few studies have described the effects of the interaction of temperature with oxygen, salinity, or flow (Lawrence et al. 2010, Verberk and Calosi 2012, Verbrugge et al. 2012, McCue and De Los Santos 2013) on invertebrate communities in streams, but at a small scale of 1-4 streams or rivers or in the lab. Two studies in the western United States predicted how changes in stream hydrology and temperature may affect trout (Wenger et al. 2011, Pingram et al. 2014), but only for 2-4 species. An additional study (Buisson and Grenouillet 2009) predicted distributional shifts in the 35 common fish taxa in France using temperature and precipitation, but did not use any direct measure or climate prediction of flow. Our study aims to project the aquatic insect community response to climate change through both runoff and temperature across a large study area. Additionally, particular regions, such as the Mediterranean region in Europe (Filipe et al. 2013), are expected to be particularly vulnerable to climate. We assessed how community responses to multiple climate-driven variables may vary across climatic regions, or ecoregions, in the western United States.

Methods

Dataset

Our aquatic insect richness dataset came from U.S. Environmental Protection Agency's (USEPA) Environmental Monitoring and Assessment Program – Western Pilot Study (WEMAP), which selected sites in 12 western states (Stoddard et al. 2005). Although over 1300 sites were sampled in the WEMAP study, we limited our analysis to 252 sites that were least-

impacted by anthropogenic disturbance. The reason for this was two-fold. First, we wanted to focus on temperature and hydrology changes from climate change without needing to account for the confounding factors of other anthropogenic disturbances. Second, the method used to calculate mean annual runoff from catchment characteristics could not be accurately estimated if anthropogenic hydrological disturbances dominated catchment hydrology. At each site, biological data were collected mostly during the summer (June–September), with a few sites sampled in May or October, following the procedures in (2006). We used genus level designations for most taxa, but grouped some of the taxa according to family due to their difficulty in identification (Capniidae, Leuctridae, and Taeniopterygidae). Chironomids were grouped according to sub-family.

The climate models make predictions concerning precipitation, air temperature, and hydrology and we focused on the latter two. Most of the biological data were collected during summer months and stream taxa are most likely to be negatively affected by the thermal maximums during this period, particularly in the context of climate change, with July being the warmest month for most of our sites. Mean annual July air temperature was calculated for each site's catchment from the 800-m-resolution Parameter-elevation Regressions on Independent Slopes Model (PRISM) database (30-y period of record from 1971–2000; PRISM Climate Group, Oregon State University, Corvallis, Oregon; <http://www.prismclimate.org>) using methods from Cuhaciyar (2006). Mean annual runoff (mean annual flow/catchment area) was derived using a random forest technique that derived hydrological variables from catchment-scale variables (e.g., precipitation, geology, land use, etc.; see Carlisle et al. 2010 for details).

Taxa tolerances

We determined the thermal and runoff tolerances of individual taxa using the biological inference techniques described in Yuan (2006). First, we classified taxa as sensitive or tolerant to changes in temperature and hydrology. Classifications were made according to the shape of logistic general additive models (GAM) for each taxon, which estimated the probability of observing a taxon along an environmental gradient using richness data. A generalized additive model is based on the assumption that the response variable has a non-linear relationship with the predictor variable. The model estimates the response variable by 1) modifying the response variable using a function (e.g., logistic function) and 2) summarizing the relationship between the response and predictor variable using a non-parametric function of the predictor instead of simple linear coefficient (Zuur et al. 2007). The non-parametric function is usually some sort of smoothing function, such as moving average (a simple smoothing function). We decided to use the GAM model, as opposed to other niche models, to be consistent with results found in Yuan (2006). We developed two GAMs for each taxon, with mean July air temperature as the explanatory variable for one model and mean annual runoff for the other. The response variable, the probability of occurrence for a taxon, in our GAMs could have four possible responses: 1) continually decrease, 2) continually increase, 3) have no relationship, or 4) have a unimodal relationship with increasing temperature or runoff. The use of GAM is sensitive to the number of observations in the model, so we only performed this analysis for aquatic insects found at 20 or more sites in our dataset, as suggested in Yuan (2006). Yuan (2006) performed a similar analysis for stream temperature using 392 WEMAP sites and assigned taxa to three possible thermal tolerance curve shape categories, which we used for this analysis. Thermally tolerant (T) taxa had an increasing curve or a uniform distribution with increasing temperatures.

Thermally intermediately tolerant (I) taxa had a unimodal distribution with probability of occurrence declining in very low and very high temperatures. Thermally sensitive (S) taxa had a decreasing curve with increasing temperatures. We determined curve shape graphically; if the highest probability was higher than the 95% confidence intervals at each end of the environmental gradient, then the curve was defined as unimodal. Under climate change scenarios, taxa designated as I or S were expected to be negatively affected by increases in temperature. We then fit GAMs using mean annual runoff as the explanatory variable and assigned taxa to four possible runoff tolerance curve shape categories. High runoff (H) tolerant taxa have an increasing curve, low runoff (L) tolerant taxa have a decreasing curve, intermediate maxima (M) taxa have a unimodal curve, and taxa with no response (N) are present in most runoff conditions. Under climate change scenarios, categories H and M are expected to be negatively affected by loss of runoff and categories L and N are expected to be negatively affected by increases in runoff.

We calculated the area under the receiver operating characteristic curve (AUC) for each GAM to determine model fit. The AUC measures the ability of a model to discriminate between true positives and false positives (Hosmer and Lemeshow 2000) and accepted rule for adequate model discrimination is 0.70, but this is intended for models that would be used in a predictive fashion. Our GAM models were only used to classify taxa instead of being used predictively, so we used a smaller AUC value of 0.55 as an acceptable measure of model fit for classification purposes, as suggested by Yuan (2006). If taxa met this criterion, the model was deemed acceptable for investigations of taxon vulnerability to temperature or runoff. All taxa except *Acentrella* met the model assessment criterion for temperature, which we assigned as tolerant. The GAM models were produced using the *gam* library (Hastie 2013) in R (R Core Team 2012).

Examples of GAM models are shown in Figure 4.1. Our GAM analysis assigned 57 taxa in the same thermal tolerance category as Yuan (2006). Eleven of our taxa were not found in his paper. Fourteen of the remaining 20 taxa had somewhat ambiguous results. For example, Yuan detected a unimodal relationship for the genus *Optioservus* and our results appeared unimodal as well, but the maximum probability of our analysis was not greater than the uppermost 95% confidence interval on the right side of the graph, indicating a tolerant relationship. For the remaining six taxa, our results strongly contradicted Yuan's. These six are indicated in Table 4.2. For the remainder of our analysis, we decided to use the Yuan (2006) designations for the ambiguous and contradictory taxa, since his dataset encompassed a larger range of temperature values than ours.

Once we classified each taxon, we defined a value along each environmental gradient where the taxon would be theoretically vulnerable to extirpation due to climate change. We designated these risk threshold values using the cumulative percentile technique, in which the proportion of sites where a taxon is present is summed along an environmental gradient. We then ran a logistic regression model on each cumulative percentile to estimate the temperature or runoff values at a specific cumulative percentile, such as 0.95. These temperature and runoff values are thresholds, points along the environmental gradient where the taxon is near their environmental limits, would be ecologically or physiologically stressed, and at high risk of local extinction. The selection of a cumulative percentile is based on our opinion when a taxon would be near its environmental limits in its current range and is thus somewhat arbitrary. The selection of the cumulative percentile value also presents a tradeoff, with percentiles closer to 1 or 0 more likely representing a true threshold, but the error also increases due to the fewer data points on the other side of the threshold value (Yuan 2006). Since the objective of this paper is

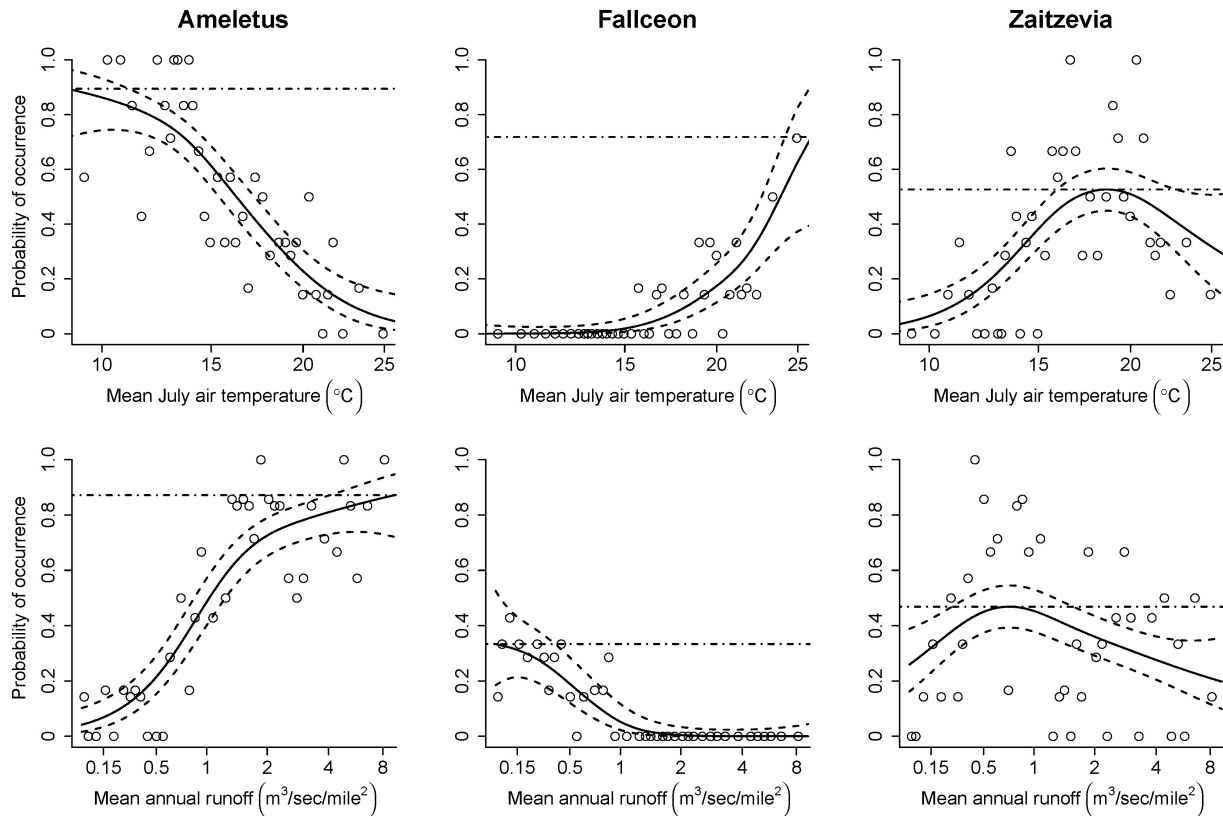


Figure 4.1: General additive models for three representative taxa with the model for mean July air temperature on the top row and mean annual runoff on the bottom row. The genus *Ameletus* is classified as vulnerable to high temperature (S) and tolerant to high runoff (H). *Fallceon* is tolerant to high temperature (T) and low runoff (L). *Zaitzevia* is intermediately tolerant to temperature (I) and runoff (M). The solid line is the GAM model, the two dashed lines represent the 95% confidence interval, and the horizontal dot-and-dashed line represents the highest response value in the GAM model.

to estimate the community vulnerability, we felt it more important to estimate thresholds using cumulative percentiles near the edge of each taxon's current distribution along the environmental gradients. We picked the 0.95 cumulative percentile to represent the point in a taxon's distribution where it would become vulnerable to increases in temperature or flow and the 0.05 cumulative percentile to represent the point in a taxon's distribution where it would become vulnerable to decreases flow. Examples of threshold models are shown in Figure 4.2.

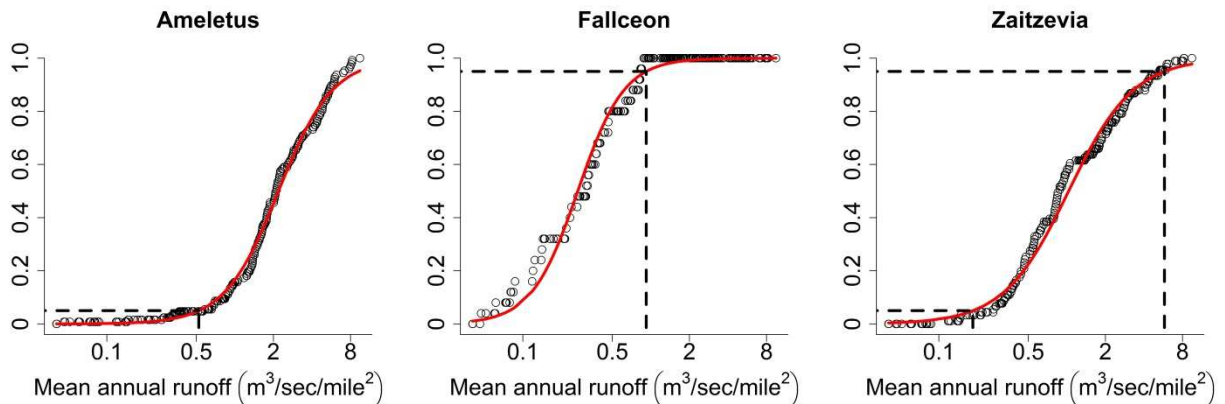


Figure 4.2: The cumulative percentiles of three representative taxa for mean annual runoff using the 0.05 and 0.95 cumulative percentiles. The red line is the logistic regression model; the dashed lines represent the mean annual runoff value that corresponds with the cumulative proportions of 0.05 or 0.95, according to the logistic regression. *Ameletus* is high runoff tolerant (H), so we calculated the 0.05 threshold. *Fallceon* is low runoff tolerant (L), so we calculated the 0.95 threshold. *Zaitzevia* has an intermediate runoff tolerance (M), so we calculated both 0.05 and 0.95 threshold values.

To account for the uncertainty with our selection of 0.05/0.95 cumulative percentiles, we also ran our analysis using thresholds estimated from 0.10/0.90 and 0.01/0.99 cumulative percentiles. The 0.10/0.90 cumulative percentiles would represent a situation where taxa are less resilient or resistant to climate change and the 0.01/0.99 cumulative percentiles would represent a situation where they are more resilient/resistant. The use of 0.01/0.99 cumulative percentiles presents an additional issue since the logistic regression extrapolates the environmental threshold values beyond current distribution of the taxon. Thus, the 0.01/0.99 cumulative percentiles would represent the best-case scenario, but should be viewed with caution. It is also important to understand that this technique assumes that the current distribution of a taxon already includes a proportion of sites that we designated as vulnerable, with taxa likely being extirpated from the site. Taxa sensitive to increases in temperature of flow were assigned an upper threshold using a

cumulative percentile of 0.95 (or 0.90, 0.99), taxa sensitive to loss of runoff were assigned a lower threshold (using 0.01, 0.05, or 0.1), and taxa intermediately tolerant to runoff, such as *Zaitzevia* in Figure 4.2, were assigned both an upper and a lower threshold, with the taxon becoming extirpated from the site if either runoff threshold is crossed.

Climate ecoregions

We modified Omernik's level-I ecoregions (Omernik 1987) in a way we felt that best grouped sites in the context of temperature and hydrological alteration due to climate change. Our desert, Mediterranean, and plains ecoregion designations are the same as Omernik's. The remaining five ecoregions were carved from the west's mountainous and more temperate regions. The Southern Dry Highlands ecoregion consists of the mountainous regions in Arizona with drier climatic conditions than other mountains to the north. The Northwestern Wet Forests ecoregion consists of the western and northern Cascade Mountains and the coastal rainforests of eastern Oregon, Washington, and northern California. This region experiences some of the highest precipitation in the 48 states with markedly different hydrological and thermal regimes than other, drier mountainous areas in the western United States. We broke the remaining western mountains into three ecoregions. The Klamath Mountains ecoregion in northern California and southern Oregon contain mountainous flora and fauna, but have very dry, warm summers and may be particularly sensitive to climate change. The two remaining mountainous regions were divided according to latitude. The Middle Temperate Mountains ecoregion (consisting of the Sierra Nevadas, Wasatch and Uinta Mountains, and the southern Rockies of Colorado) is lower in latitude with warmer summers. The Northern Temperate Mountains

ecoregion (consisting of the northern and middle Rockies, eastern Cascades, and Blue mountains) has generally shorter, cooler summers. Ecoregions and sites are shown in Figure 4.3.

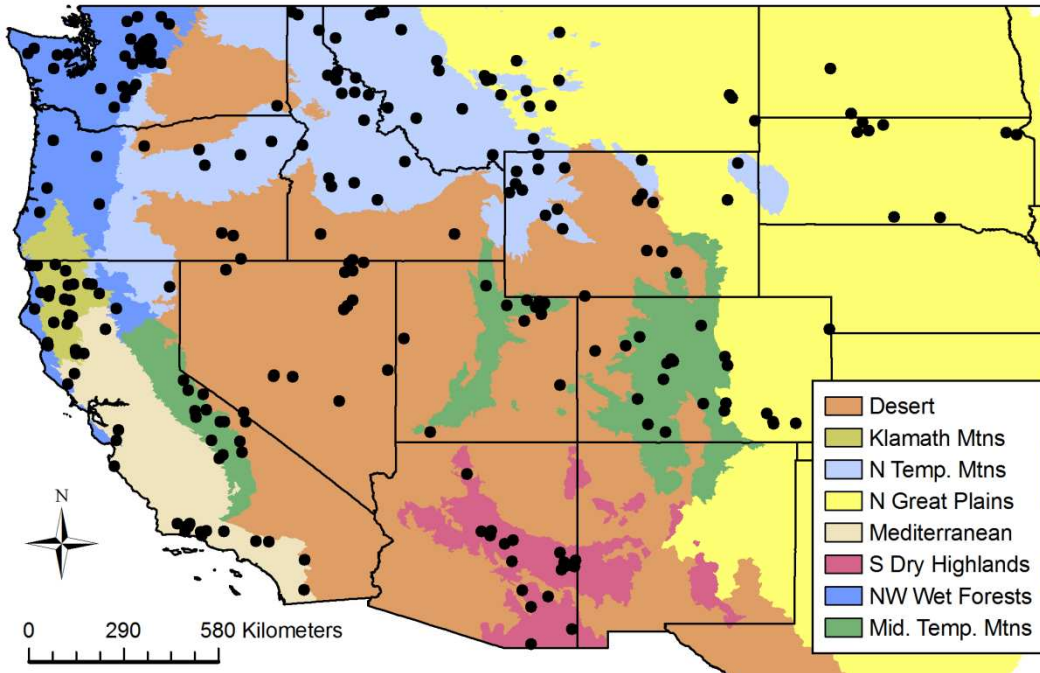


Figure 4.3: Ecoregions, represented by color, and the location of sites in the western United States (black dots; n = 252).

Climate predictions

Once we designated tolerance classifications and threshold values for each taxon, we wanted to assess how climate change predictions may affect 1) individual taxa and 2) communities grouped according to ecoregion. We used two approaches to do this. First, at each site we incrementally increased the mean annual July air temperature by four degrees Celsius and incrementally changed mean annual runoff by $\pm 80\%$, values that encompassed the range of temperature and flow changes predicted by the climate models. Once changes in temperature or runoff crossed a taxon threshold, the taxon was removed from the site. We added a stochastic element to this process by allowing the removed taxon to be randomly added back to the site

based on the distance the temperature or runoff is from the taxon's threshold. For example, if the temperature value crosses threshold based on the 0.05/0.95 cumulative percentile for a taxon, then that taxon could be re-inserted if a value drawn from a uniform distribution (minimum 0, maximum 1) is less than 0.05. The probability of being re-inserted decreases according to the cumulative percentile after the threshold is crossed (e.g. 4% chance of re-insertion at the 0.04/0.96 thresholds, 3% chance at 0.03/0.97 thresholds) and a taxon cannot be re-inserted after temperature or runoff equal the value associated with the taxon's 0.001/0.999 cumulative percentile. For the taxon analyses, we summed sites now missing the once-present taxon and divided by the initial number of sites with the taxon. This was the proportion of sites that are considered lost for each taxon. For community analysis, we summed the total number of taxa removed from each site and divided by that site's initial number of common taxa. This was the mean proportion of taxa that are considered lost at each site. Stream community composition is shaped by both the regional species pool (dispersal, colonization) and species interactions under local stream conditions (Townsend and Hildrew 1994, Poff 1997), and we would therefore expect stream communities in some climatic regions to be more sensitive to climate change than others. To account for this, we averaged the proportion of lost taxa per site within each of eight ecoregions. We presented the proportion of lost taxa per community and lost sites per taxa for each ecoregion as contour graphs.

A second approach to assess how climate change affects our communities and taxa was to use actual climate model predictions, projected temperature and hydrology data from the World Climate Research Programme's (WCRP) Coupled Model Intercomparison Project phase 3 (CMIP3) multimodel data set. We used a middle climate scenario (A1b), with CO₂ emissions leveling off in the mid-21st century. We selected four climate change projections, each

representing the extremes in projected runoff and temperature change, and I averaged all 16 climate models as a 5th mean model for both the taxa and ecoregion analyses. The four extreme model projections represented mild increases in temperature and reduced runoff (warm-dry), mild increases in temperature and increased runoff (warm-wet), high increases in temperature and decreased runoff (hot-dry), and high increases in temperature and increased runoff (hot-wet). Taxa are not constrained to a particular ecoregion, so we selected models that represented extremes for the entire dataset in the taxa analyses, while we selected models for the ecoregion analyses that represented extremes for each ecoregion. The individual models used for each analysis are identified in Table 4.1. For each site's upstream catchment, we computed the mean air temperature and runoff from 1971-2000 for each of the five models as a baseline climate value, calculated the mean air temperature and runoff from 2041-2070 as a future value, and calculated the difference between the two values. The difference was retained as a value in Celsius for temperature and a proportional change for runoff. The climate model analyses were produced using ArcMapTM 9.3 GIS software (ESRI, Redlands, California). We then applied the changes in temperature and runoff to the mean July temperature and mean annual runoff variables at each site and calculated the number of thresholds crossed for each site and taxon.

In addition to analyzing shifts in community composition, we also assessed the shifts in the functional composition of aquatic insect communities at sites across ecoregions using the 0.05/0.95 cumulative percentile thresholds. We assigned each taxon the following traits according to Poff et al. (2006): functional feeding group (FFG), voltinism (i.e., number of generations per year), development time and seasonality, adult life span, and adult female dispersal distance. We calculated the proportion of taxa lost from each trait category according

to the five climate change model scenarios and found distinct functional changes according to ecoregion.

Table 4.1: The models used to represent extremes in projected changes in temperature and runoff. All taxa were found across multiple ecoregions, so the extreme models for all sites were used for the taxa analyses. For the community analyses, we selected climate models that best represented extremes at sites for each ecoregion.

Analysis	Warm-wet	Warm-dry	Hot-wet	Hot-dry
Taxa (all sites)	ncrp2	mri4	ipsl	ncrc6
NW Wet Forests	mri2	mri4	ipsl	ncrc3
N. Temp. Mtns	cccm2	csiro	ipsl	ncrc6
Mid. Temp. Mtns	ncrp4	mri4	ipsl	miro2
Klamath Mtns	mri1	mri4	ipsl	ukmo
Mediterranean	ncrp2	mri2	ipsl	ukmo
S. Dry Highlands	ncrp2	mri4	inmcm	miro1
Desert	ncrp2	mri4	ipsl	miro2
Great Plains	ncrp3	giss4	ukmo	ipsl

cccm2 = Canadian Centre for Climate Modeling and Analysis, Canada, CGCM3.1 (T47) model, run 2

csiro = Commonwealth Scientific and Industrial Research Organization, Atmospheric Research, Australia, CSIRO-Mk3.0 model

giss4 = NASA/Goddard Institute for Space Studies, USA, GISS-ER model, run 4

inmcm = Institute for Numerical Mathematics, Russia, INM-CM3.0 model

ipsl = Institut Pierre Simon Laplace, France, IPSL-CM4 model

miro1 = Center for Climate System Research (The University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change, Japan, MIROC3.2 (medres) model, run 1

miro2 = Center for Climate System Research (The University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change, Japan, MIROC3.2 (medres) model, run 2

mri1 = Meteorological Research Institute, Japan, MRI-CGCM2.3.2 model, run 1

mri2 = Meteorological Research Institute, Japan, MRI-CGCM2.3.2 model, run 2

mri4 = Meteorological Research Institute, Japan, MRI-CGCM2.3.2 model, run 4

ncrc3 = National Center for Atmospheric Research, USA, CCSM3 model, run 3

ncrc6 = National Center for Atmospheric Research, USA, CCSM3 model, run 6

ncrp2 = National Center for Atmospheric Research, USA, PCM model, run 2

ncrp3 = National Center for Atmospheric Research, USA, PCM model, run 3

ncrp4 = National Center for Atmospheric Research, USA, PCM model, run 4

ukmo = Hadley Centre for Climate Prediction and Research/Met Office, UK, UKMO-HadCM3 model

Results

Our dataset had 88 aquatic insects found at 20 or more sites. Sixty-two of these taxa had tolerance curves indicating they were vulnerable to (i.e., probability of occurrence decreased

with) increases in temperature, 59 were vulnerable to proportional decreases in runoff, and 23 were vulnerable to proportional increases in runoff. Thermal and runoff tolerance classifications and the threshold values based on the 0.05/0.95 cumulative percentiles for each taxon are in Table 4.2. The use of different thresholds (e.g., 0.9, 0.95, 0.99) showed a wide range of possible responses by an individual taxon to climate change, but the incremental method revealed about ten groups of taxa with similar responses to increases in temperature and changes in runoff. Five taxa were tolerant to changes in both temperature and runoff, showing no response. Two groups were tolerant of temperature increases with four taxa losing sites as runoff decreased and 16 taxa losing sites as runoff increased (a representative of this latter group is shown in row A in Figure 4.4). Eight taxa were tolerant of changes in runoff, but lost sites with temperature increases (row B in Figure 4.4). The largest contingent of taxa, 34, showed a gradual loss of sites as temperature increased and runoff declined, some with amplified loss at about 75% runoff reduction (row C in Figure 4.4). Six taxa lost sites as runoff decreased or increased, most having the loss further amplified as temperature increased (row D in Figure 4.4). Six taxa showed only a slight loss of sites as temperature increased, but loss became more severe as runoff decreased (row E in Figure 4.4). Six taxa showed the opposite effect, with increases in temperature having the strongest effect and runoff only minimally amplifying the loss (row F in Figure 4.4). Two taxa experience a moderate loss of sites with increases temperature, but experienced much greater losses with decreases in runoff (row G in Figure 4.4). Finally, one taxon, the stonefly family Taeniopterygidae, lost most sites with even slight increases in temperature and loss of runoff (row H in Figure 4.4). The loss of sites varied greatly among taxa for the five climate model projections as well, with 24 taxa having less than 15% of sites lost for any model while Taeniopterygidae had 72% of sites lost for the two hot models (see Table 4.2).

Table 4.2: Thermal and runoff tolerance curve shapes, thresholds, and proportion of sites lost predictions for aquatic insects found at 20 or more sites. The thresholds and proportion of sites lost are based on the 0.05/0.95 cumulative percentiles. We used the three thermal curve shape classifications described in Yuan (2006): thermally tolerant (T), intermediately tolerant (I), and sensitive (S). The four mean annual runoff curve shape classifications are: tolerant to high runoff (H), tolerant to low runoff (L), intermediate maxima along the runoff gradient (M), and no response to runoff (N). The thermal threshold is in °C and computed for taxa sensitive to increases in temperature (S and I). The mean annual runoff thresholds are in ft³/sec/mile² with the 0.05 threshold computed for taxa sensitive to runoff reductions (H and M) while the 0.95 threshold was computed for taxa sensitive to runoff increases (L and M). The proportion of risky sites are those sites where the taxon is present in the dataset, but subsequently crossed the taxon's thermal tolerance or mean annual runoff thresholds when predictions from the five climate models were applied.

Taxa	Thermal tolerance		Mean annual runoff tolerance			Prop. of sites lost - climate models:				
	Curve shape	0.95 threshold	Curve shape	0.05 threshold	0.95 threshold	Warm, wet	Warm, dry	Mean	Hot, wet	Hot, dry
Coleoptera										
<i>Cleptelmis</i>	I	21.496	M	0.227	4.928	0.135	0.108	0.081	0.216	0.243
<i>Eubrianax</i>	I ^a	24.102	H	0.496	-	0.129	0.258	0.194	0.194	0.323
<i>Heterlimnius</i>	S	20.002	H	0.442	-	0.139	0.190	0.165	0.228	0.291
<i>Microcylloepus</i>	T	-	L	-	1.009	0.156	0.000	0.031	0.125	0.000
<i>Narpus</i>	I	20.292	H	0.289	-	0.208	0.208	0.208	0.375	0.333
<i>Optioservus</i>	I	23.867	L	-	5.403	0.132	0.088	0.132	0.228	0.167
<i>Ordobrevia</i>	T	-	H	0.396	-	0.036	0.143	0.071	0.071	0.179
<i>Oreodytes</i>	T	-	H	0.263	-	0.029	0.086	0.029	0.057	0.114
<i>Zaitzevia</i>	I	23.137	M	0.184	5.775	0.176	0.132	0.187	0.297	0.275
Diptera										
<i>Antocha</i>	I	22.010	H	0.244	-	0.117	0.091	0.195	0.208	0.286
<i>Bezzia</i>	T	-	L	-	8.037	0.008	0.000	0.000	0.008	0.000
<i>Chelifera</i>	S	19.916	H	0.262	-	0.121	0.152	0.167	0.227	0.258
Chironominae	T	-	L	-	9.744	0.004	0.000	0.004	0.008	0.000
<i>Clinocera</i>	S	21.007	H	0.372	-	0.128	0.191	0.170	0.170	0.234
Diamesinae	S	19.671	H	0.347	-	0.123	0.180	0.189	0.254	0.270
<i>Dicranota</i>	S	21.755	H	0.212	-	0.128	0.141	0.167	0.192	0.244

Taxa	Thermal tolerance		Mean annual runoff tolerance			Prop. of sites lost - climate models:				
	Curve shape	0.95 threshold	Curve shape	0.05 threshold	0.95 threshold	Warm, wet	Warm, dry	Mean	Hot, wet	Hot, dry
<i>Dixa</i>	S ^b	24.483	N	-	-	0.057	0.086	0.086	0.086	0.086
<i>Glutops</i>	S	23.158	H	0.773	-	0.030	0.091	0.121	0.152	0.303
<i>Hemerodromia</i>	T	-	L	-	4.560	0.000	0.000	0.000	0.095	0.000
<i>Hexatoma</i>	I	21.437	H	0.243	-	0.163	0.174	0.233	0.267	0.291
<i>Limnophila</i>	S ^b	27.170	N	-	-	0.000	0.000	0.000	0.000	0.000
<i>Maruina</i>	T	-	N	-	-	0.000	0.000	0.000	0.000	0.000
<i>Neoplasta</i>	T	-	N	-	-	0.000	0.000	0.000	0.000	0.000
<i>Oreogeton</i>	S	17.654	H	0.932	-	0.147	0.176	0.206	0.353	0.294
Orthoclaadiinae	T	-	N	-	-	0.000	0.000	0.000	0.000	0.000
<i>Pericoma</i>	S ^b	22.859	M	0.219	5.238	0.054	0.162	0.189	0.189	0.324
<i>Prosimulium</i>	S	16.551	H	0.430	-	0.241	0.241	0.310	0.345	0.379
<i>Simulium</i>	T	-	L	-	6.666	0.031	0.019	0.019	0.044	0.013
Tanypodinae	T	-	N	-	-	0.000	0.000	0.000	0.000	0.000
<i>Tipula</i>	S	21.233	N	-	-	0.125	0.167	0.250	0.292	0.292
<i>Wiedemannia</i>	S	19.391	H	0.675	-	0.179	0.143	0.179	0.179	0.250
Ephemeroptera										
<i>Acentrella</i>	T	-	L	-	3.675	0.033	0.033	0.033	0.067	0.033
<i>Ameletus</i>	S	19.945	H	0.522	-	0.134	0.157	0.173	0.236	0.236
<i>Baetis</i>	S	23.222	H	0.184	-	0.069	0.111	0.120	0.152	0.194
<i>Caenis</i>	T	-	L	-	1.644	0.054	0.054	0.054	0.054	0.054
<i>Caudatella</i>	S	17.781	H	0.835	-	0.176	0.196	0.216	0.294	0.314
<i>Centroptilum</i>	T	-	N	-	-	0.000	0.000	0.000	0.000	0.000
<i>Cinygmula</i>	S	19.880	H	0.512	-	0.126	0.176	0.193	0.252	0.244
<i>Dipheter</i>	I	23.694	N	-	-	0.024	0.024	0.037	0.098	0.134
<i>Drunella</i>	S	20.598	H	0.510	-	0.145	0.178	0.217	0.217	0.263
<i>Epeorus</i>	S	21.467	H	0.350	-	0.138	0.151	0.191	0.211	0.257
<i>Ephemerella</i>	S	20.610	H	0.293	-	0.117	0.200	0.150	0.200	0.267
<i>Fallceon</i>	T	-	L	-	0.918	0.160	0.000	0.000	0.080	0.000

Taxa	Thermal tolerance		Mean annual runoff tolerance			Prop. of sites lost - climate models:				
	Curve shape	0.95 threshold	Curve shape	0.05 threshold	0.95 threshold	Warm, wet	Warm, dry	Mean	Hot, wet	Hot, dry
<i>Ironodes</i>	S	23.193	H	0.532	-	0.063	0.156	0.125	0.125	0.281
<i>Paraleptophlebia</i>	S	23.346	H	0.241	-	0.044	0.080	0.097	0.142	0.195
<i>Rhithrogena</i>	S	20.078	H	0.777	-	0.139	0.165	0.191	0.209	0.235
<i>Serratella</i>	I	21.944	H	0.342	-	0.108	0.189	0.176	0.216	0.270
<i>Tricorythodes</i>	T	-	L	-	3.248	0.098	0.073	0.073	0.146	0.049
Megaloptera										
<i>Sialis</i>	T	-	L	-	8.246	0.026	0.000	0.000	0.026	0.000
Odonata										
<i>Argia</i>	T	-	L	-	1.909	0.033	0.033	0.033	0.033	0.033
Plecoptera										
<i>Calineuria</i>	I	24.188	H	0.473	-	0.098	0.216	0.137	0.157	0.255
Capniidae	S	19.290	H	0.523	-	0.128	0.205	0.205	0.205	0.231
<i>Doroneuria</i>	S	17.968	H	0.497	-	0.192	0.212	0.250	0.269	0.365
<i>Hesperoperla</i>	I	22.468	N	-	-	0.065	0.043	0.065	0.174	0.152
Leuctridae	S	19.757	H	0.746	-	0.161	0.145	0.194	0.194	0.258
<i>Malenka</i>	I	23.170	H	0.230	-	0.062	0.077	0.154	0.215	0.292
<i>Megarcys</i>	S	16.446	H	0.924	-	0.232	0.161	0.286	0.464	0.464
<i>Pteronarcys</i>	S	20.305	H	0.350	-	0.182	0.182	0.227	0.273	0.318
<i>Skwala</i>	S	20.868	H	0.382	-	0.160	0.240	0.240	0.240	0.280
<i>Suwallia</i>	S	16.644	H	0.632	-	0.130	0.130	0.217	0.348	0.348
<i>Sweltsa</i>	S	20.305	H	0.494	-	0.154	0.169	0.185	0.231	0.262
Taeniopterygidae	S	15.167	H	0.965	-	0.409	0.318	0.545	0.727	0.727
<i>Visoka</i>	S	17.850	H	0.972	-	0.156	0.156	0.222	0.311	0.289
<i>Yoraperla</i>	S	18.719	H	0.784	-	0.175	0.211	0.246	0.246	0.298
<i>Zapada</i>	S	19.911	H	0.378	-	0.133	0.178	0.193	0.274	0.274
Trichoptera										
<i>Agapetus</i>	I	23.889	N	-	-	0.077	0.077	0.077	0.115	0.154
<i>Apatania</i>	S	20.463	H	0.838	-	0.171	0.244	0.171	0.195	0.293

Taxa	Thermal tolerance		Mean annual runoff tolerance			Prop. of sites lost - climate models:				
	Curve shape	0.95 threshold	Curve shape	0.05 threshold	0.95 threshold	Warm, wet	Warm, dry	Mean	Hot, wet	Hot, dry
<i>Arctopsyche</i>	S	21.500	H	0.765	-	0.111	0.111	0.194	0.194	0.389
<i>Brachycentrus</i>	S	19.993	M	0.201	4.059	0.190	0.143	0.214	0.286	0.310
<i>Cheumatopsyche</i>	T	-	L	-	3.661	0.043	0.043	0.043	0.087	0.043
<i>Dicosmoecus</i>	T ^c	-	H	0.648	-	0.000	0.050	0.050	0.000	0.050
<i>Dolophilodes</i>	S	19.943	M	0.372	5.255	0.167	0.167	0.167	0.333	0.417
<i>Ecclisomyia</i>	S	19.922	H	1.113	-	0.190	0.238	0.286	0.333	0.333
<i>Glossosoma</i>	S	21.331	H	0.704	-	0.171	0.145	0.211	0.211	0.276
<i>Gumaga</i>	T	-	M	0.271	4.597	0.040	0.160	0.040	0.120	0.280
<i>Helicopsyche</i>	T	-	L	-	1.657	0.074	0.037	0.037	0.148	0.037
<i>Hydropsyche</i>	T	-	L	-	5.857	0.059	0.000	0.010	0.108	0.000
<i>Hydroptila</i>	T	-	L	-	3.796	0.063	0.021	0.042	0.125	0.021
<i>Lepidostoma</i>	S	23.346	H	0.248	-	0.051	0.093	0.102	0.127	0.203
<i>Micrasema</i>	S	22.875	H	0.290	-	0.058	0.115	0.135	0.163	0.288
<i>Neophylax</i>	S	19.230	H	0.547	-	0.219	0.156	0.313	0.344	0.344
<i>Neothremma</i>	S	15.818	H	0.908	-	0.171	0.257	0.286	0.486	0.486
<i>Ochrotrichia</i>	T	-	L	-	3.231	0.128	0.051	0.051	0.128	0.026
<i>Oligophlebodes</i>	S	17.326	H	0.471	-	0.136	0.136	0.227	0.318	0.273
<i>Parapsyche</i>	S	19.374	H	0.827	-	0.145	0.161	0.194	0.194	0.226
<i>Polycentropus</i>	T	-	H	0.311	-	0.000	0.129	0.065	0.032	0.194
<i>Rhyacophila</i>	S	20.982	H	0.470	-	0.136	0.191	0.210	0.216	0.272
<i>Wormaldia</i>	I ^a	24.889	N	-	-	0.038	0.038	0.077	0.154	0.154

A = Our analysis indicated a this taxon as thermally tolerant. Yuan's (2006) analysis designated the taxon as intermediately tolerant. We used the Yuan (2006) designation for this paper.

B = Our analysis indicated this taxon as thermally tolerant. Yuan's (2006) analysis designated the taxon as sensitive. We used the Yuan (2006) designation for this paper.

C = Our analysis indicated this taxon as thermally sensitive. Yuan's (2006) analysis designated the taxon as tolerant. We used the Yuan (2006) designation for this paper.

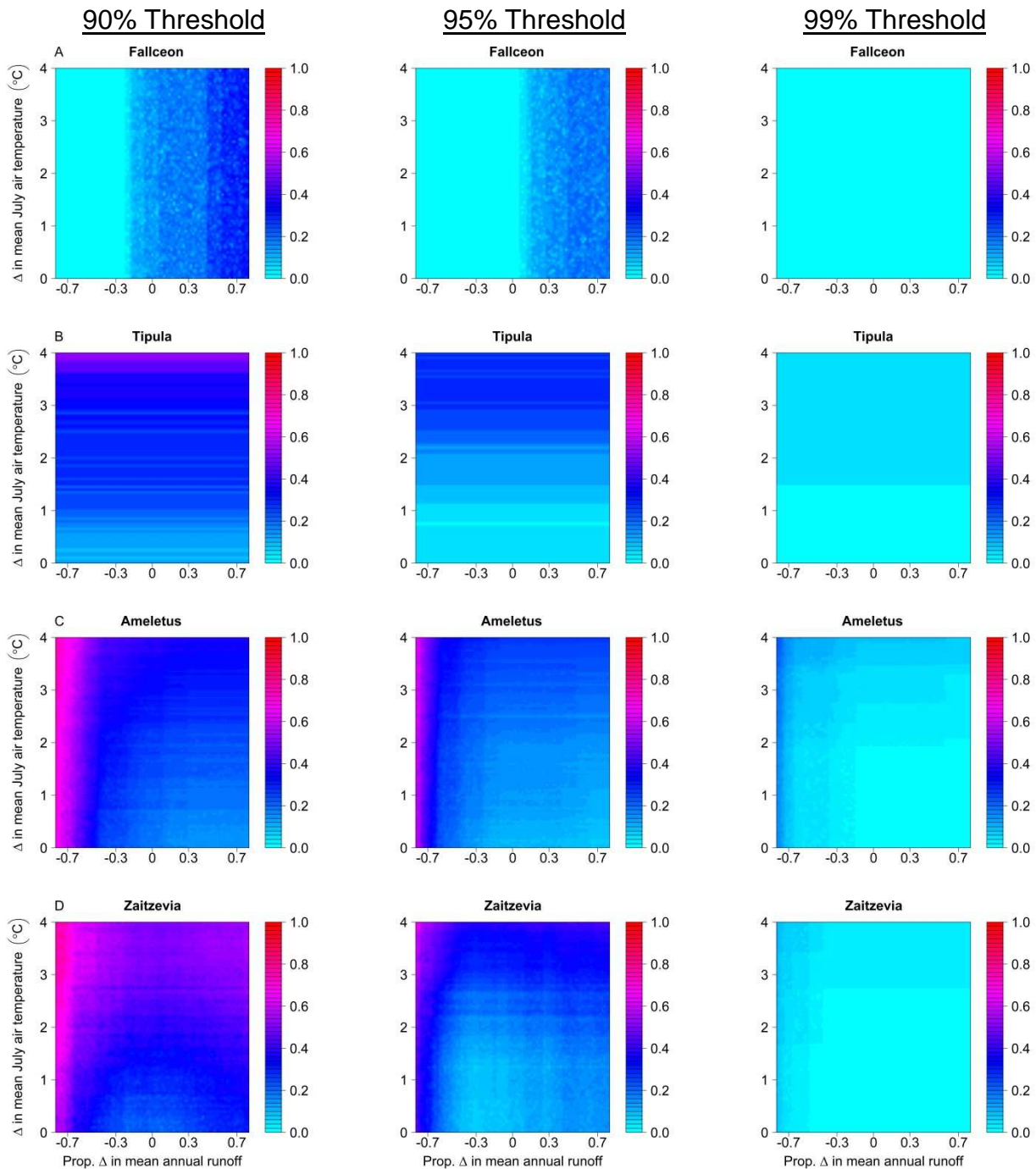


Figure 4.4: Projected proportions of sites considered “vulnerable” for representative taxa from eight of the ten taxa groups that showed similar responses to projected climate change. Each row represents a single taxon and each column represents a different threshold scenario. The colors represent the projected proportion of sites per taxa that were defined as “vulnerable” as temperature increased and runoff increased or decreased, with light blue representing 0 and bright red representing 1. Each row represents a taxon and each column represents a different threshold designation for the taxon.

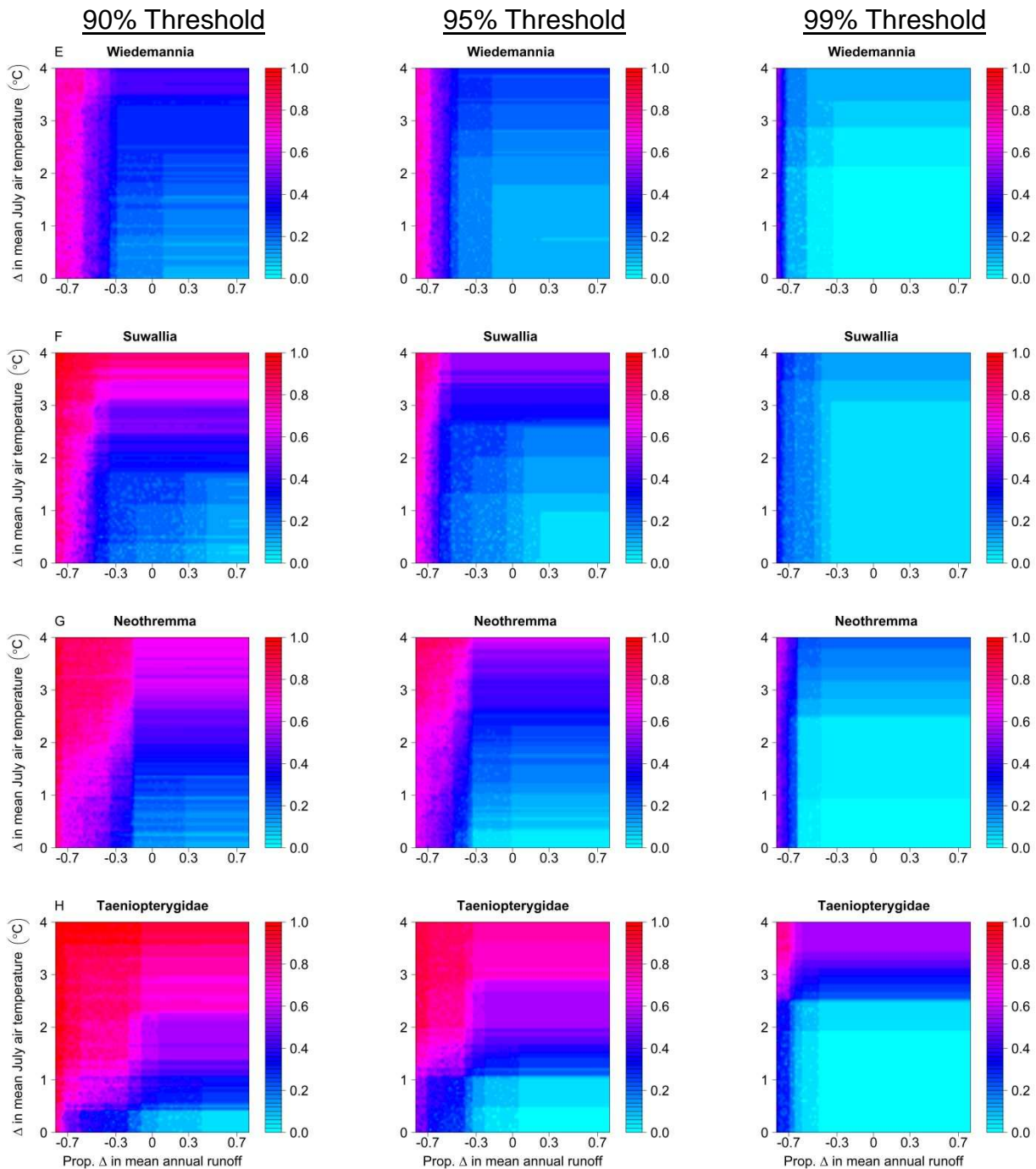


Figure 4.4, continued: Projected proportions of sites considered “vulnerable” for representative taxa from eight of the ten taxa groups that showed similar responses to projected climate change. Each row represents a single taxon and each column represents a different threshold scenario. The colors represent the projected proportion of sites per taxa that were defined as “vulnerable” as temperature increased and runoff increased or decreased, with light blue representing 0 and bright red representing 1. Each row represents a taxon and each column represents a different threshold designation for the taxon.

The mean proportion of taxa vulnerable to changes in runoff and temperature varied across ecoregions (Table 4.3). The Northwestern Wet Forests, Northern Temperate Mountains, Middle Temperate Mountains, and Klamath Mountains all had high proportions of taxa vulnerable to temperature increases and runoff decreases, followed by Desert, Mediterranean, and Southern Dry Highlands with moderate proportions and the Northern Great Plains with low proportions. Although some ecoregions have similar proportions of vulnerable taxa, such as the Middle Temperate and Klamath Mountains, the incremental analysis revealed very different ecoregion-scale community responses to changes in temperature and runoff (Figure 4.5). Adjusting the environmental threshold values based on different cumulative percentiles resulted in very different responses, with almost no loss of taxa at the 0.01/0.99 cumulative percentiles (right column in Figure 4.5) and increasing loss with the 0.05/0.95 (middle column in Figure 4.5) and 0.1/0.9 (left column in Figure 4.5) cumulative percentile scenarios. We felt that the 0.1/0.9 cumulative percentile scenario may have designated taxa as too sensitive to climate change (with 10% of their current distribution being vulnerable) and the 0.01/0.99 scenario may not be sensitive enough. With regards to the 0.05/0.95 scenario, the proportion of taxa lost in the Northern Great Plains slightly with runoff decreases and temperature decreases (05-15% of taxa lost), although this includes most vulnerable taxa in that ecoregion (row A in Figure 4.5). The Desert ecoregion had a similar pattern to the Northern Great Plains, but with a greater loss of taxa, up to 50% in the most extreme temperatures increases and runoff loss (row B in Figure 4.5). The proportion taxa lost in the Southern Dry highlands increased moderately (10-30%) with either increases or decreases in runoff coupled with temperature increases (row D in Figure 4.5). The proportion taxa lost in the Northern and Middle Temperate Mountains showed little response to temperature increases, with loss of runoff eliciting a greater, although minimal (0-

20%) response (rows F and G in Figure 4.5). The proportion of taxa lost in the Northwestern Wet Forests increased slightly as temperature and runoff increased (row H in Figure 4.5). Finally, the Klamath Mountains and Mediterranean ecoregions were the most severely affected by changes in temperature (rows C and E in Figure 4.5), while changes in runoff had little impact. The proportion of taxa lost in these two ecoregions ranged from 20-60%. The five climate model predictions (represented by the symbols in Figure 4.5 and shown in Table 4.3) demonstrate a range of reasonable scenarios for each ecoregion, with Middle Temperate Mountains having the lowest proportion taxa lost (0-10% according to the 0.05/0.95 threshold scenario) and the Klamath Mountains having the highest proportion of taxa lost (21-43% according to the 0.05/0.95 threshold scenario).

Trait responses

In addition to taxa lost from ecoregions, this analysis also demonstrated shifts in the trait composition of stream communities. For functional feeding groups, the collector-filterers appeared to be most sensitive to most climate change scenarios in the Northwestern Wet Forests (Figure 4.6). This may be due to increased runoff in the region and sensitivity of some filter-feeders, such as *Brachycentrus* and *Simulium* to extremely high runoff. Shredders appeared to be most sensitive in desert, plains, and the Southern Dry Highlands ecoregions, since most shredders in these regions were classified as sensitive to temperature increases. For the voltinism trait, univoltine (one generation per year) and semivoltine (one generation over multiple years) were most sensitive in the Klamath, Mediterranean, Desert, Great Plains, and Southern Dry Highlands ecoregions (Figure 4.7). Semivoltinism is often associated with organisms that prefer colder streams and may be at their thermal limits in these ecoregions. For

Table 4.3: The number of sites (n), mean proportion of thermally and runoff vulnerable taxa per ecoregion, and mean proportion of taxa lost for each ecoregion for five climate change scenarios. The mean proportion of taxa lost per site is based threshold values derived from the 0.05/0.95 cumulative percentiles. The numbers in parentheses are the standard errors.

Ecoregion	n	Prop. of common taxa vulnerable to:			Prop. of common taxa vulnerable to climate model predictions:				
		High Temp.	High runoff	Low runoff	Warm, wet	Warm, dry	Mean	Hot, wet	Hot, dry
NW Wet Forests	45	0.82 (0.02)	0.12 (0.02)	0.80 (0.02)	0.04 (0.01)	0.03 (0.01)	0.06 (0.01)	0.10 (0.02)	0.06 (0.01)
N. Temp. Mtns	50	0.82 (0.01)	0.15 (0.02)	0.80 (0.02)	0.04 (0.01)	0.04 (0.01)	0.05 (0.01)	0.09 (0.02)	0.09 (0.02)
Mid. Temp. Mtns	30	0.77 (0.02)	0.19 (0.02)	0.72 (0.02)	<0.01 (0)	0.04 (0.02)	0.03 (0.01)	0.05 (0.02)	0.09 (0.03)
Klamath Mtns	22	0.74 (0.02)	0.20 (0.01)	0.70 (0.02)	0.28 (0.03)	0.21 (0.03)	0.33 (0.04)	0.42 (0.04)	0.43 (0.04)
Mediterranean	19	0.51 (0.03)	0.39 (0.03)	0.46 (0.03)	0.25 (0.03)	0.29 (0.03)	0.30 (0.03)	0.34 (0.03)	0.40 (0.03)
S. Dry Highlands	15	0.38 (0.05)	0.48 (0.05)	0.35 (0.04)	0.08 (0.03)	0.10 (0.02)	0.09 (0.03)	0.11 (0.03)	0.16 (0.03)
Desert	43	0.60 (0.04)	0.39 (0.03)	0.51 (0.03)	0.11 (0.02)	0.19 (0.03)	0.17 (0.03)	0.16 (0.03)	0.26 (0.03)
Great Plains	28	0.21 (0.05)	0.62 (0.03)	0.16 (0.04)	0.03 (0.01)	0.12 (0.03)	0.09 (0.02)	0.10 (0.02)	0.11 (0.02)

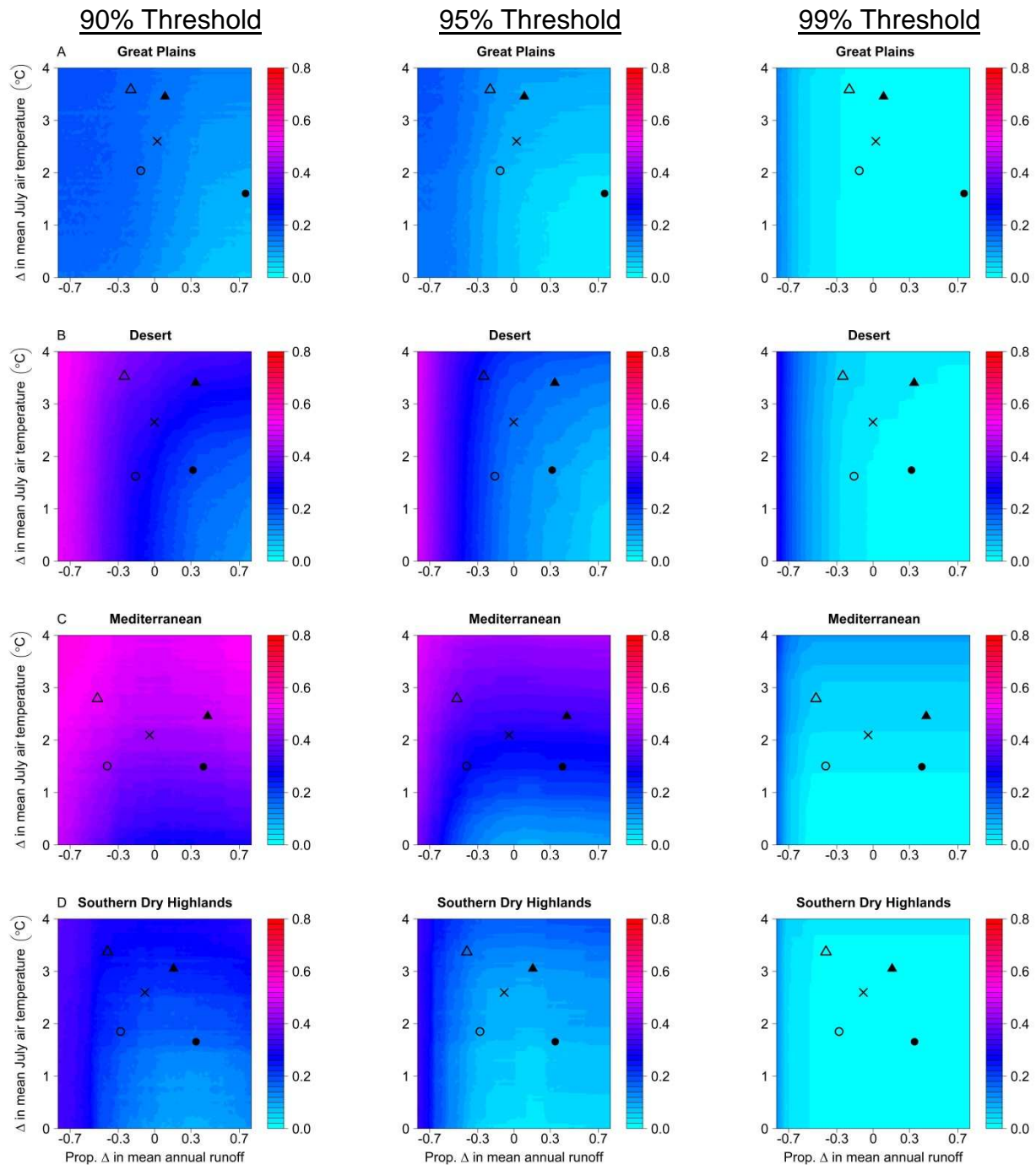


Figure 4.5: The projected proportion of taxa per site, averaged across ecoregions, which were defined as “vulnerable” as temperature increased and runoff increased or decreased, with light blue representing 0 and bright red representing 0.8. The five symbols represent the five climate change scenarios, with triangles representing high temperature increases, circles mild temperature increases, open symbols representing low runoff, closed symbols representing high runoff, and the X representing the mean of all climate models. Each row represents an ecoregion and each column represents a different threshold designation for the taxa in the ecoregion.

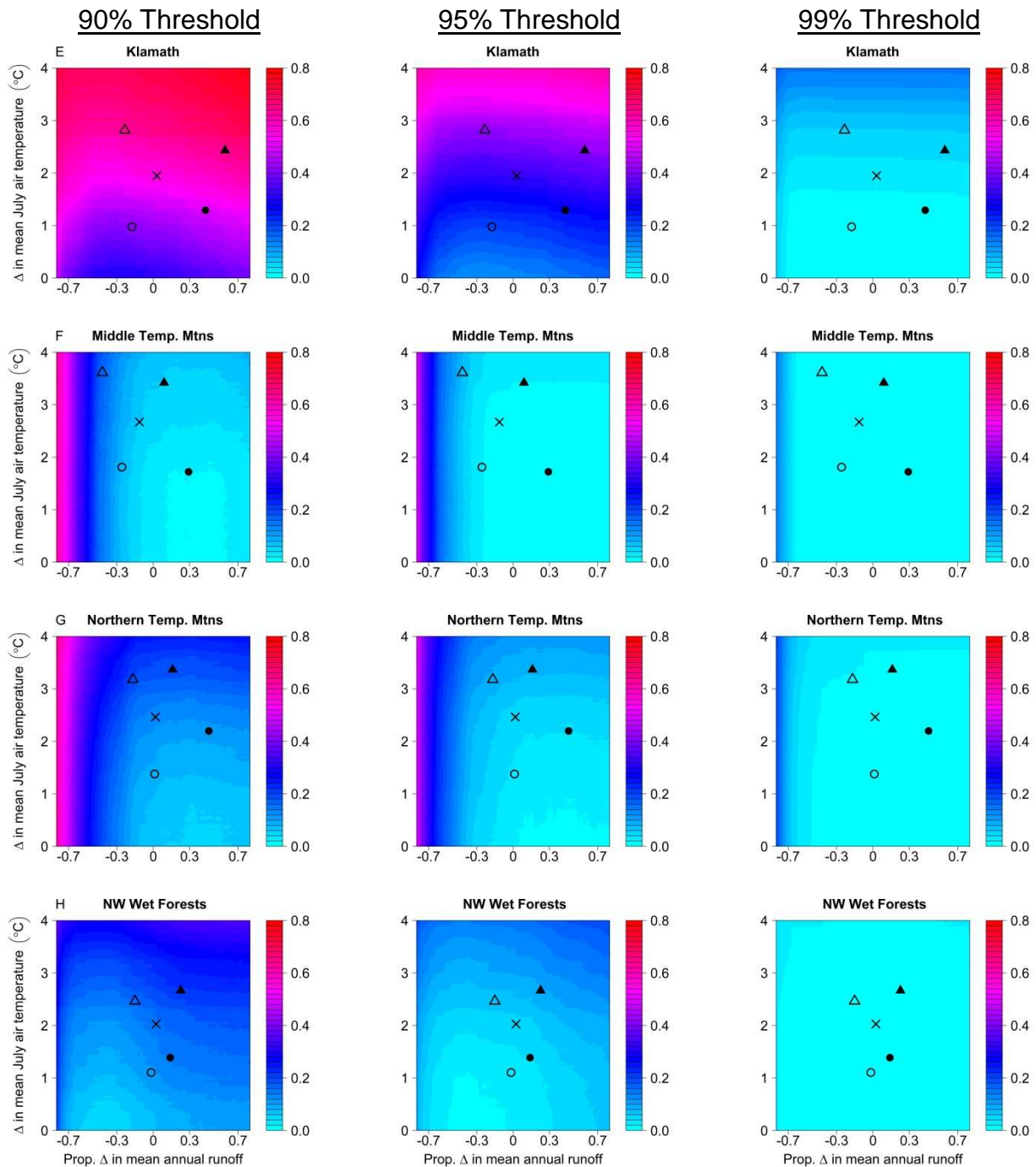


Figure 4.5, continued: The projected proportion of taxa per site, averaged across ecoregions, which were defined as “vulnerable” as temperature increased and runoff increased or decreased, with light blue representing 0 and bright red representing 0.8. The five symbols represent the five climate change scenarios, with triangles representing high temperature increases, circles mild temperature increases, open symbols representing low runoff, closed symbols representing high runoff, and the X representing the mean of all climate models. Each row represents an ecoregion and each column represents a different threshold designation for the taxa in the ecoregion.

the development trait, greater proportions of slow seasonal and nonseasonal taxa were lost in most ecoregions under most climate scenarios (Figure 4.8). For adult life span, long and short lifespans were lost in greater proportions in the drier and warmer ecoregions (Figure 4.9). For the adult female dispersal trait, the Klamath Mountains, Mediterranean, Desert, Southern Dry Highlands, and Great Plains ecoregions lost much greater proportions of low dispersal ability (Figure 4.10). Low dispersal, long adult lifespans, and semivoltinism are often associated with organisms that may not be able to adapt to changing stream conditions and sites in the Great Plains, Southern Dry Highlands, and Mediterranean ecoregions may experience a significant shift in the functional composition of organisms, with weedy organisms – organisms with faster life cycles and better dispersal abilities becoming more prominent.

Discussion

This analysis revealed that the relative influence of discharge and temperature on aquatic insect communities varies according to taxa and ecoregion and that both, producing very different community responses per ecoregion. Other studies have developed species distribution models for stream macroinvertebrates using temperature-only climate change scenarios and found that up 60% of European taxa will have decreases in distribution (Domisch et al. 2013) and some regions in Korea may lose up to 60% of taxa (Li et al. 2013), similar to our own results for the Klamath and Mediterranean ecoregions. But, experimental approaches in other ecosystems have found that that simple species distribution models based only on current temperatures did not perform well when temperatures were artificially increased (Diamond et al. 2012). To reason for this discrepancy is not known, but the fact that the inclusion of both temperature and runoff in our analysis resulted in unique responses taxa to climate change indicated that biological

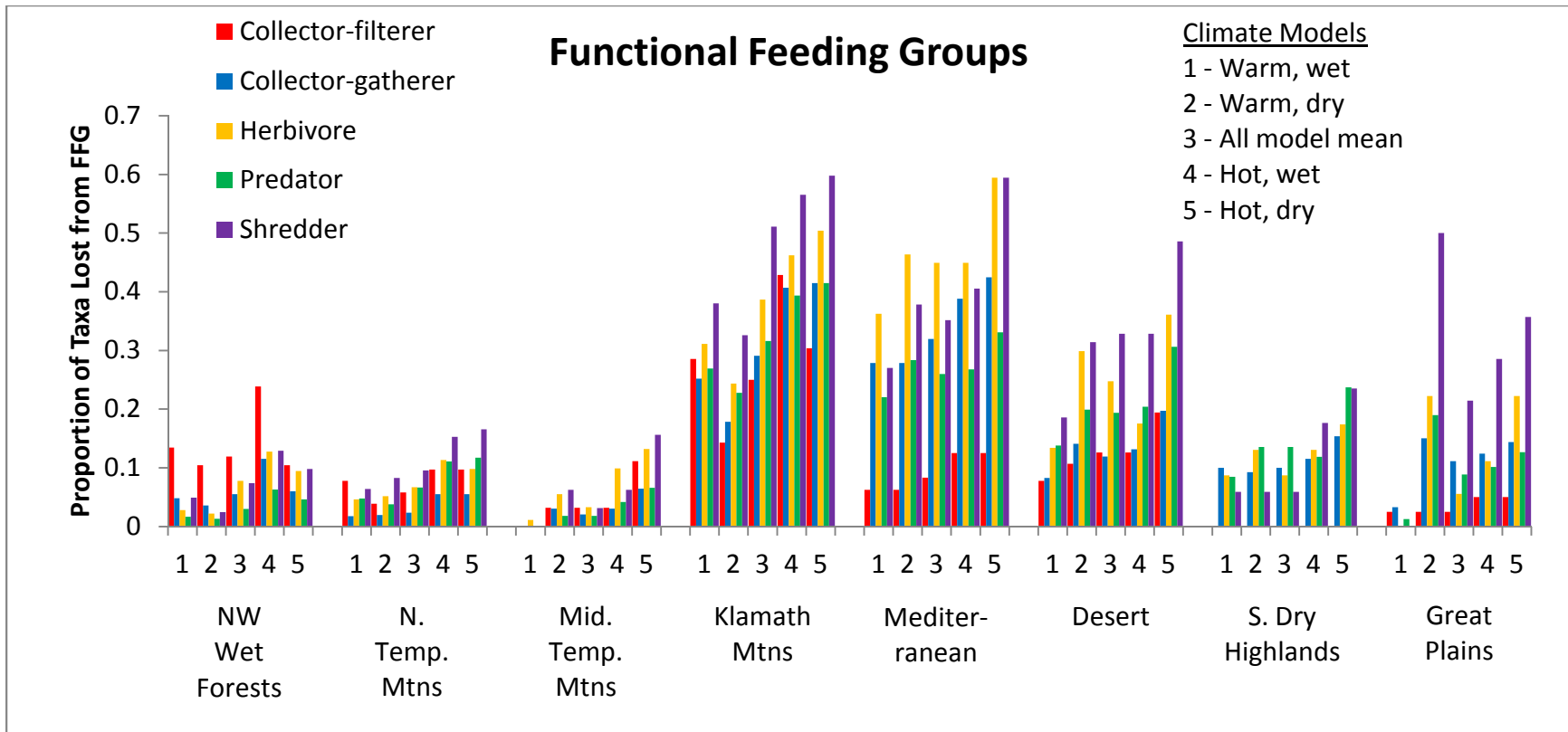


Figure 4.6: The mean proportional loss of taxa from functional feeding groups for each ecoregion using thresholds from the 0.05/0.95 cumulative percentile scenario. Numbers 1-5 on the x-axis represent the five climate change model scenarios for each ecoregion.

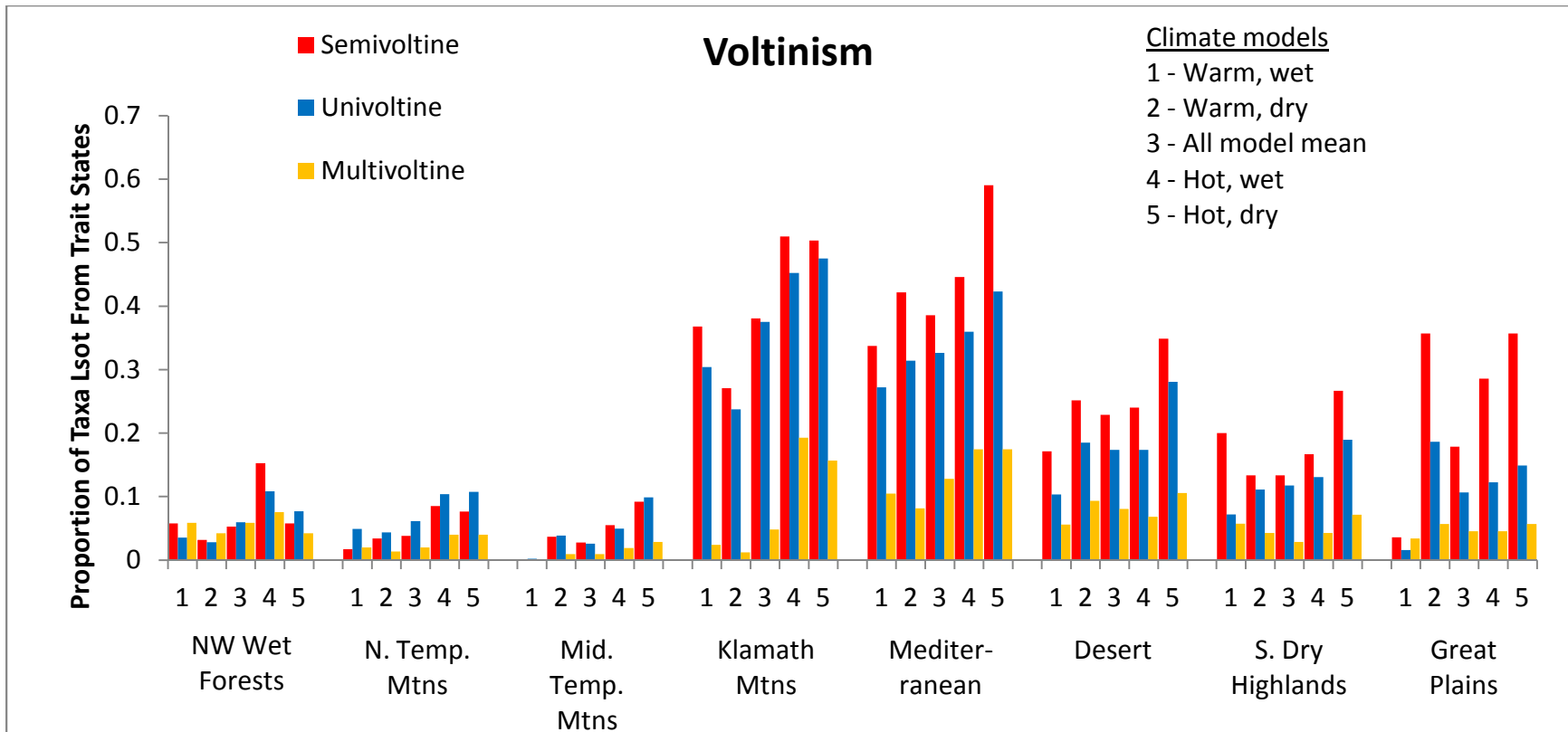


Figure 4.7: The mean proportional loss of taxa according to voltinism for each ecoregion using thresholds from the 0.05/0.95 cumulative percentile scenario. Numbers 1-5 on the x-axis represent the five climate change model scenarios for each ecoregion.

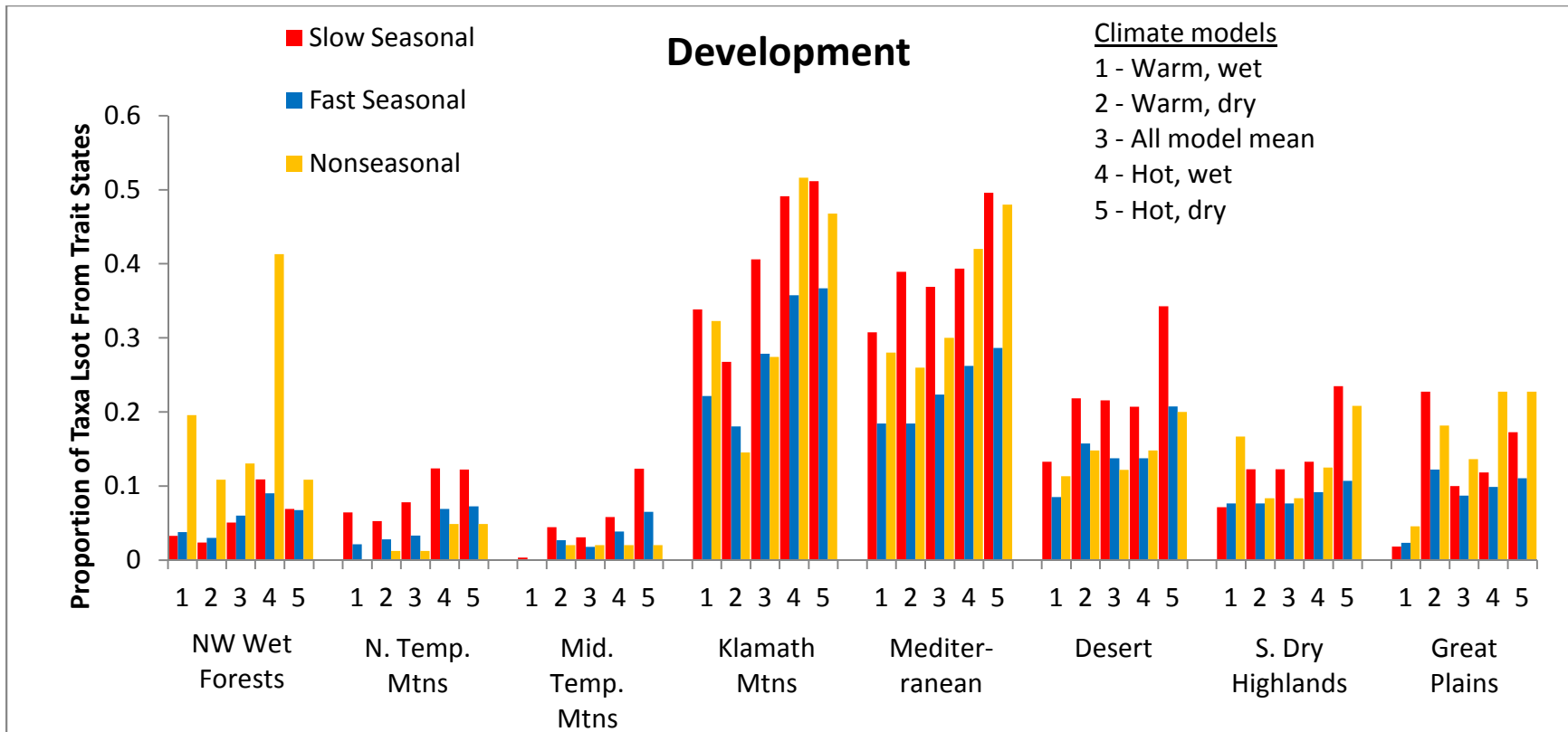


Figure 4.8: The mean proportional loss of taxa according to development time and seasonality for each ecoregion using thresholds from the 0.05/0.95 cumulative percentile scenario. Numbers 1-5 on the x-axis represent the five climate change model scenarios for each ecoregion.

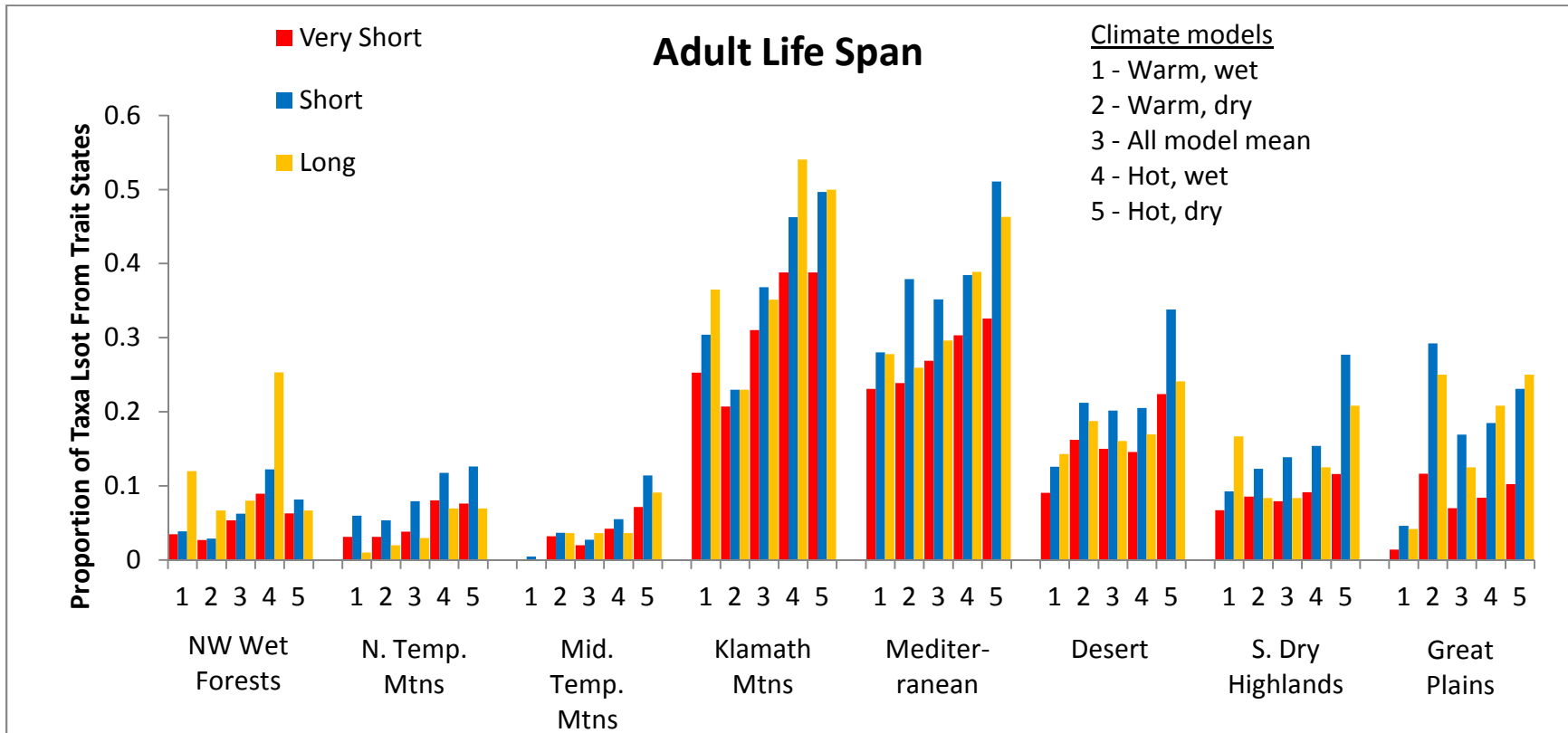


Figure 4.9: The mean proportional loss of taxa according to adult life span for each ecoregion using thresholds from the 0.05/0.95 cumulative percentile scenario. Numbers 1-5 on the x-axis represent the five climate change model scenarios for each ecoregion.

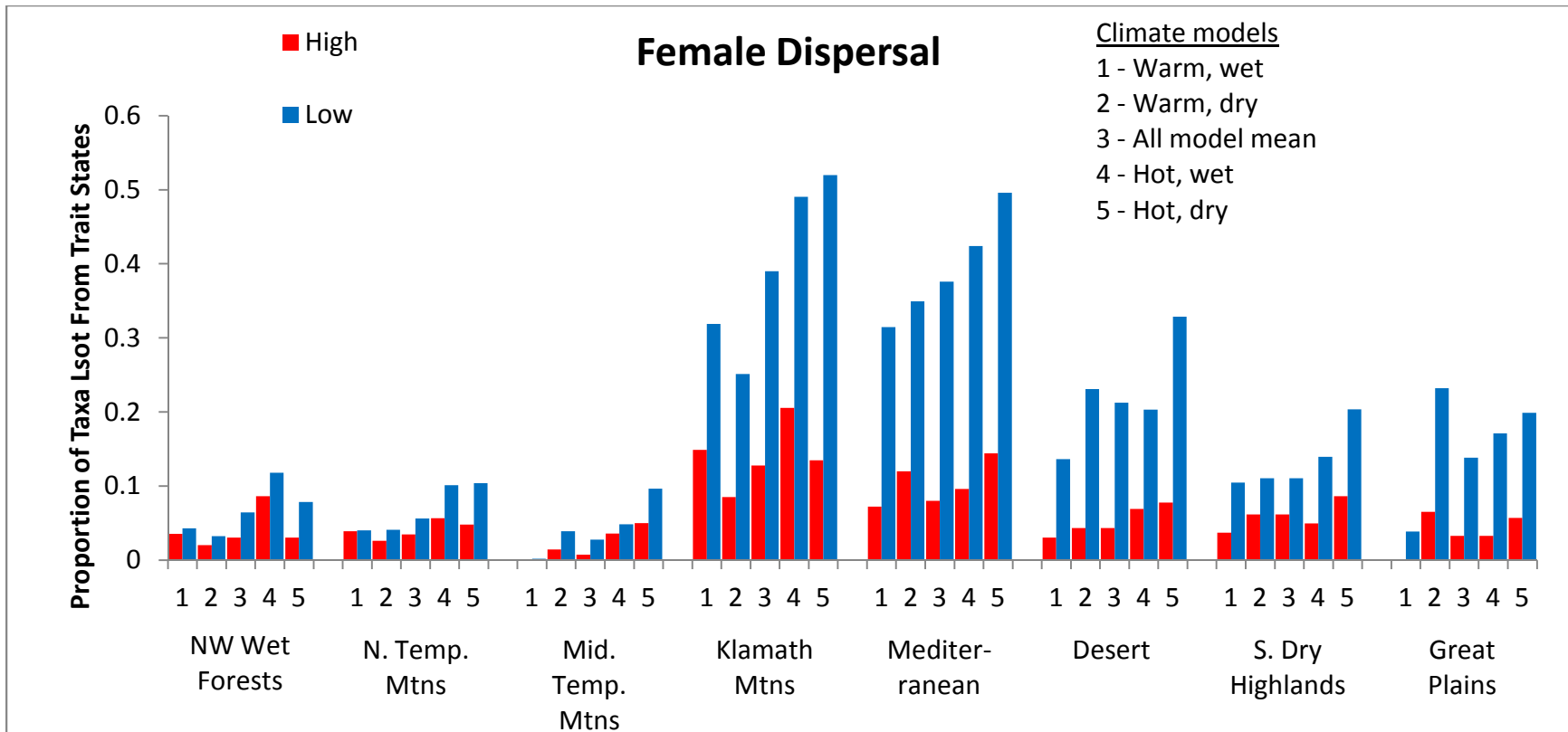


Figure 4.9: The mean proportional loss of taxa according to female dispersal ability for each ecoregion using thresholds from the 0.05/0.95 cumulative percentile scenario. Numbers 1-5 on the x-axis represent the five climate change model scenarios for each ecoregion.

inference models may need to incorporate the effect of multiple environmental factors related to climate change to effectively predict range shifts in stream taxa and communities.

Our analysis indicated that communities in the Mediterranean and Klamath ecoregions may be the most detrimentally impacted by climate change. Multiple studies have argued that communities with the most cold-adapted and/or high runoff-dependent taxa should be the most adversely affected by climate change and predicted range reductions and distribution shifts in cold-water regions (Mohseni et al. 2003, Buisson and Grenouillet 2009, Fenoglio et al. 2010, Poff et al. 2010), such as the interior mountain and northwestern ecoregions in the western United States. Our analysis, however, indicated that these ecoregions should be the least susceptible to climate change. Although many mountain and northwestern taxa are found in cold-water streams, they may be tolerant of a wide range of thermal conditions. A thermal ramping experiment on a single stonefly species restricted to alpine and glacial streams in Montana showed high tolerances for temperature increases, maintaining behavior in temperatures up to 2X original stream temperatures (Treanor et al. 2013). One possible explanation is that the variability in temperature and runoff in mountain systems may result in greater tolerance breadth and greater adaptability to climate change (i.e., the climate variability hypothesis in Stevens 1989, Williams et al. 2008). This hypothesis has been upheld in some aquatic systems (Hossack et al. 2013, Xu et al. 2014), but not in others (Mermillod-Blondin et al. 2013). A second possible explanation is that mountainous taxa are living in conditions well below their environmental limits. An experiment on ants in North Carolina and Massachusetts (Diamond et al. 2012) found that the southern species, near their upper thermal tolerances, responded negatively to experimental changes in temperature while the northern species, found well below their upper thermal limits, did not.

A third possible explanation for the relative insensitivity of mountain and northwestern streams to possible climate change is that taxa living in cold, hydrologically variable streams may be able to adjust life history traits to cope with changes in climate. A study in Toronto, Canada, increased temperature in a small spring-fed stream for two years and found no change in richness nor extirpation of taxa from the stream, but did find that life history characteristics of some taxa, particularly size, timing of emergence, and breeding times, did change (Hogg et al. 1995). In the Mediterranean and Klamath ecoregions, many typically cold-water species may be at their environmental limits and have already made such life-history adaptations to survive. Extreme thermal conditions in the Mediterranean and Klamath ecoregions coupled with low thermal variability may make California communities more sensitive thermal increases. Additionally, the mean proportion of taxa lost in the Klamath and Mediterranean ecoregions did not show much change when we altered projected runoff. Fauna in Mediterranean regions often have to deal with stream intermittency and may be better adapted to changes in runoff, particularly in mountainous regions such as the Klamath Mountains, which have regular cycles of flooding (Fenoglio et al. 2010). Some streams in this climate can cycle through low flow-adapted and high flow-adapted communities (Bêche and Resh 2007) which might make them more resilient to changes in flow, which our results suggest. But, Bêche et al. (Bêche et al. 2009) found that many aquatic organisms could not persist in a prolonged 5-year drought.

The Mediterranean and Klamath ecoregions are two of the three ecoregions in this study (along with the Northern Great Plains) that have the highest mean temperatures and our results might be an artifact of the cumulative percentile technique; since temperatures at these sites are already high they are already amongst the sites that have crossed the thermal thresholds. This is a legitimate concern and our dataset was too small in most ecoregions to separate into calibration

and evaluation datasets. There is, however, a marked difference between the Klamath/Mediterranean ecoregions and the Northern Great Plains ecoregion. The Northern Great Plains sites had much lower proportions of taxa lost due to changes in temperature and runoff, even though they exhibited some of the highest July temperatures and lowest runoff in the dataset. This is due to the fact that Northern Great Plains sites have very few taxa that we designated as being vulnerable to increases in temperature or changes in runoff (Table 4.3). In contrast, the majority of taxa in the Mediterranean and Klamath ecoregions are vulnerable to these changes. The California ecoregions represent the known environmental limits for many climate-sensitive taxa, while these taxa are not present in the plains. It is important to incorporate a large enough region to appropriately estimate entire distribution of a species (Sánchez-Fernández et al. 2011) when estimating climatic tolerances and while we are unsure if the western United States is large enough, the area of our study was indeed large and indicates that many taxa residing in much of California are at their known thermal limit.

Our models indicate risk, but do not incorporate other possible scenarios, such as range expansions, which have been recorded for some families of aquatic insects during periods of general temperature increases (Chessman 2009, 2012). We did not incorporate range expansions into our models, but our results do indicate the unique nature of taxon responses to both temperatures and runoff. Thus, possible range expansions may need to be analyzed on a taxon-by-taxon basis. Additionally, some aquatic species appear to be able to experience increased temperature tolerances once they are acclimated to higher temperatures (Galbraith et al. 2012, Majhi et al. 2013). The vulnerability of a taxon to climate change depends not just on its physiological tolerance limit, but also on its behavioral responses, genetic diversity, phylogeographic diversity, interspecific interactions, dispersal ability, population size dynamics,

and trait plasticity (Williams et al. 2008, Wenger et al. 2011, Chessman 2012). Stochastic environmental processes influenced by temperature and precipitation change, such as fire, can also have a large impact on taxon survival.

Most studies have estimated the effect of climate change by estimating the response of one or a few organisms to temperature change. Some studies have incorporated flow or precipitation in predicting fish responses climate change, but ours is the only analysis that incorporated both temperature and runoff changes for an animal community as large and as complex as aquatic insects in streams. This analysis demonstrated that community responses to multiple climate-driven variables can vary across ecoregions and that the use of temperature alone is not adequate in predicting the effect of climate change on aquatic communities.

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