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Relationships between Riparian Vegetation, Hydrology, Climate and Disturbance across the Western United States

Nathaniel Hough-Snee

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RELATIONSHIPS BETWEEN RIPARIAN VEGETATION, HYDROLOGY, CLIMATE, AND DISTURBANCE ACROSS THE WESTERN UNITED STATES

by

Nate Hough-Snee

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

Joseph M. Wheaton Major Professor	Brett B. Roper Committee Member
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UTAH STATE UNIVERSITY
Logan, Utah

2016

ABSTRACT

Relationships between Riparian Vegetation, Hydrology, Climate and Disturbance across the Western United States

by

Nate Hough-Snee, Doctor of Philosophy

Utah State University, 2016

Major Professor: Dr. Joseph M. Wheaton
Department: Watershed Sciences and Ecology Center

Flow regime, the magnitude, duration and timing of streamflow, controls the development of floodplain landforms on which riparian vegetation communities assemble. Streamflow scours and deposits sediment, structures floodplain soil moisture dynamics, and transports propagules. Flow regime interacts with environmental gradients like climate, land-use, and biomass-removing disturbance to shape riparian plant distributions across landscapes. These gradients select for groups of riparian plant species with traits that allow them to establish, grow, and reproduce on floodplains – *riparian vegetation guilds*. Here I ask, *what governs the distributions of groups of similar riparian plant species across landscapes?* To answer this question, I identify relationships between riparian vegetation guilds and communities and environmental gradients across the American West. In Chapter One, I discuss guild-based classification in the context of community ecology and streams. In Chapter Two, I identified five woody riparian vegetation guilds across the interior Columbia and upper Missouri River Basins, USA, based on species’ traits and morphological attributes. I modeled guild occurrence across environmental gradients, including climate, disturbance, channel form attributes that reflect hydrology, and relationships between guilds. I found guilds’ distributions were related to hydrology, disturbance, and competitive or complementary interactions (niche partitioning) between co-occurring guilds. In Chapter Three, I examine floodplain riparian vegetation across the American West, identifying how hydrology, climate, and floodplain alteration shape riparian vegetation communities and their guilds. I identified eight distinct plant communities ranging from high elevation mixed conifer forests to gallery cottonwood forests to *Tamarisk*-dominated novel shrublands. I aggregated woody species into four guilds based on their traits and morphological attributes: an evergreen tree guild, a mesoriparian shrub guild, a mesoriparian tree guild, and a drought and hydrologic disturbance tolerant shrub guild. Communities and guilds’ distributions were governed by climate directly, and indirectly as mediated through streamflow. In Chapter Four, I discuss the utility of guild-based assessments of riparian vegetation, current limitations to these approaches, and potential future applications of the riparian vegetation guild concept to floodplain conservation and management. The classification of vegetation into functional trait-based guilds provides a flexible, framework from which to understand riparian biogeography, complementing other models frameworks for riparian vegetation.

(176 pages)

PUBLIC ABSTRACT

Relationships between Riparian Vegetation, Hydrology,
Climate and Disturbance across the
Western United States

Nate Hough-Snee

Floodplain riparian ecosystems, the interface between streams and uplands, are distinct habitats that harbor unique plant communities. The factors that control riparian plant species composition along streams and rivers, including climate, streamflow, and watershed management, are largely unexplored at landscape scales. I conducted two studies to identify how riparian vegetation guilds, sets of species that respond similarly to streamflow and floodplain disturbance, are distributed across the western United States. Using riparian vegetation data from the Columbia and Missouri River Basins, I aggregated woody species into guilds with similar adaptations to stream hydrology and linked guilds to gradients in climate, watershed management, and channel form.

I also compared how riparian vegetation guilds and communities, sets of species that occur together on the landscape, relate to hydrology, climate, and floodplain alteration across most of the western U.S. I identified woody, riparian plant guilds that correspond to flow magnitude, duration, and timing, and delineated riparian vegetation communities from floodplain vegetation data collected at U.S. Geological Survey stream gages. I found guilds and communities corresponded to conditions that select for species' traits that allow them to persist in distinct climatic, hydrologic, and disturbance settings. Because streamflow interacts with floodplain alteration to shape riparian vegetation,

managers should consider how flow-based guilds interact with disturbance and landscape variability when guilds are used to support watershed and floodplain management.

DEDICATION

To Mike - the best older brother that a pair of dirt shirt twins could ever ask for. Thanks to you, I will always embrace the grind, whatever form it may take.

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Nate Hough-Snee

CONTENTS

Page

ABSTRACT.. iii

PUBLIC ABSTRACT v

DEDICATION.. vii

ACKNOWLEDGMENTS viii

LIST OF TABLES.. xiii

LIST OF FIGURES xv

CHAPTER

1. INTRODUCTION 1
    - 1.1 Background 1
    - 1.2 Figures 9

2. MULTI-SCALE ENVIRONMENTAL FILTERS AND NICHE PARTITIONING GOVERN THE DISTRIBUTIONS OF RIPARIAN VEGETATION GUILDS 13
    - Abstract 13
    - 2.1 Introduction 14
    - 2.2 Methods 19
    - 2.3 Results 25
    - 2.4 Discussion 29
    - 2.5 Acknowledgements 36
    - 2.6 Tables and Figures 37

3. THE ROLES OF CLIMATE, FLOW REGIME, AND FLOODPLAIN ALTERATION IN SHAPING RIPARIAN VEGETATION COMMUNITY AND GUILD DISTRIBUTIONS ACROSS THE WESTERN UNITED STATES 53
    - Abstract 53
    - 3.1 Introduction 54
    - 3.2 Methods 59

  - 3.3 Results....68
  - 3.4 Discussion....76
  - 3.5 Conclusion....85
  - 3.6 Acknowledgments....85
  - 3.7 Tables and Figures....87

4. SUMMARY, FUTURE APPLICATIONS, AND CONCLUSIONS....105

  - 4.1 Guilds and ecological inference across the western United States....105
  - 4.2 Limitations to determining guilds....107
  - 4.3 Future application and opportunities....109
  - 4.4 Conclusions....110

REFERENCES....112

APPENDICES....129

APPENDIX A....130

APPENDIX B....140

APPENDIX C....150

VITA....157

LIST OF TABLES

Table Page

2.1 Functional and morphological attributes used in the determination of riparian functional guilds 39

2.2 Summaries of environmental filters used to predict riparian guild presence and absence across the Columbia and Missouri River Basins 41

2.3 Riparian functional guilds identified based on clustering species morphological and physical attributes into common life history strategies 42

2.4 Generalized linear models for the presence and absence of each habitat guild 44

3.1 Summary of environmental variables considered for inclusion in models describing relationships between climate, flow and riparian vegetation communities and guilds 87

3.2 Initial functional and morphological attributes used in the determination of riparian vegetation-flow response guilds 89

3.3 Woody plant communities determined through cluster analysis and indicator species analysis 91

3.4 Structural hypotheses between climate and hydrology, and climate, hydrology, and floodplain alteration and riparian vegetation 92

3.5 Woody plant communities determined through cluster analysis and indicator species analysis 93

3.6 Summary of morphological attributes and traits by guild 94

S.2.1. Summary of the categorical, morphological and physical attributes by guild 131

S.2.2. Correlations between species' life history traits and the principal coordinate analysis ordination. 133

S.2.3. Goodness-of-fit statistics for environmental filters and riparian guilds fit to the NMDS ordination solution for guild assemblages 134

S.2.4. Alternative plausible generalized linear models as determined by AIC 135

S.3.1. Full environmental summary of the 433 study reaches across the western United States 143

S.3.2. Full multi-level pattern analysis results for the eight communities identified through cluster analysis 144

S.3.3. Species functional and morphological attributes used in determining guilds 146

LIST OF FIGURES

Figure Page

1.1 Active floodplain schematic diagram 9

1.2 Examples of structures that modify natural flow regimes 10

1.3 Timeline of plant classifications and the origin of the guild concept 11

1.4 Watershed disturbances that can influence floodplain vegetation 12

2.1 Study reaches in the Missouri and Columbia River basins where riparian vegetation and stream attributes were sampled 47

2.2 Dendrogram of species clustered by their traits using Gower's dissimilarity 48

2.3 Principal coordinates analysis (PCoA) of species clustered by traits into guilds 49

2.4 Summaries of the six morphological and physical attributes most strongly correlated to the principal coordinates analysis of species and guilds........50

2.5 Nonmetric multi-dimensional scaling (NMDS) ordination of trait assemblages 51

2.6 Conditional inference trees (CITs) for the presence of riparian guilds 52

3.1 Study area map of USGS stream gages where floodplain vegetation was sampled between 1997-2002........96

3.2 Structural metamodel of hypotheses tested using causal models 97

3.3 Communities displayed in a DCA ordination of individual reaches' species composition........98

3.4 Distributions of the eight identified riparian vegetation communities across the western United States........99

3.5 Riparian vegetation guilds identified using cluster analysis of species by traits and morphological attributes........100

3.6 Principal coordinates analysis of plant species clustered into riparian vegetation-flow response guilds 101

3.7 Riparian vegetation community and guild distributions across the western U.S. ..102

3.8 Principal component analysis of flow variables 103

3.9 Causal models explaining relationships between climate, hydrology, floodplain alteration and riparian communities and guilds 104

S.2.1. Map of combinations of guild assemblages across the Columbia and Missouri River basins showed that a majority of reaches contained all possible guilds 139

S.3.1. Eight riparian vegetation communities were identified by cluster analysis of floodplain reaches by floodplain woody plant species abundance 141

S.3.2. Relationships between date of peak flow, flow dispersion, community type and guild abundance showed that both communities and individual riparian vegetation guilds were linked to the timing of streamflow.....................................142

CHAPTER 1

INTRODUCTION

1.1. Background

What environmental conditions determine where different plant communities occur? Are these communities comprised of similar groups of species? How are these species similar? How are they different? How do species’ stress responses and resource acquisition influence their abundance and distributions? Within this dissertation, I address these questions in riparian plant communities along streams and rivers of the western United States. I set out to determine what common groups of woody plant species exist along low-order streams of the Columbia and Missouri River basins, and, more broadly, along floodplains of the western United States (U.S.). I explore how groups of plant species are related to climate, streamflow, and channel form, all of which have been dramatically altered by human water and land use across the U.S. To answer these questions within floodplain plant communities, one must understand how hydrologic and geomorphic processes physically shape riparian ecosystems, the interface between aquatic and terrestrial ecosystems.

Flow regime – the magnitude, duration, and timing of water flowing through a stream – is the primary control on floodplain ecosystem assembly (Figure 1.1). Streamflow controls geomorphic processes that shape stream and floodplain physical habitats that plants colonize (Bendix and Hupp 2000). Regular floods disturb established vegetation (Kyle and Leishman 2009), provide soil moisture (Lite et al. 2005), and sort and distribute sediment and propagules (Nilsson et al. 2010) across floodplains. Along streams, floods decrease in recurrence and magnitude from frequently inundated, geomorphically active surfaces adjacent to the active channel, to rarely inundated, geomorphically inactive surfaces higher above the channel (Leopold et al. 1995, Steiger et al. 2005, Corenblit et al. 2010, Wheaton et al. 2015; Figure 1.1). As flood hydraulics reshape landforms near the active channel more frequently than outlying landforms, floodplain mosaics evolve with landforms that correspond to distinct flow regimes (Steiger et al. 2005, Whited et al. 2007, Mouw et al. 2013, Wheaton et al. 2015, Kleindl et al. 2015).

These stream- and landform-scale flow regimes select for groups of species that have evolved to establish, grow, and reproduce under specific flow regimes that control landforms' flooding, drying, erosion, deposition, and nutrient pulses. Recent studies have presented models of riparian vegetation-flow response guilds – sets of plant species with common adaptations to streamflow and flooding – that attempt to identify generalizable relationships between riparian vegetation and streamflow (Merritt et al. 2009, 2010). Specifically, riparian vegetation-flow response guilds (riparian guilds) attempt to link plant traits to flow regimes. Numerous traits allow plants to disperse, establish, and grow in floodplain environments: dispersal mechanisms (Kehr et al. 2014), seed mass, root depth, flower and seed phenology (Greet et al. 2011), water balance (Amlin and Rood 2002), photosynthetic and growth rates (Kozlowski 2002), and tissue construction and maintenance costs (Westoby 1998, Westoby et al. 2002). Species can be grouped into guilds that respond to floodplain hydrology and disturbance based on these traits or their categorical surrogates (Chapters Two and Three; Sarr et al. 2011, Bejarano et al. 2012, Hough-Snee et al. 2015a).

For example, many mesic riparian guilds have evolved traits that allow them to tolerate frequent flooding and sediment erosion and deposition. Mesic riparian guilds' flood tolerance, seed dispersal, and seedling establishment and growth should coincide with natural streamflow regimes (Stromberg and Merritt 2015). Xeric riparian guilds are adapted to drought, reduced streamflow duration, and less adapted to frequent fluvial disturbance. Xeric riparian guilds may have dispersal strategies that do not depend on streamflow. Mesic guilds should hypothetically occur more frequently along rivers with natural flow patterns that match species' adaptations to historic flow regimes (Merritt et al. 2010). The opposite should be true for xeric guilds, as they would be more prevalent along streams with intermittent flow and limited flood disturbance (Stromberg and Merritt 2015).

The riparian vegetation-flow response guild framework provides a convenient lens through which to understand and predict how riparian vegetation communities differ in their response to streamflow-dependent processes (Merritt et al. 2009, 2010). Flow alteration from dams or water diversions modify natural flow regimes (Figure 1.2), which often favor the establishment of non-riparian species (Dynesius et al. 2004, Bejarano et al. 2012). The basis for using riparian vegetation-flow response guilds to describe floodplain plant communities has arisen from a long history of plant classification. The origins of riparian guilds and their use in understanding riparian ecosystems are closely linked to the larger history and objectives of plant classification.

Plant classification along streams and rivers

Plants have been classified based on their functional types, growth forms or life history strategies for millennia (Figure 1.3). Greek naturalists like Aristotle and Theophrastus initially classified plants based on their life forms in *De Historia Plantarum* (Theophrastus 1813). Pliny the Elder, a Roman, followed early Greek classifications with his botanical chapter of *Naturalis Historia* that identified plant species' general character and horticultural uses (reprinted as Pliny the Elder and Healy 1991). Centuries later, Linnaeus taxonomically organized how species were related to one another, introducing binomial classification to systematically categorize organisms into discrete species (Linnaeus 1758). However, the sheer global diversity and number of species led to further frameworks to group species into guilds and explain how and why guilds and species existed in different environments.

In 1895, Eugenius Warming coined the term "life form" to describe how plants differ in their physical form and growth strategies (Warming 1895). Warming's student, Christen Raunkiær, formally introduced the plant life-form classification (Raunkiaer 1904). This scheme grouped species based on plant growth during the active growing season and the dormant (cold) season, using their allocation to structures like flowers, buds, woody tissue, roots, tubers, and rhizomes. The life-form classification provided plant functional context to ecological concepts like succession and competition that were developing rapidly in the early 20th century (Clements 1916, 1928, Gleason 1917, 1926). In an era of limited computing power, Raunkiaer attempted to explain biogeographic patterns based on life forms' various adaptations to climate, soils, and physical habitat.

The guild concept was introduced by Root (1967) who felt it provided a generalizable framework for understanding birds' feeding strategies. Root (1967) defined a guild as "…a group of species that exploit the same class of resources in a similar way." Guilds do not incorporate species' phylogenetic relationships, which allows for the study of distantly related species that possess similar strategies for growth, resource acquisition, reproduction or dispersal. Guild-based models attempt to reduce the species within a biota to discrete groups of similar, representative strategies. From these discrete groups, general inference can be made about groups of similar organisms and their habitats.

Within plant ecology, the guild concept provides a convenient taxonomic resolution from which to compare multiple species' responses to environmental change. Guild frameworks can be used to better understand how a resource, disturbance, or stressor controls a community's composition, diversity, or stability (Diamond 1975, Toner and Keddy 1997, Weiher et al. 1998). Work to identify guilds in other taxa and ecosystems have provided great insight into how various communities assemble (Johnson et al. 2003, Cornwell and Ackerly 2009), respond to environmental change (Welcomme et al. 2006, Mims and Olden 2013), and in some cases, may respond to future environmental change (Keddy 1992). While Root's guild concept provided the conceptual basis for identifying riparian vegetation-flow response guilds, plant ecology theory has refined their application.

Grime (1977, 1979) presented the CSR theory of how different strategies allow plant species to persist, reproduce, and perpetuate their genes under various stress, disturbance, and resource gradients. Specifically, CSR theory identified trade-offs between species in their capacity to compete (C), tolerate stress (S) and quickly complete a ruderal lifecycle (R). Grime's CSR model has been built upon to describe how species persist across stress, disturbance, and resource gradients in wetland and riparian environments (van der Valk 1981, Keddy 2000). The riparian guild framework is an extension of Grime's CSR framework (Merritt et al. 2009) that identifies trade-offs between species that may not be equally adapted to streamflow-mediated stress, disturbance, and resources.

While many riparian vegetation studies examine communities and their component species, community patterns are often explained *post hoc* based on individual species' general morphological characteristics or environmental tolerances (Hough-Snee et al. 2015b). These relationships, while informative, may not link species' measured traits to the riparian environment. This allows many interpretations of community patterns to be based on species' environmental associations or successional patterns rather than identifying the specific traits that allow a species to occur in a floodplain environment. The identification of trait-based guilds explicitly links plant performance to environmental processes, allowing for generalization about what species occur at a given location and why.

Scaling riparian guilds to landscapes

Because floodplain surfaces are created and reworked by streamflow and colonized by biota within a larger landscape context, multiple environmental gradients, including climate (Sarr and Hibbs 2006), geology (Harris 1988), and biomass-removing disturbance (Kleindl et al. 2015), interact with flow regimes to shape riparian guilds' distributions. When examined at landscape scales, riparian guilds are likely shaped by climate or disturbance, either directly, or indirectly, as they shape streams' hydrology and floodplain physical habitats (Figure 1.3). Here, I quantitatively determine riparian vegetation-flow response guilds and identify their relationships with additional floodplain alteration, climate, and hydrology, to better understand what processes correspond to riparian guilds' distributions across the American West (Figure 1.4).

Dissertation Objectives and Organization

The objective of this dissertation is to use field-based vegetation, floodplain alteration, and hydrology data and remotely-sensed climate data to identify relationships between riparian vegetation guilds and climate, hydrology, and floodplain alteration across the western U.S. I attempt to make inference beyond similar reach-scale studies and link landscape-scale environmental gradients to the distributions of guilds that exhibit similar morphological traits that allow them to occur near streams and in floodplains.

Chapters Two and Three use riparian vegetation data from large-scale riparian monitoring and inventory projects and coarse estimates of species traits to group species into guilds that respond to floodplain alteration, hydrology, and climate. Chapter Two explores woody riparian vegetation-disturbance response guilds of the interior Columbia and upper Missouri River basins in the northwest United States. I discuss which traits and morphological attributes relate to non-fluvial disturbances that occur at the riparian-upland interface and identify guilds using clustering and ordination methods. I use generalized linear models to explore what environmental filters drive guild presence and absence, and how associations between guilds explain guilds' distributions.

In Chapter Three, I identify riparian vegetation-flow response guilds for woody species that occur on floodplains of the western United States. I use structural equation models to test hypotheses about how riparian vegetation guilds and communities are related to climate, hydrology, and disturbance. This approach tests hypotheses about the direct and indirect effects of climate on vegetation guilds and communities, and effects of streamflow and floodplain alteration on vegetation guilds and communities. I discuss how community and guild-based approaches complement one another, and how their applications may inform watershed and floodplain management. In Chapter Four I conclude by discussing how guild-based models complement existing approaches to assessing plant diversity and distributions along streams and rivers. I discuss shortcomings of the methods used in Chapters Two and Three, and prescribe frameworks for future trait-based studies of riparian vegetation in the context of rapid global change.

1.2. Figures

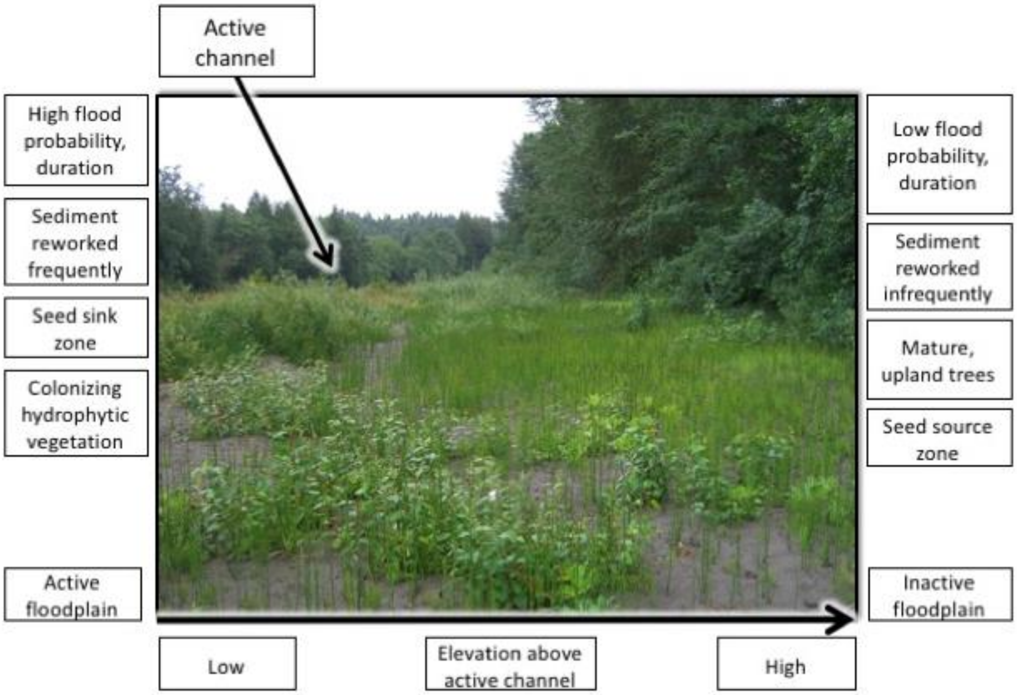

Fig. 1.1. Floodplain surfaces near the active channel (left) are frequently reworked by flood disturbance, allowing disturbance and flood tolerant hydrophytic plant species to colonize. Inactive floodplain surfaces further from the channel (right) select for flood and disturbance intolerant upland species based on the low recurrence and duration of floods.

Fig. 1.2. Examples of structures that modify natural flow regimes. The Grand Coulee Dam on the Columbia River, WA, USA, (upstream - A, downstream - B) has a flow regime designed for irrigation water storage and hydroelectric power. The irrigation canal diversion on the lower Logan River, UT, USA, (upstream – C, downstream – D), diverts a majority of flow to agriculture during the growing season, significantly reducing downstream flows.

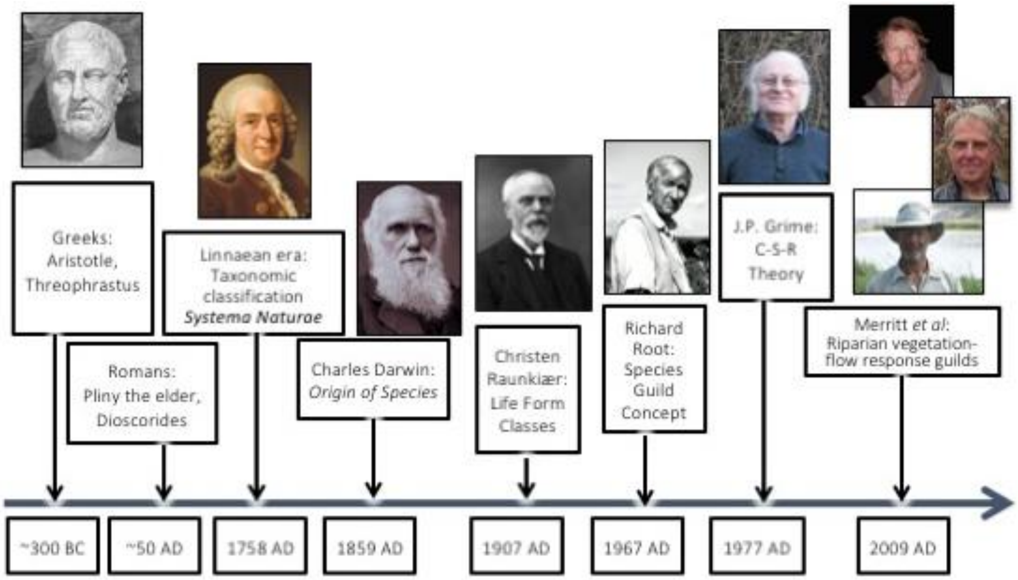

Fig. 1.3. Timeline of various plant classifications throughout history and the 2009 origin of the riparian vegetation-flow response guild concept discussed in the text.

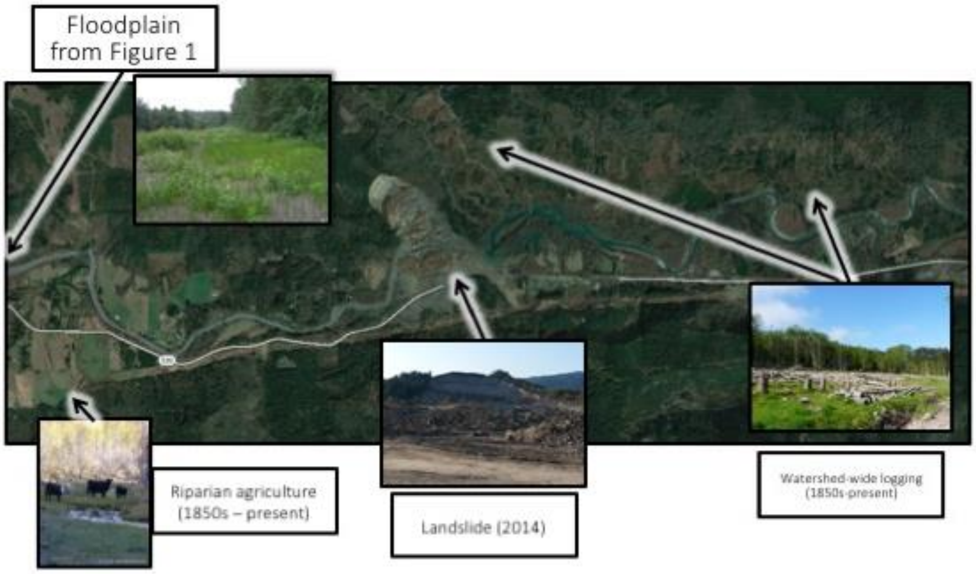

Fig. 1.4. Watershed disturbances that can influence floodplain vegetation include flooding, row crop and livestock agriculture, logging, and landslides, among others. These disturbances interact with climate, geomorphic setting, and streamflow, as well as species' traits, to determine what species comprise different floodplain riparian plant communities. This floodplain example is from the Stillaguamish River, near Oso, Washington, USA.

CHAPTER 2

MULTI-SCALE ENVIRONMENTAL FILTERS AND NICHE PARTITIONING GOVERN THE DISTRIBUTIONS OF RIPARIAN VEGETATION GUILDS.

Abstract

Across landscapes, riparian plant communities assemble under varying levels of disturbance, environmental stress, and resource availability, leading to the development of distinct riparian life-history guilds over evolutionary timescales. Identifying the environmental filters that exert selective pressures on specific riparian vegetation guilds is a critical step in setting baseline expectations for how riparian vegetation may respond to environmental conditions anticipated under future global change scenarios. In this study, I ask: (1) What riparian plant guilds exist across the interior Columbia and upper Missouri River basins? (2) What environmental filters shape riparian guild distributions? (3) How does resource partitioning among guilds influence guild distributions and co-occurrence? Woody species composition was measured at 703 stream reaches and each species' morphological and functional attributes were extracted from a database in four categories: (i) life form, (ii) persistence and growth, (iii) reproduction, and (iv) resource use. I clustered species into guilds by morphological characteristics and attributes related to environmental tolerances, modeling these guilds' distributions as a function of environmental filters – regional climate, watershed hydrogeomorphic characteristics, and stream channel form – and guild co-existence. I identified five guilds: (i) a tall, deeply rooted, long-lived, evergreen tree guild, (ii) a xeric, disturbance tolerant shrub guild, (iii) a hydrophytic, thicket-forming shrub guild, (iv) a low-statured, shade-tolerant, understory shrub guild, and (v) a flood tolerant, mesoriparian shrub guild. Guilds were most strongly discriminated by species' rooting depth, canopy height and potential to resprout and grow following biomass-removing disturbance (e.g. flooding, fire). Hydro-climatic variables, including precipitation, watershed area, water table depth, and channel form attributes reflective of hydrologic regime, were predictors of guilds whose life history strategies had affinity or aversion to flooding, drought, and fluvial disturbance. Biotic interactions excluded guilds with divergent life history strategies and/or allowed for the co-occurrence of guilds that partition resources differently in the same environment. I conclude that the riparian guild framework provides insight into how disturbance and bioclimatic gradients shape riparian functional plant diversity across heterogeneous landscapes. Multiple environmental filters should be considered when the riparian vegetation-flow response guild framework is to be used as a decision-support tool framework across large spatial extents.

2.1 Introduction

Riparian zones are globally threatened ecosystems due to widespread hydrologic alteration, watershed degradation, and the introduction of novel disturbance regimes and biota (Patten 1998, Shafroth et al. 2002, Stromberg et al. 2012, Dalldorf et al. 2013). A consequence of riparian vegetation degradation is the decline of vegetation-mediated ecosystem processes including allocthonous energy subsidies to aquatic ecosystems (Delong and Brusven 1994), contribution of large wood to stream channels (Hough-Snee et al. 2014), temperature regulation by mature overstory vegetation (Pollock et al. 2009), and valuable terrestrial wildlife habitat (Merritt and Bateman 2012). Accordingly, any disturbance or ecosystem process that alters the composition or structure of riparian vegetation is also likely to alter channel form (Gurnell 2014) and riparian (Scott et al. 2003, Cooke and Zack 2008) and aquatic habitats (Herbst et al. 2012). The interrelationships between riparia, hydrogeomorphic processes, and ecosystem services pose a fundamental question in watershed management: what environmental factors are most responsible for governing the characteristics of riparian vegetation across landscapes? Additionally, how can these factors be managed to sustain the functions and habitat values of riparian ecosystems?

To address these questions, ecologists have suggested that by aggregating individual species into groups based on common life history strategies (Box 1) broad inference can be made about the environmental drivers of riparian plant diversity and used to predict ecosystem change (Merritt et al. 2009, 2010). This approach to riparian plant community assembly provides a framework to identify how functional vegetation guilds assemble across environmental gradients that filter species and life history strategies from biological communities. Environmental filtering, in its most simple form, assumes that as environmental conditions change, specific life history strategies and traits will be selected for at a given location, leading to the assembly of communities with morphological and physiological tolerances suited to a given environment (Keddy 1992, Díaz et al. 1998). When the dominant environmental filters that shape riparian biodiversity are known, then riparian guilds can be probabilistically modeled to predict ecosystem change as environmental filters shift (Merritt et al. 2009). While many environmental filters shape riparian plant communities (Hough-Snee et al. 2015b), the most commonly studied environmental drivers of riparian vegetation are hydrology and fluvial processes in large, alluvial rivers (Naiman et al. 2000, Merritt and Cooper 2000, Stella et al. 2013).

Not coincidentally, riparian plant communities have commonly been characterized based on relationships between species composition and the magnitude, duration, and timing of stream flow or surrogate flow measurements like stream order (Ekness and Randhir 2007, Stella and Battles 2010, Viers et al. 2012) or hydrologic and substrate characteristics of fluvial surfaces (Hupp and Osterkamp 1996, Bendix and Hupp 2000). Indeed, within large rivers, hydrogeomorphic processes that dictate intra- and interannual shifts in overbank flooding, erosion, deposition, and hydrologic recession play a strong role in shaping vegetation functional diversity, including guilds (Shafroth et al. 2002, Katz et al. 2009). The historic focus on riparian plant diversity in large, alluvial rivers has left much to be learned about how environmental processes shape riparian ecosystems, especially in unregulated, low-order streams.

While headwaters make up disproportionate amounts of stream area within watersheds (Lowe and Likens 2005), the environmental filters that control riparian plant functional diversity in low-order streams have rarely been elucidated at broad spatial scales (Hough-Snee et al. 2015b). Many riparian ecosystems, especially those along small streams, can be linked to landscape to local-scale processes such as climate, land management, and fluvial disturbance (Richardson and Danehy 2007, Dunn et al. 2011, Hough-Snee et al. 2015b) and biotic interactions (Whigham et al. 2012). Riparian plant communities assemble through both biotic and abiotic environmental filters that limit which species and functional traits can occur at a given location within a stream network (Díaz et al. 1998). While riparian environmental filters may occur at multiple spatial and temporal scales within a given environment (e.g. process domains; Montgomery 1999), filtering can select for comparable sets of traits or guilds with shared life history strategies, regardless of the dominant processes at work. These filters, whether they originate from stream or upland processes, exert selective pressures on traits that allow species to persist and reproduce in a given environment.

Identifying trait-based plant assemblages provides a novel approach for assessing plant functional diversity where numerous species with similar realized niches and corresponding life history strategies may occur (Grime 1977, Merritt et al. 2010). Riparian guilding (Merritt et al. 2010) allows for the identification of groups of species with shared functional traits, morphological characteristics, or environmental preferences that correspond to distinct life history strategies. These guilds may respond to individual or multiple environmental filters, including water availability and the frequency and magnitude of fluvial disturbance (Merritt et al. 2010), depending on the attributes used in guilding species (Catford and Jansson 2014). Within riparian ecosystems, guild-based approaches have been used to identify how functional riparian vegetation assemblages respond to flow regulation (Bejarano et al. 2012, 2013). However, riparian guild determination, or “riparian guilding,” may also provide insights into the broad environmental filters that shape riparian plant functional diversity across landscapes. By assessing riparian plant diversity based on attributes representative of shared life history strategies rather than individual species, theories may be made about what filters drive different life history strategies across regions with large species pools.

Riparian guilding provides a powerful tool for explaining how different niches are occupied by specific life history strategies across landscapes. While environmental filtering may broadly explain how species, traits, and assemblages occupy a stream reach, niche partitioning within communities may be based on the complementarity or divergence of guilds' functional traits and life history strategies, enabling multiple trait syndromes to coexist. That is, multiple life history strategies and guilds may co-exist in the same community due to their different strategies for tolerating environmental stress, responding to disturbance, and acquiring nutrients and water (Grime 1977, Catford and Jansson 2014).

To investigate relationships between riparian functional plant diversity and environmental filtering, in this chapter I pose two sets of questions:

1. Can meaningful riparian woody plant guilds be identified based on species' shared morphological and life history attributes or are traits distributed along a continuum of individualistic attributes? If meaningful guilds can be identified, what are the functional differences between guilds and the nature of each guild's dominant life history strategies?

2. How do environmental filters and the presence and absence of complementary guilds shape the distribution of *individual* riparian guilds across landscapes? How do environmental filters shape *guild assemblages*, the combination of guilds present at a given site, across landscapes?

2.2 Methods

Study Sites

I selected 703 low-order stream reaches within the interior Columbia and upper Missouri River basins (Figure 2.1) for inclusion in the study. These reaches were sampled under a spatially balanced, probabilistic sampling design (Kershner et al. 2004). All reaches were low-gradient (average < 2%) and occur within USGS 6th order hydrologic unit code sub-watersheds with > 50% federal ownership upstream of the sampled reach. Study reaches are managed by the U.S. Bureau of Land Management (BLM) or Forest Service (USFS) and occur across the physical and climatic gradients representative of the interior Columbia and upper Missouri River basins.

Vegetation field data

Riparian vegetation was sampled during the growing season at base flow conditions (June - September). Greenline vegetation data were collected in 42–50 evenly spaced quadrats (50cm x 20cm) per reach, based on reach length and bankfull width (PIBO EM 2012a). The greenline is the point at which the first rooted perennial vegetation is present along a stream (Winward 2000, PIBO EM 2012a) and is located on flat, floodplain-like or depositional features at or near bankfull stage. Vascular plants were measured in a lower vegetation layer (< 1m in height) and an upper woody species layer (> 1m in height). If a species was observed in either vegetation layer, then it was classified as present at a site, otherwise it was classified as absent.

Riparian plant attributes for defining life history strategy and guilds

I identified functional groups by allocating species to groups based on life history strategies as a product of their shared functional and morphological attributes, selecting attributes based on their importance in maintaining individual plants and populations within a typical low-order stream's riparian environment. Smaller, wadeable streams are exposed to multiple stressors from fluvial (overbank flooding, erosion, deposition, etc.) and terrestrial processes (wildfire, grazing, forest fragmentation, etc.) as well as climatic variability across landscapes. Accordingly, the plant attributes I selected for guilding aligned with multiple environmental filters across the riparian environment and study landscape (Table 2.1). I used the USDA Plants database (USDA NRCS 2010) to identify functional attributes that pertained to each plant species' life-form, persistence and growth, disturbance and stress responses, resource use, and reproductive strategy (Table 2.1). For simplified description, each attribute was allocated to a primary life history stage based on that attribute's dominant role in defining a species general life form, survival and growth, resource use, or reproduction in the riparian environment (Table 2.1). Generally, plant traits may be categorized as biological traits measured on individual plants, or ecological traits that reflect species' responses to the environment. The ecological attributes used here may be thought of as surrogates for, or integrators of, traits that reflect environmental adaptation.

For example, adaptation to different soil textures and grain sizes illustrates the capacity for a plant to persist and grow in an environment where interannual differences in deposition and erosion may deposit a range of sediment size classes in the same location. This same functional attribute is also representative of a species’ reproduction potential because deposited sediment provides sites where hydrochorous propagules (seeds, sprigs, etc.) collect and germinate following spring flooding. Moisture use, drought tolerance, and anaerobic soil tolerance are all tied to species’ abilities to germinate, persist, photosynthesize, and grow amid intra-annual and interannual hydrologic variability. The timing and duration of flowering, seed set and seed dormancy (persistence) are all tied to a species’ reproductive life history strategy in riparian areas, namely the timing of hydrochorous and post-flood seed dispersal (Merritt and Wohl 2006).

I use the term morphological or functional "attribute" as opposed to "trait," because traits are defined as empirically measured physiological and morphological parameters that change in response to the physical environment (Box 1; Mcgill et al. 2006), whereas many species’ attributes were categorizations and not empirical measurements. It is worth noting that of the small number of attributes selected for guild analysis, many often covary with other traits. A limited number of attributes (or when available, measured traits) may be used in such guild analyses, providing the advantage that a parsimonious set of traits may actually represent a family of traits (Duckworth et al. 2000). For example, wood density is easy to measure yet represents a complex set of physiological traits that are strongly correlated with water use efficiency in plants (Reich 2014).

Environmental metrics

Stream gradient, bankfull width, bank stability, channel sinuosity, bank angle, median particle size, wood frequency, wetted width-depth ratio, residual pool depth, hydraulic radius, and percent undercut banks were field measured at each reach using standardized protocols (Table 2.2; PIBO EM 2012b). I identified a 30m buffer surrounding each stream in GIS and calculated the proportion of each buffer polygon that was grazed by livestock in the last 30-years using USFS grazing allotment data. Because forest patches serve as corridors for propagule dispersal and tree canopies shape understory light and humidity, I identified the proportion of each watershed and reach covered by overstory forest vegetation using LANDFIRE (USGS 2012). I also used LANDFIRE data to estimate the proportion of each watershed that had burned between 1997 and 2007. I calculated road density (km/km^2) within each buffer and watershed because roads serve as plant dispersal vectors and alter local hydrology. I used 10m digital elevation models to define watershed boundaries and calculate watershed area, stream density and the average slope of the watershed and buffer surrounding each reach. An erosivity index – a unitless, continuous measure of the uniaxial compressive strength of lithology types – was calculated to estimate the relative erosion potential at each reach (Cao et al. 2007). Average soil thickness and depth to the seasonal high water table, indicators of hydric soils, were estimated at each reach (NRCS 2012). All landscape and watershed-scale filters were summarized for the watershed area upstream of each reach (Table 2.2).

Riparian guild identification

Riparian guilds were identified by clustering species into groups based on their morphological and physical attributes (Table 2.1). I calculated a distance matrix of species and species' attributes using Gower's distance (Gower and Legendre 1986), which scales variables between 0 and 1 and allows for the use of continuous and ordinal variables. I clustered species based on this distance matrix using Ward's method and examined cluster results for three to ten guilds, settling on a five-guild (cluster) solution. I visualized the resulting guilds, and the attributes that differentiated them, using a three-dimensional principal coordinate analysis (PCoA). Guild fidelity was tested using permuational analysis of variance (PERMANOVA) models (Anderson 2001) with the null hypothesis that the attribute composition of each species guild did not differ. Species' life history strategy attributes were correlated to the ordination solution using multiple regression and plotted to illustrate relationships between life history attributes and species within the ordination space ("envfit" function; *vegan* package in R statistical software; Oksanen et al. 2015). I determined guild presence by creating lists of woody species that occurred at each reach. If any species from a given guild was field identified at a reach, then that guild was categorized as present. The combined species list for all reaches was reduced to common woody species that occurred at 5% or more of reaches (McCune and Grace 2002). Guild presence was not weighted based on species abundance or frequency.

Environmental drivers and riparian guild coexistence

To identify relationships between guilds within each guild assemblage I performed non-metric multidimensional scaling (NMDS) on a matrix of guild presence and absence at each reach, using Euclidean distance. To identify relationships between guild assemblages and stream, watershed, buffer, and landscape-scale variables I correlated environmental filters to the final NMDS solution using multiple regression models. Environmental vectors were considered significant fits to the guild assemblages with an alpha of $P < 0.05$.

A systematic approach was taken to model each guild's presence and absence across the study region. Generalized linear models were fitted for each guild using environmental attributes as predictors of guild presence and absence (binomial function; Table 2.2). Prior to model building, I removed environmental variables with correlations $> |0.65|$ to avoid collinearity between predictors, retaining the variable with a stronger hypothesized relationship to plant persistence in riparian zones. I included interaction terms for variables with spatial codependence including bank angle and buffer slope, sinuosity and gradient, and bankfull width and wetted width to depth ratio. I used an iterative, systematic approach to compare models for each guild, removing variables and/or interaction terms with hypothesized weak relationships with guild presence to minimize the Akiake Information Criterion (AIC) and negative log-likelihood for each model. This approach maintained an information theoretic approach that retained key hydrologic and climatic variables that were thought to have strong, meaningful biological relationships with plant life history strategies (guilds) and their component plant attributes.

To further explore how guild distributions were related to co-occurring guilds and environmental filters, I built conditional inference (classification) trees for each guild from the variables retained in that guild's final generalized linear model ("ctree" function; party package; R statistical software; Hothorn et al. 2006). Conditional inference trees are a machine-learning method that can operate on mixed variable types and are well suited to modeling non-linear and non-additive relationships common in trait or categorical morphological attribute data (De'ath and Fabricius 2000). Classification maximizes the heterogeneity between nodes based on the variable with the strongest association with the response variable. I assessed conditional inference tree performance by fitting the observed data to the model and used Cohen's Kappa statistic to see if each tree performed better than random at predicting guild presence and absence.

2.3 Results

Riparian guilds

I identified five riparian guilds comprised of woody species with distinct life history strategy characteristics: (1) a long-lived, deeply-rooted, tall, shade tolerant, evergreen tree guild, (2) a rapidly growing, multi-stemmed, rhizomatous and thicket-forming, shrub guild, (3) a short-moderate stature, hydrophytic, multi-stemmed, thicket-forming shrub guild, (4) an obligate riparian, medium-deeply rooted, vegetatively reproducing, alluvial substrate preferring, shrub and tree guild, and (5) a short-statured, shade-tolerant, water stress and flooding intolerant understory shrub guild (Table 2.3;

Figure 2.2; Figure 2.3). Guilds were given abbreviated names for simplicity of presentation: (1) evergreen tree, (2) upland disturbance, (3) mesic shrub, (4) mesoriparian shrub and tree, and (5) understory shrub (Table 2.3). The clustered guilds and their representative species separated based on their component functional attributes. This was apparent in the cluster dendrogram, summaries of guilds' functional attributes, and PCoA plot of species, and guild by functional attributes (Figure 2.2; Figure 2.4; Appendix A). Morphological attribute composition differed significantly between guilds (PERMANOVA pseudo-F = 8.79; $P < 0.001$). Species height at maturity and rooting depth were the two strongest drivers of the species by life history attribute (guild) ordination, followed by leaf retention, moisture use, growth form, growth rate, fire tolerance, vegetative spread rate, lifespan, bloom period, resprouting ability, drought tolerance and live-staking (Figure 2.3; Figure 2.4; Appendix A). Life form, resource use, persistence and growth traits were more reflective of guild differences than species' reproductive duration and timing.

Environmental gradients and guild distributions

The five riparian guilds occurred in 32 different combinations of assemblages at the 703 study reaches (Figure 2.5; Appendix A). A three-dimensional NMDS ordination solution of guild assemblages converged after 17 tries (principal components rotation; Euclidean distance; stress = 0.047, $P = 0.009$). The combinations of guilds that assembled at each reach and individual guilds were strongly correlated to multiple environmental gradients (Figure 2.5, Table 2.4, Appendix A). Buffer slope, reach elevation, sinuosity, stream gradient, buffer forest cover, and average and annual precipitation were most strongly correlated to the guild assemblage ordination solution (Figure 2.5A-C; Appendix A). The guild assemblages within the NMDS ordination space (Figure 2.5D) and the fitting of individual guilds' presence and absence showed a clear and significant ($P < 0.05$; PERMANOVA) separation between all five guilds. The individual upland disturbance, mesoriparian shrub and tree, and understory shrub guilds were most strongly correlated to guild assemblages in the final NMDS solution (Figure 2.5; Appendix A). These correlations between guilds and guild assemblages were two to three-times stronger than any of the correlations between environmental filters and the guild assemblage ordination (Appendix A), indicating strong relationships between individual guilds and the full guild assemblages at each reach.

Environmental filters and riparian guild coexistence

The presence and absence of individual riparian guilds corresponded to many of the same environmental filters that correlated to guild assemblages in the NMDS ordination (Table 2.4). Generalized linear models (GLMs) and conditional inference trees (CITs) showed that for most guilds, in addition to environmental filtering effects from hydrologic and channel form attributes, the presence and absence of other guilds were significant predictors of guild presence and absence (Table 2.4). The final evergreen tree guild GLM showed that hydrologic variables, watershed area and average water table depth, and the channel-form variables, sinuosity and buffer slope, were negatively correlated to evergreen guild presence. Annual precipitation, wetted width-depth ratio, buffer forest cover and the presence of the upland disturbance and understory shrub guilds were positively correlated to evergreen tree guild presence (Table 2.4). The evergreen tree guild’s CIT confirmed that multi-scale environmental filters and the presence of the upland disturbance guild were strong predictors of the evergreen tree guild’s presence (Figure 2.6; 82.2% correctly classified).

The final GLM for the upland disturbance guild showed that channel form variables were the most important filters related to guild presence. The model showed positive relationships between guild presence and buffer forest cover, average watershed temperature, bankfull width and gradient, and the buffer slope-bank angle interaction and negative relationships with bank angle, water table depth, and the bankfull width-wetted width depth ratio interaction. Presence of the evergreen tree guild was also positively correlated to upland disturbance guild presence in the GLM (Table 2.4, Appendix A). The upland disturbance guild’s CIT showed that the presence of the evergreen tree guild was a major predictor of upland disturbance guild presence behind buffer slope. The final CIT successfully predicted upland disturbance guild presence at 71.6% of reaches (Figure 2.6).

The final mesic shrub guild model showed that this guild corresponded to multi-scale environmental filters and two other riparian guilds. Average temperature, elevation, and buffer slope-bank angle interaction were negatively correlated to guild presence, while buffer slope, bank angle, bankfull width and the mesoriparian shrub and tree and understory guilds’ presence positively correlated to this guild. The mesic shrub guild’s CIT was solely comprised of the understory shrub and mesoriparian shrub and tree guilds’ presence and absence. This model correctly predicted mesic shrub guild presence at 89.9% of reaches, but failed to successfully predict any absences and did not show more predictive power than random chance (Kappa = 0; Z = 0; *P* = 0.5).

The understory shrub guild was inversely correlated to average temperature, annual precipitation, minimum elevation, buffer forest cover and bank angle, predominantly landscape scale environmental filters, within its final GLM. This guild was positively correlated to the presence of all other guilds, except the upland disturbance guild, which was not included in the final GLM. Gradient and buffer slope were also positively correlated to the presence of this guild indicating a preference toward steeper streams and riparian areas. The presence and absence of the mesoriparian shrub and tree guild was significant in the CIT modeling of the understory shrub guild's distribution (Figure 2.6). The final understory guild CIT successfully predicted guild presence and absence at 82.7% reaches.

The mesoriparian shrub and tree guild was positively related to the mesic shrub and understory shrub guilds, but negatively associated with the evergreen tree guild. This guild was also negatively related to temperature and elevation and positively related to bankfull width, buffer slope, and grazing frequency in the buffer. The CIT model for the mesoriparian shrub and tree guild showed that in less steeply sloped reaches the mesic shrub and understory shrub guilds corresponded to mesoriparian shrub and tree guild presence (Figure 2.6). This CIT correctly classified 78.2% of reaches.

2.4 Discussion

I identified riparian plant guilds based on component species' distinctive life history strategies that reflect each guild's resource use, reproduction, persistence, and growth in the riparian environment. The characteristics that differentiated guilds were those that allowed guilds to tolerate flooding disturbance, acquire soil moisture and nutrition, and reproduce while coexisting with guilds of different life history strategies. Distinct life history strategies were tied to species' canopy height and root depth that allow for persistence and growth in competitive aboveground and belowground environments. Species moisture use and drought tolerance, commonly limiting factors in arid and semi-arid rivers (Shafroth et al. 2000, 2002, Horton et al. 2001), were important in differentiating guilds' with adaptations to fluvial and wetland environments (e.g., mesic shrub, mesoriparian shrub and tree) from guilds adapted to upland disturbances like fire or herbivory. Resprouting potential, vegetative spread, and live-staking capabilities, common adaptations to the riparian environment where species are buried, washed away or broken off by floods (Catford and Jansson 2014), differentiated the mesoriparian and mesic shrub guilds from the more upland evergreen tree, upland disturbance, and understory guilds. Shade and drought tolerance, upland forest stressors that limit species distributions, differentiated the understory shrub and upland disturbance guilds from more hydrophytic guilds and the larger-statured evergreen tree guild.

Riparian functional guilds' distributions affirm that life-history strategies are selected for by multiple environmental filters (selective pressures) that are reflective of particular process domains (Montgomery 1999), such as hydrogeomorphic processes, local disturbance, and climate patterns that vary across large watersheds. For example, stream width, gradient, and sinuosity were predictors of multiple guilds, suggesting that hydrogeomorphic processes that shape channel form also eliminate or allow the persistence of local life history strategy diversity. This finding corresponds to research that showed wetland and riparian communities comprised of co-existing species were similarly correlated to multiple environmental filters (Lemly and Cooper 2011, Hough-Snee et al. 2015b) and that riparian forest regeneration strategies are tied to both environmental gradients and biotic interactions (Sarr et al. 2011). Functional guilds that respond to such gradients serve as good indicators of particular climatic and disturbance regimes. Such characterizations of typical suites of guilds for a particular process domain may provide sound reference states from which to understand departures from natural conditions and to set goals for restoration.

Individual guilds were often found either to be complementary to, or mutually exclusive with other guilds, suggesting that some guilds' species differentially partition their niches within similar environments. For example, the evergreen tree guild was positively associated with both the upland disturbance guild and the canopy understory guild, likely because these guilds acquire resources differently when co-existing in similar environments. The evergreen tree guild is unlikely to occupy disturbed forest edges suitable for the upland disturbance guild, and thus the two were often found together at a site, that is, the two guilds occupied different unique locations within a site, averting competitive exclusion. The understory shrub guild is positively associated with the evergreen tree guild because the tall, mature overstory trees provide suitable habitat for the shade-tolerant understory guild. The evergreen tree, upland disturbance and understory shrub guilds' rooting depths differ enough to suggest that each guild acquires soil resources independently within the soil profile.

Previous work identifying riparian guilds has focused on guild relationships to flow modification within a single stream network (Bejarano et al. 2011, 2012). I build upon these efforts by considering riparian functional plant diversity across large watersheds with diverse climatic and hydrogeomorphic settings, and disturbance regimes. I used extensive vegetation and stream monitoring data to show that the riparian guild concept can and should be extended to landscapes with diverse physiographic and bioclimatic settings such as the Columbia and Missouri River basins. For example, I showed that riparian guilds were structured directly by flow-related channel metrics, and that many guilds with upland life-history strategies were linked to upland disturbances and bioclimatic factors that influence species' broad environmental niches.

To extend the riparian guild concept as a tool for understanding how riparian communities are structured across landscapes, traits used in guilding should include those that respond to spatially and temporally relevant environmental filters, including multiple disturbances (flooding, wildfire, grazing) and limiting resources (soil moisture, nutrition, light). Whenever possible, these traits should represent species' multiple life history stages (dispersal, establishment, persistence) and size classes (*e.g.* seedling, sapling, mature tree). For example, in low-order streams where riparia blend into uplands (Hagan et al. 2006), traits that comprise versatile non-riparian life history strategies will be important in identifying distinct guilds. When appropriate, guild-based forecasts should also incorporate biotic interactions between guilds – especially when guilds consist of species that modify their environment and/or facilitate establishment of later successional guilds. Linking these distinct guilds to multiple environmental filters and process domains should improve understanding of how riparian communities may respond to future climate and disturbance regimes within and between stream reaches.

By extending the guild concept, this approach provides a basis for quantifying trait-based vegetation groups and community assembly, which can be used to model probable riparian vegetation outcomes in future disturbance and climate scenarios (Kominoski et al. 2013). The multi-scale approach used here shows utility across diverse landscapes where stream physical setting and local management (e.g., grazing and logging pressure) vary within large catchments, and regional-scale drivers such as climate and climate-induced flow alteration shape riparian plant guilds and guild assemblages. The riparian guild framework, as applied in this study, provides a powerful, flexible approach to identify and prioritize the responses of functional plant diversity to multiple environmental filters. Because riparian ecosystems will respond to multiple environmental stressors under future global change scenarios, managers should consider building guild models that account for both flow-related habitat creation or maintenance and disturbance regimes that will change under probable land use, water management and climatic scenarios.

The utility of the riparian guild framework is developing rapidly and will improve as additional stream morphology, riparian vegetation, and measured plant trait data become available. The riparian vegetation data in this study are relatively coarse, using reach-level species presence without linking guild locations to hydraulics that differentiate landforms' hydrogeomorphic settings along a reach. Because riparian plants respond to micro-site differences in environmental parameters such as groundwater elevation, flood exceedance probability, and patchy soil nutrient availability (Biederman and Whisenant 2011, Hough-Snee et al. 2011), the utility of guilding will increase as fine-scale geomorphic and vegetation data are paired with specific landscape filters relevant to individual catchments. Thus, future research should, whenever possible, incorporate spatially explicit, reach-scale hydrogeomorphic diversity with broader bioclimatic data. Future research can also build guilds using measured plant trait data on individuals, incorporating phenotypic plasticity into functional riparian guilds. Using average or ordinal ecological trait values for guilding may render environmental filters too narrowly, missing sub-optimal trait levels that indicate reduced plant performance caused by water-table declines (Cooper and Merritt 2012) or human disturbance. This sub-optimal performance in response to shifting local environmental conditions may be captured by trait plasticity information and measured trait data, building more informative guilds.

Riparian vegetation is structured by hydrogeomorphic processes operating at a hierarchy of scales (from watersheds to reaches), but also influences the operation of such processes through feedback mechanisms (Merritt 2013). For example, large wood accumulation alters local hydraulics and the subsequent sediment deposition that forms bars and islands. These newly-created landforms provide suitable germination sites for new riparian communities that further stabilize the landform (Wohl 2013). Identification and modeling of key riparian guilds that influence hydrogeomorphic processes could help predict habitat changes in both aquatic and riparian habitats. If keystone guilds are predictors of specific habitat types (e.g. canopy bird habitat), this could provide information for predicting changes in aquatic and riparian habitat quality for endangered species (Merritt and Bateman 2012). In watersheds like the Columbia, where endangered salmonid habitat conservation and restoration are national management priorities, the ability to predict habitat processes or habitat condition based on riparian guild dynamics could explicitly link riparian ecology to aquatic conservation (*sensu* Kominoski et al. 2011, Hough-Snee et al. 2014).

The identification and modeling of riparian vegetation guilds and communities in explanatory capacities provides baseline information on the diversity of plant life history strategies that occur across landscapes. This baseline will be of increasing importance as land use, water management, and climate change reshape many environmental filters. While understanding the relationships between riparian species, their component traits, and environmental filters is a fundamental priority in riparian ecology, land and water-resource managers require informed hypotheses on how changes in environmental filters will change the ecosystems that they steward. Probabilistic, predictive models of trait-based plant guilds' responses to anthropogenic flow-regime modification, changes in climate, and anthropogenic and natural disturbance filters can provide these hypotheses. As thorough conceptual and empirical models enhance the understanding of how riparian ecosystems function and confer ecosystem services, they should be expeditiously employed to predict and forecast how riparian guilds, habitats, and ecosystem services may change in response to likely watershed management and global change scenarios.

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2.6 Tables and Figures

Box 1. Glossary of terms used in this paper to describe guilds

Riparian guild – (noun) A group of species with a common life history strategy based on species morphological and/or functional traits. This common life history strategy allows a guild to occupy a unique niche within a riparian environment (Merritt et al. 2009, 2010). For example, riparian *vegetation-flow response guilds* (*sensu* Merritt et al. 2009, 2010) are organized into guilds based on species' traits that respond predominantly to hydrologic and hydrogeomorphic variability.

Riparian guilding – (verb) The process of quantitatively identifying groups of species with shared life history strategies through the clustering of species by their functional and morphological traits or attributes (Merritt et al. 2009, 2010).

Functional trait – A quantitatively measured plant trait that is used to describe a species' physiological performance e.g. stem water potential, wood density, photosynthesis, seed size (Keddy 1992, Grime 2001).

Functional or morphological attribute – Any categorical or semi-quantitative estimate used to describe a plant species' environmental tolerances or general morphology. These can be ordinal or categorical e.g. flooding tolerance, flower timing, rhizomatous vs. taproot rooting strategies. etc.

Life history strategy – a species' or guild's life history strategy is comprised of various investments in individuals' persistence and growth, survival, and reproduction (Grime 1977). Species' measured functional traits, or categorized/estimated functional or morphological attributes are all used to describe species life history strategies. Here I describe species life history strategies using life form, persistence and growth, reproduction, and resource use.

Life history stages – thresholds between component functional traits or attributes (life history strategies) within or between species or guilds (*sensu* (Huston and Smith 1987). I relate these thresholds to four coarse categories: life form, persistence and growth, reproduction, and resource use. For example, mature cottonwood trees have different physical habitat and physiological requirements for survival and reproduction than younger, smaller, reproductively immature seedlings of the same species.

Life form – pertains to the dominant aboveground and belowground strategies employed by a species. Life form can be tied to longevity through direct age estimates or categorical variables that correspond to major differences in dominant life history strategies e.g. perennial vs. annual, forb vs. shrub, etc.

Box 1. (cont.)

Persistence and growth – pertains to the potential for a species to persist, and grow in the riparian environment where environmental disturbance and resource gradients provide diverse conditions that species/guilds must survive within.

Reproduction – pertains to the strategies by which species reproduce and the relative timing of these strategies in response to predominantly fluvial disturbance and fluctuating hydrologic regimes.

Resource use – pertains to the potential of each species or guild to acquire limiting resources, namely water and nitrogen as used here.

Table 2.1. Functional and morphological attributes used in the determination of riparian functional guilds. Species' functional and morphological attribute levels and values were acquired from the USDA PLANTS database (USDA NRCS 2010) except for live-staking, which was acquired from (Burgdorf 2007). Each attribute is broken into one of four coarse life history stages: life form, persistence and growth, reproduction, and resource use.

Species' functional and morphological attributes	Variable type	Dominant life history category	Plant-environment associations in the riparian environment
Growth form	Categorical	Life form	Overbank flooding response, light and water acquisition within canopies
Lifespan	Categorical		Temporal response to flooding, drying, etc.
Adapted to coarse textured soils	Categorical	Persistence and growth	Seed dispersal, germination and plant water relations in alluvial substrate
Adapted to fine textured soils	Categorical		Seed dispersal, germination and plant water relations in alluvial substrate
Adapted to medium textured soils	Categorical		Seed dispersal, germination and plant water relations in alluvial substrate
Anaerobic tolerance	Categorical		Depth, duration and timing of soil saturation from overbank flooding
Drought tolerance	Categorical		Response to seasonal soil drying and moisture deficit
Fire tolerance	Categorical		Ability to for stems to resprout, and/or seeds to disperse or germinate following fire
Growth rate	Categorical		Biomass production from photosynthetic carbon gains minus respiration costs
C:N ratio	Categorical		Leaf-level photosynthesis, tissue construction and maintenance from soil nutrition and atmospheric light, H_2O and CO_2
Height at maturity	Continuous		Ability to acquire atmospheric light and CO_2; response to flooding and fluvial shear stress
Leaf retention	Categorical		Maintenance and construction costs of photosynthetic tissues
Resprout ability	Categorical		Response to flooding and fluvial shear stress, fire, and herbivory
Shade tolerance	Categorical		Capability to account for cellular respiration costs and gain carbon in reduced light environments like forest understories
Vegetative spread rate	Categorical		Ability to reproduce and grow rapidly following disturbance

Table 2.1. (cont.)

Species' functional and morphological attributes	Variable type	Dominant life history category	Plant-environment associations in the riparian environment
Bloom period	Categorical	Reproduction	Timing of flowering in response to environmental cues (flooding, fire, climate, etc.)
Fruit/seed abundance	Categorical		The amount of seed corresponds to the dispersal and reproductive strategy of a species during flood recession
Fruit/seed period begin	Categorical		Timing of seed set relative to freshet and peak floods in snow-melt dominated streams
Fruit/seed persistence	Categorical		How long propagules remain viable and persist following dispersal
Live-staking	Categorical		The capability of a species to adventitiously root when placed into an anaerobic soil environment
Moisture use	Categorical	Resource use	Required moisture to support transpiration and maintain whole plant water balance
Root depth	Continuous		Potential for an individual to acquire soil resources, including deep moisture, nutrients, etc.
Nitrogen fixation	Categorical		Symbiotic relationships with atmospheric nitrogen-fixing bacteria in plant roots allows nitrogen acquisition in nutrient-poor alluvial substrates

Table 2.2. Summaries of environmental filters used to predict riparian guild presence and absence across the Columbia and Missouri River Basins. Buffer variables were summarized within a 90-m buffer of the stream reach, while watershed and landscape variables were summarized for the upstream area above each field-sampled reach. Stream variables were field-sampled at individual reaches.

Variable scale	Environmental variable	Abbreviation in figures	Data source	Mean	SD	Min	Max
Landscape	Elevation (m)	MinElev	USGS NED	1429.3	455.8	186.0	2714.0
	30-year average precipitation (m)	AvgPrecip	PRISM	0.93	0.32	0.27	1.86
	30-year average temperature (°C)	AvgTemp	PRISM	3.74	1.93	-2.50	11.87
	Annual precipitation (m)	AnnPrecip	PRISM	0.91	0.34	0.25	2.10
Watershed disturbance and hydrology	Watershed area (km^2)	Watershed Area	USGS NED	45.97	73.59	0.57	886.82
	Watershed burned (%)	Watershed Burned	LAND-FIRE	10.21	25.04	0.00	100.0
	Average depth water table (m)	AvgWater Table	NRCS	1.15	0.28	0.36	1.52
	Soil thickness (m)	AvgSoil Thick	NRCS	1.78	0.11	0.77	1.82
Stream buffer (30 m riparian buffer)	Forested in buffer (%)	BufForested	LAND-FIRE	70.24	17.32	0.48	100.0
	Grazing in buffer (%)	BufGrazed	USFS BLM	49.34	47.06	0.00	100.0
	Roads in buffer (%)	BufRoads	USFS BLM	1.34	1.49	0.00	7.91
	Buffer slope (°)	BufSlope	USGS NED	34.03	11.09	3.00	64.95
Hydro-geomorphic (stream channel form)	Bank angle (°)	BankAngle	Field measured	109.70	19.41	53.0	157.0
	Gradient (%)	Gradient		1.97	1.20	0.01	8.64
	Bankfull width (m)	BfWidth		6.62	3.75	0.78	23.67
	Sinuosity (%)	Sinuosity		1.27	0.33	1.00	5.66
	Hydraulic radius (m)	Hydraulic Rad		0.41	0.14	0.08	1.00
	Wetted width:depth ratio	WetWD Ratio		25.57	14.57	1.40	192.82
	Undercut banks (%)	Undercut Bank		32.93	17.34	0	95

Table 2.3. Riparian functional guilds identified based on clustering species morphological and physical attributes into common life history strategies. Guilds were given descriptive names and shorthand names for reference in the text. Descriptions broadly generalize each guild’s environmental tolerances and attributes observed in the species within that guild.

Guild (Short guild name)	Description	Species
Long-lived, deeply-rooted, shade tolerant, evergreen tree (Evergreen tree guild)	Evergreen, shade tolerant, overstory conifer tree species; long life spans, short-moderate growth rate, tall stature, deep roots, high drought tolerance, no asexual reproduction, nitrogen fixing, or live-staking, high seed abundance, short seed persistence and low anaerobic tolerance.	*Abies grandis*
		Abies lasiocarpa
		Picea engelmannii
		Pinus contorta
		Pinus ponderosa
		Pseudotsuga menziesii
		Thuja plicata
Rapidly growing, multi-stemmed, rhizomatous and thicket-forming, drought-plastic shrub guild (Upland disturbance shrub guild)	Deciduous, moderate lifespan, multiple stem, thicket forming and rhizomatous species; Poorly adapted to fine textured soils, well adapted to moderate-coarse soils; Variable anaerobic tolerance, moderate drought tolerance, moderate to rapid growth rates and moderate-high seed abundance and low seed persistence.	*Acer glabrum*
		Alnus viridis
		Dasiphora fruticosa
		Menziesia ferruginea
		Philadelphus lewisii
		Ribes hudsonianum
		Salix exigua
		Spiraea douglasii
		Vaccinium scoparium
Low-moderate stature, hydrophytic, multi-stemmed thicket forming shrubs (Mesic shrub guild)	Deciduous, short-moderate lived, low to moderate stature, multiple stem, thicket-forming shrubs; moderate shade tolerance, slow-moderate vegetative spread rate; moderate root depth, high fire tolerance, low-moderate anaerobic tolerance, high moisture use, medium-high C:N ratio, variable seed abundance and low seed persistence.	*Alnus incana*
		Betula occidentalis
		Rosa acicularis
		Rosa nutkana
		Rubus parviflorus
		Salix drummondiana
		Salix geyeriana
		Salix lucida
		Vaccinium membranaceum
Medium-deeply rooted, vegetatively reproducing, alluvial substrate preferring shrubs and trees (Mesoriparian shrub and tree guild)	Deciduous shrubs and trees with moderate-high stature and moderate-deep roots; Adapted to all soil textures, low-moderate anaerobic tolerance, low drought tolerance, moderate-rapid growth rates, high moisture use, high live-staking potential, medium-high fire tolerance	*Amelanchier alnifolia*
		Cornus sericea
		Populus balsamifera
		Salix bebbiana
		Salix boothii
		Salix melanopsis
		Salix sitchensis
		Salix wolfii

Table 2.3. (cont.)

Guild (Short guild name)	Description	Species
Short-statured, shade-tolerant, water stress and flooding intolerant understory shrubs (Understory shrub guild)	Low stature, shade-tolerant, slow-spreading species with moderate rooting depths. Medium-high fire tolerance, generally adapted to medium-textured soils, and lacking drought and anaerobic tolerance. Medium soil moisture use and C:N ratio.	*Cornus canadensis*
		Lonicera involucrata
		Rhamnus alnifolia
		Ribes inerme
		Ribes lacustre
		Rosa woodsii
		Rubus idaeus
		Spiraea betulifolia
		Symphoricarpos albus

Table 2.4. Generalized linear models for the presence and absence of each habitat guild. Bold parameters were significant in the final model. Models were selected with an information theoretic approach, iteratively comparing model AIC and log-likelihood as the variables with the weakest hypothesized relationships with guild presence/absence were removed. Pseudo R^2 are reported using Cragg and Uhler (1970) and maximum likelihood methods. Model AIC, ΔAIC, log-likelihood Alternative models are presented in Appendix A.

Guild (Short guild name)	Final model terms				Pseudo R^2	
	Variable scale	Terms	Estimate	Std. error	Cragg-Uhler	Maximum likelihood
Long-lived, deeply-rooted, shade tolerant, evergreen tree (Evergreen tree guild)	Landscape	AvgTemp	-0.10	0.07	0.42	0.28
		AnnPrecip	1.04	0.44		
	Watershed	WatershedArea	-0.01	0.00		
		AvgWaterTable	-0.97	0.42		
		WatershedBurned	-0.01	0.00		
	Buffer	BufForested	0.06	0.01		
		BufRoads	0.17	0.10		
		BufSlope	-0.05	0.01		
	Stream	WetWDRatio	0.03	0.01		
		Sinuosity	-0.95	0.40		
		Gradient	0.18	0.11		
	Biotic	UD	0.61	0.24		
		US	0.88	0.27		
		MR	-0.51	0.30		
Rapidly growing, multi-stemmed, rhizomatous and thicket-forming, drought-plastic shrub guild (Upland disturbance shrub guild)	Landscape	AvgTemp	0.11	0.05	0.23	0.16
	Watershed	WatershedArea	-0.00	0.00		
		AvgWaterTable	-0.83	0.35		
	Buffer	BufForested	0.01	0.00		
		BufSlope	-0.10	0.05		
	Stream	BankAngle	-0.05	0.02		
		BfWidth	0.20	0.05		
		WetWDRatio	0.02	0.01		
		Gradient	0.40	0.10		
		BufSlope:BankAngle	0.00	0.00		
		BfWidth:WetWDRatio	-0.00	0.00		
	Biotic	ET	0.57	0.23		

Table 2.4. (cont.)

Guild (Short guild name)	Final model terms				Pseudo R^2	
	Variable scale	Terms	Estimate	Std. error	Cragg-Uhler	Maximum likelihood
Low-moderate stature, hydrophytic, multi-stemmed thicket forming shrubs (Mesic shrub guild)	Landscape	AvgTemp	-0.39	0.14	0.31	0.15
		AnnPrecip	-0.80	0.56		
		MinElev	-0.00	0.00		
	Watershed	WatershedArea	-0.00	0.00		
	Buffer	BufSlope	0.28	0.08		
	Stream	BankAngle	0.04	0.08		
		BfWidth	0.17	0.08		
		WetWDRatio	-0.00	0.02		
		Sinuosity	-0.56	0.34		
		BfWidth:WetWDRatio	-0.00	0.00		
		BufSlope:BankAngle	-0.00	0.00		
	Biotic	US	0.63	0.31		
		MR	0.74	0.31		
Medium-deeply rooted, vegetatively reproducing, alluvial substrate preferring shrubs and trees (Mesoriparian shrub and tree guild)	Landscape	AvgTemp	-0.43	0.10	0.26	0.17
		AnnPrecip	-0.66	0.39		
		MinElev	-0.00	0.00		
	Watershed	AvgSoilThick	1.73	0.92		
	Buffer	BufGrazing	0.01	0.00		
		BufRoads	0.12	0.08		
		BufSlope	0.05	0.01		
	Stream	BfWidth	0.12	0.04		
		Gradient	0.18	0.09		
	Biotic	ET	-0.51	0.26		
		MS	0.67	0.31		
		US	0.68	0.25		

Table 2.4. (cont.)

Guild (Short guild name)	Final model terms				Pseudo R^2	
	Variable scale	Terms	Estimate	Std. error	Cragg-Uhler	Maximum likelihood
Short-statured, shade-tolerant, water stress and flooding intolerant understory shrubs (Understory shrub guild)	Landscape	AvgTemp	-0.23	0.11	0.33	0.21
		AnnPrecip	-4.12	1.44		
		MinElev	-0.01	0.00		
		AnnPrecip:Elev	0.00	0.00		
	Watershed	WatershedArea	-0.00	0.00		
	Buffer	BufForested	-0.01	0.01		
		BufRoads	0.16	0.10		
		BufSlope	0.04	0.01		
	Stream	BankAngle	-0.01	0.01		
		Gradient	0.48	0.12		
	Biotic	ET	0.87	0.27		
		MS	0.68	0.32		
		MR	0.83	0.25		

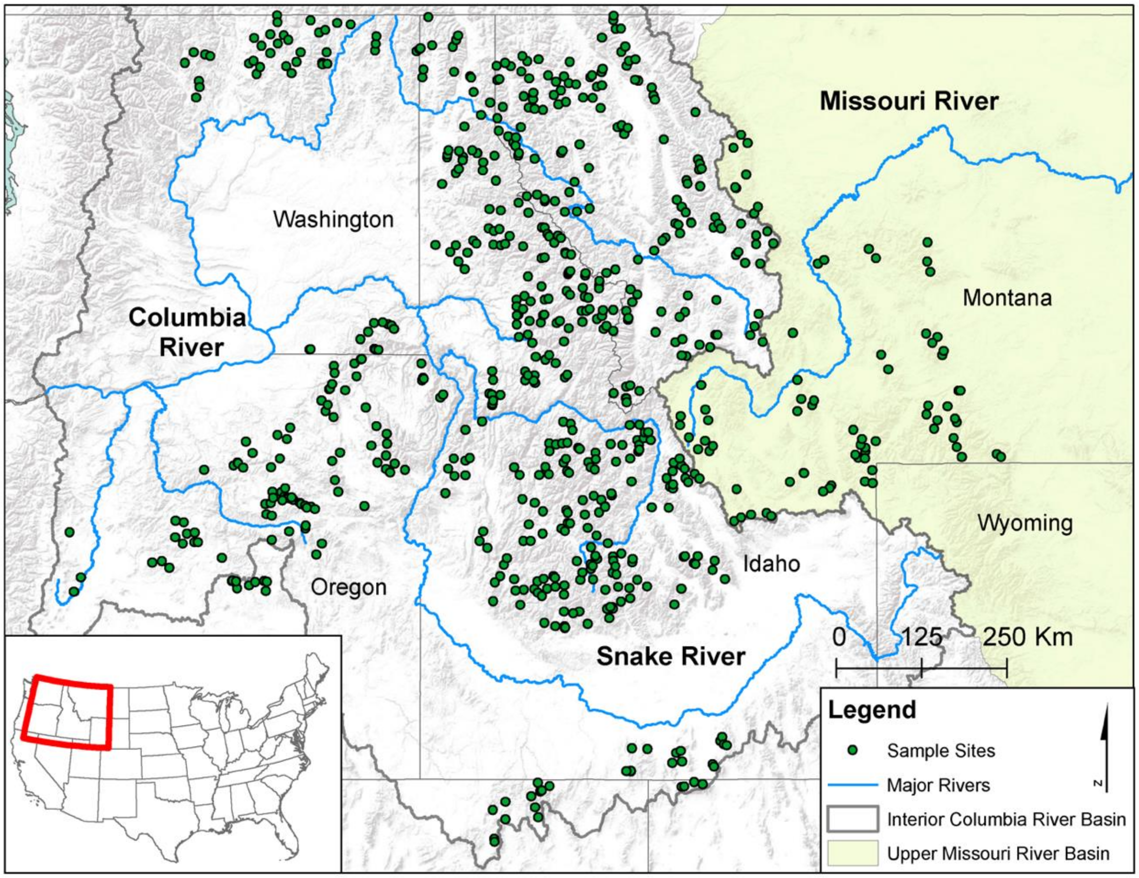

Fig. 2.1. The 703 study reaches in the Missouri and Columbia River basins where riparian vegetation and stream attributes were sampled. All reaches occurred on low-order streams in watersheds under predominantly federal ownership.

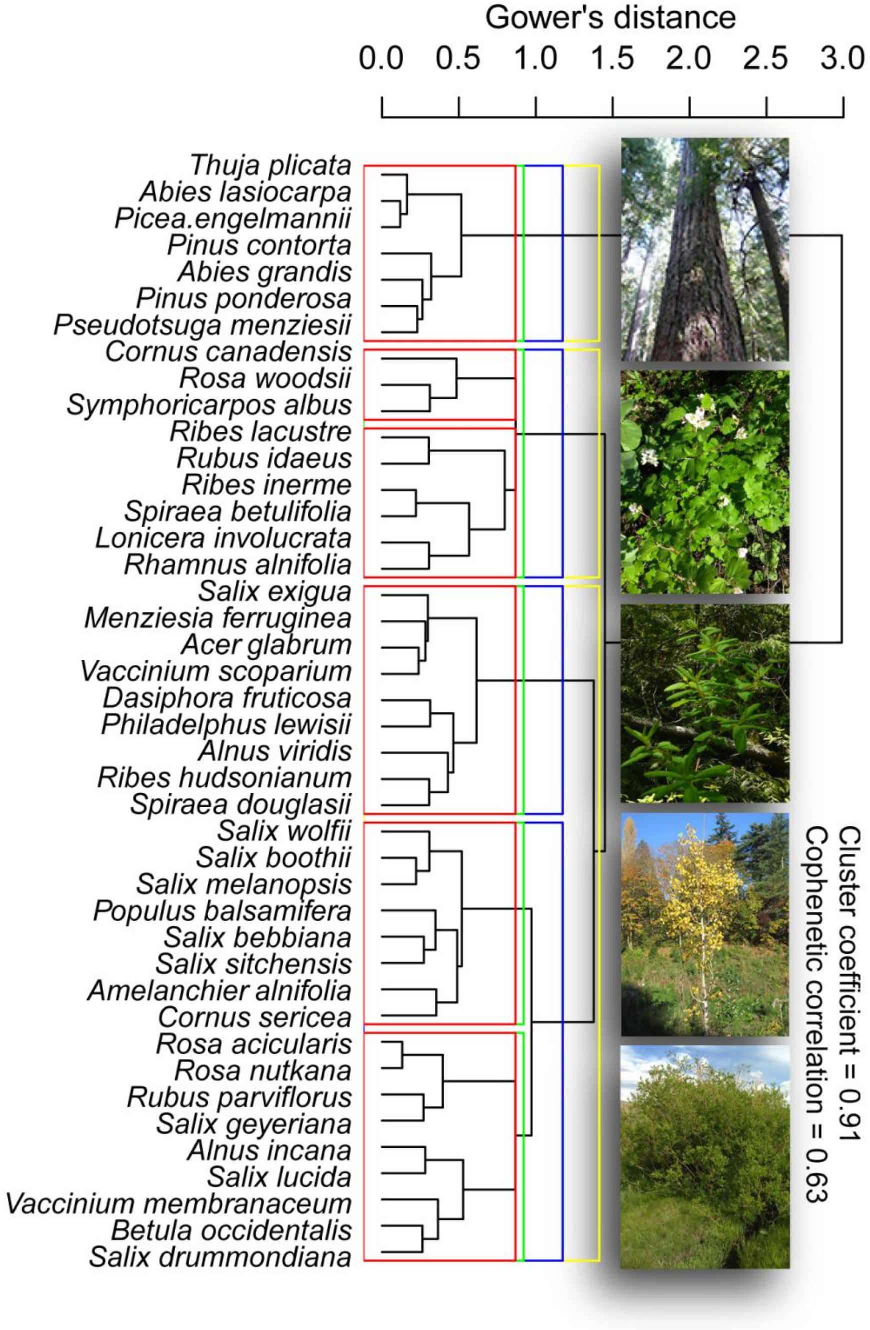

Fig. 2.2. The final dendrogram of species clustered by traits using Gower's dissimilarity. Colored bands indicate sets of three (yellow), four (blue), five (green) and six (red) guilds that were examined *post-hoc*. Five guilds were selected based on their observed ecological niches and guild fidelity using PERMANOVA: (ET) evergreen tree guild, (UD) upland disturbance guild, (US) understory shrub guild, (MR) mesoriparian shrub and tree guild, and (MS) mesic shrub guild.

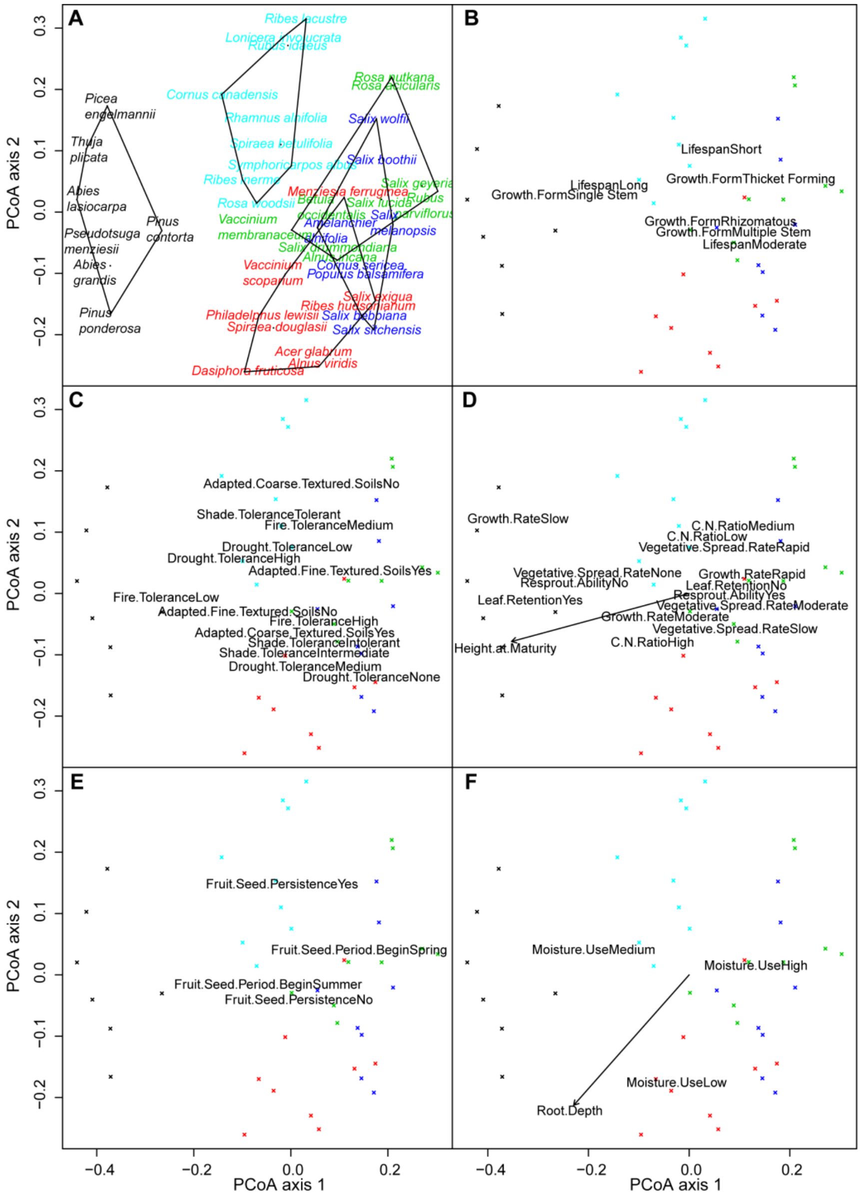

Fig. 2.3. Principal coordinates analysis (PCoA) of species clustered by traits into guilds showed that guilds have distinct life history strategies. Figure 2.3A shows the individual species by their guild membership: evergreen tree guild (black), upland disturbance guild (red), mesic shrub guild (green), mesoriparian shrub and tree guild (dark blue), and understory shrub guild (light blue). Continuous traits (vectors) and categorical traits (text only) significant at an alpha of $p < 0.01$ are plotted over the PCoA solution by life form (B), persistence and growth (C and D), reproduction (E), and resource use (F). Traits are shown in the PCoA ordination space over points that correspond to each species, colored by functional guild (A). The full suite of species and attributes used in guilding are described further in Tables 1 and 3.

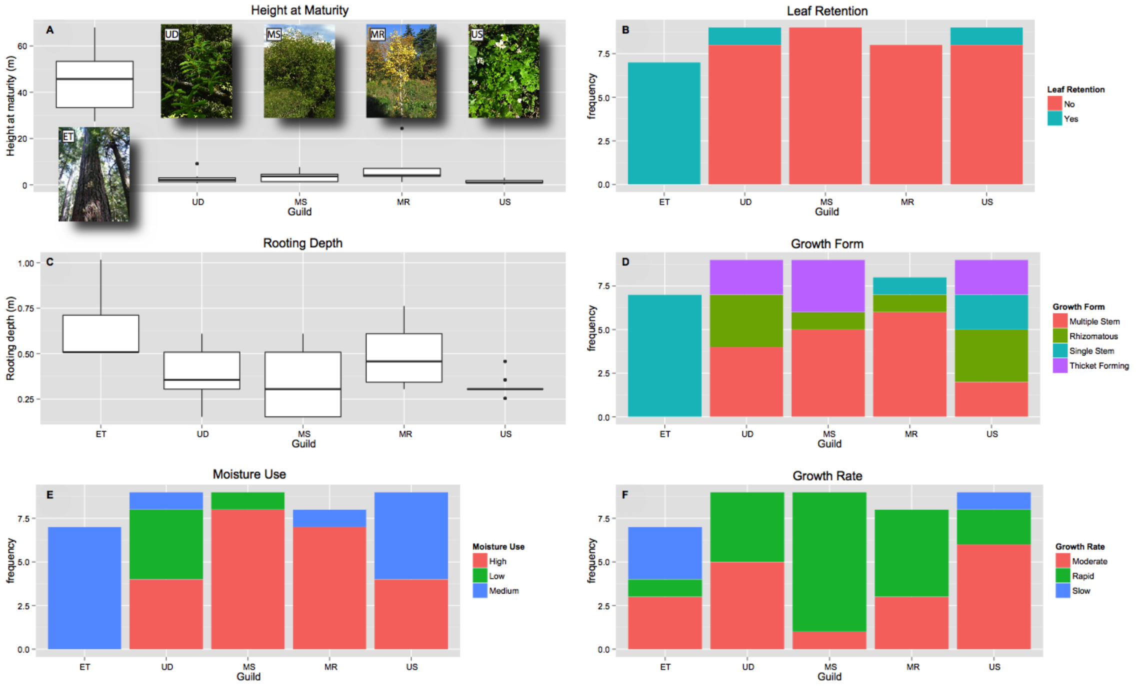

Fig. 2.4. Summaries of the six morphological and physical attributes most strongly correlated to the principal coordinates analysis of clustered species and guilds showed different life history strategies for each guild. Guilds along the horizontal axis are from left to right, (ET) evergreen tree guild, (UD) upland disturbance guild, (MS) mesic shrub guild, (MR) mesoriparian shrub and tree guild, and (US) understory shrub guild.

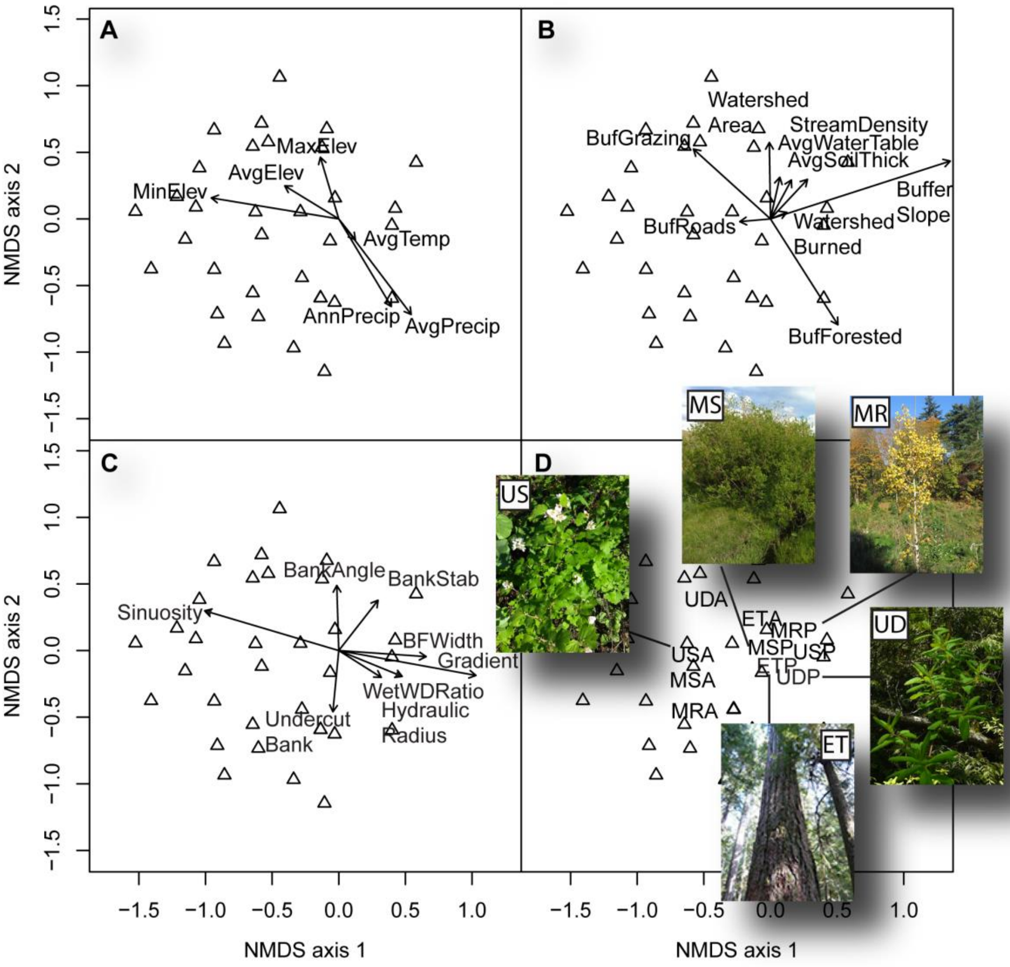

Fig. 2.5. Fitting of environmental vectors to the final nonmetric multi-dimensional scaling (NMDS) solution for trait assemblages at each reach showed that landscape (A), watershed and stream buffer (B) and stream (C) scale environmental filters were all correlated to guild assemblage composition. The presence and absence of individual guilds (D) illustrate how the presence and absence of each individual guild corresponded to guild assemblages at each reach. Abbreviations for environmental factors and guild vectors correspond to those found in tables two and three. For panel D, MRA would indicate the absence of the mesoriparian guild while UDP would indicate the presence of the upland disturbance guild. Points in the NMDS ordination reflect the 32 combinations of guild presence and absence observed at the 703 study reaches. Darker points reflect more frequently occurring guild assemblages than lighter points.

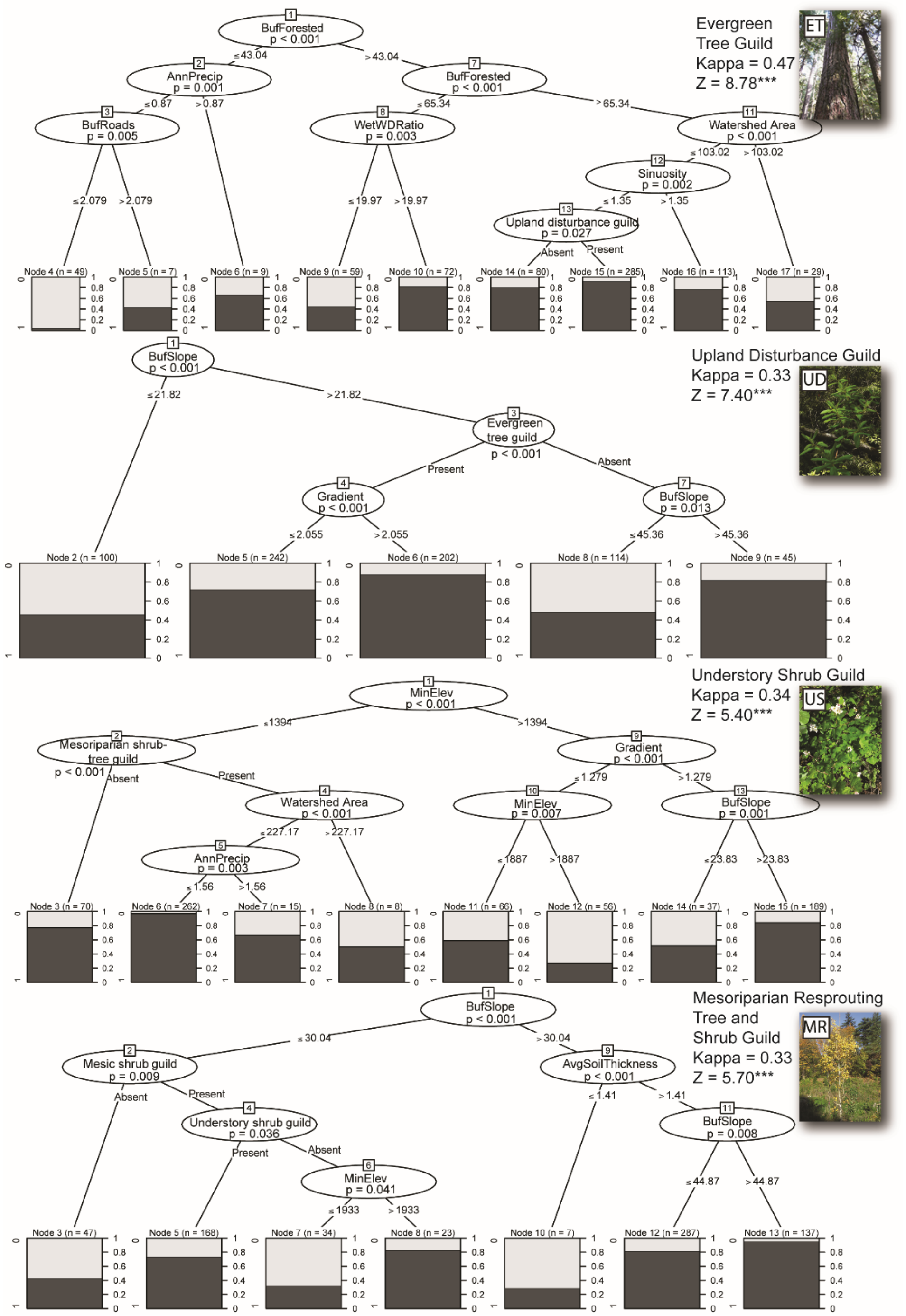

Fig. 2.6. Significant conditional inference trees (CITs) for four of the five riparian guilds showed that guild presence and absence are predicted by both environmental filters and the presence and absence of complementary functional guilds. The mesic shrub guild's final CIT was not a better predictor of guild presence or absence than random chance and is not presented here.

CHAPTER 3

THE ROLES OF CLIMATE, FLOW REGIME, AND FLOODPLAIN ALTERATION IN SHAPING RIPARIAN VEGETATION COMMUNITY AND GUILD DISTRIBUTIONS ACROSS THE WESTERN UNITED STATES.

Abstract

Streamflow alteration from human land and water use has shifted many riparian plant communities from riparian specialist species to drought-tolerant species with generalist strategies. Because climate change and future water development will further alter streamflow across the western United States, there is an urgent need to understand how climate and hydrology shape riparian plant species' distributions. Here I identify riparian plant communities – sets of species that occur together on the landscape – and riparian vegetation-flow response guilds – groups of species that have evolved life history strategies in synchrony with stream hydrologic and geomorphic processes – to determine their relationships with streamflow, climate, and floodplain alteration. I built structural equation models to test hypotheses on how climate controls the magnitude, duration, and timing of streamflow, and how climate and streamflow control floodplain vegetation communities' distributions and riparian guilds' abundance. I incorporated floodplain alteration into models when applicable. I identified eight floodplain communities, ranging from gallery *Populus* spp. forests and montane *Salix* and *Alnus* spp. shrublands, to *Tamarix* and *Elaeagnus* desert floodplains and four guilds: (1) a large, evergreen tree guild, (2) a mesoriparian, hydrochorous tree guild, (3) a mesoriparian, hydrophytic, resprouting shrub guild, and (4) a drought and disturbance-tolerant shrub guild.

Hydrology and climate explained communities' distributions and guilds' abundances. Communities dominated by the mesoriparian tree and shrub guilds, and the large, evergreen tree guild occurred in cool climates with prolonged flow duration. Communities dominated by species from the drought and disturbance-tolerant guild occurred at reaches with high flood magnitude and low interannual flow variability. Hydrophytic, mesoriparian guilds occurred at low abundance in warm climates, with high flow variability, and a late peak flow date. The drought and disturbance-tolerant shrub guild was most abundant in warm climates with variable streamflow and low flood magnitude. These models illustrate how modified streamflow and floodplain alteration favor drought-tolerant species with opportunistic dispersal strategies over riparian species with flow-based dispersal, establishment and growth strategies. As climate change alters streamflow magnitude, duration, and timing, floodplain vegetation communities' guilds may continue to shift from hydrophytic, mesoriparian species to drought tolerant guilds.

3.1 Introduction

Streamflow-mediated hydrologic and geomorphic processes create distinct riparian habitat mosaics on rivers' and streams' floodplains (Mouw et al. 2013, Kleindl et al. 2015). Floods deliver water and sediment that create floodplain landforms where riparian vegetation can colonize, grow, and reproduce (Gurnell et al. 2012, Goebel et al. 2012). Streamflow also provides water that supports riparian plant species' transpiration (Rood et al. 2003, Alstad et al. 2008), seed dispersal (Auble et al. 1994, Rood et al. 2005), and seedling establishment following competition-removing disturbance (Van Pelt et al. 2006). Many riparian plant species have traits that are adapted to distinct, natural flow regimes (Poff et al. 1997), the magnitude, frequency, timing, and duration of streamflow (Stromberg and Boudell 2013, Stromberg and Merritt 2015). Plant adaptations to flow regime include seed dispersal by wind and water (Nilsson et al. 2010), asexual reproduction (Schlosser 1995), flood and drought tolerance (Kozlowski 2002), rapid growth, and low tissue construction and maintenance costs (Wright et al. 2004). These adaptations allow species to establish, grow, and reproduce in floodplains amid flood-mediated erosion, deposition, inundation, drying, and biomass-removing disturbance.

Across the western United States, flow alteration has reduced many streams' flow duration and flood recurrence and magnitude from their historic levels (Bunn and Arthington 2002). Many rivers' natural flow regimes (Poff et al. 1997, Carlisle et al. 2010) are also at risk of modification by water diversion or withdrawal, dam regulation, land use change, or climate change (Wenger et al. 2010b, Coopersmith et al. 2014, Reynolds et al. 2015). When historic flood magnitude, frequency, timing, and duration are altered, generalist or non-riparian specialist species may encroach upon floodplains previously dominated by riparian specialist species (Merritt and Poff 2010). Drought tolerant, generalist species may be more well adapted to novel, modified flow regimes than specialist riparian species (Merritt and Cooper 2000, Birken and Cooper 2006) that may suffer reduced physiological performance (Rood et al. 2003), dispersal limitation (Merritt and Wohl 2006), and/or reduced growth (Rood et al. 2003) following flow modification. In some cases, woody species that establish following flow alteration, like *Tamarix* spp., may facilitate further hydrologic alteration through channel narrowing that disconnects floodplains from channels (Manners et al. 2014).

Ecologists have commonly assessed how riparian plant communities may change in response to hydrologic alteration by examining relationships between individual plant species (Auble et al. 2005, Merritt and Poff 2010) or plant communities (Merritt and Cooper 2000, Engelhardt et al. 2012) and flow regimes. Recently, riparian vegetation and streamflow assessment has shifted from individual species or communities with distinct species composition (Youngblood et al. 1985, Padgett et al. 1989) to riparian vegetation-flow response guilds (Merritt et al. 2009, 2010; Chapter Two). Riparian guilds are non-phylogenetic groups of plant species with shared life history strategies that have phenological, morphological, and physiological adaptations to streamflow-induced biomass-removing disturbance, flooding and drying, and sediment erosion and deposition (Merritt et al. 2009, 2010). Riparian guilds – groups of species with life history strategies adapted to stream hydrologic and geomorphic processes – are complementary to riparian plant communities – groups of species that occur together at the same reach.

Streamflow is the dominant control on vegetation composition at individual stream reaches (Auble et al. 1994, Mouw et al. 2013), so riparian vegetation-flow studies commonly occur at this scale (Merritt and Cooper 2000, Mortenson and Weisberg 2010, Bejarano et al. 2011). Recent reach-scale efforts to link streamflow and riparian guilds have examined how flow regulation changes riparian forest composition (Bejarano et al. 2012) and how guilds and species' traits differ between intermittent, ephemeral, and perennial rivers (Stromberg and Merritt 2015). Because guilds are groups of species with shared traits, not phylogenetically related species or sets of co-occurring species, they can be related to streamflow across broad geographic extents where species' ranges may not overlap.

At sub-continental scales, riparian plant communities assemble across streamflow and landscape-scale environmental gradients (Fullerton et al. 2006, Dunn et al. 2011). These gradients include local soil moisture (Dwire et al. 2004), watershed hydrology (Auble et al. 1994, Shafroth et al. 2000), channel form (Harris 1988), geology (Chambers et al. 2004, Jolley et al. 2010), land use (Hough-Snee et al. 2015a), disturbance (Hough-Snee et al. 2015b) and climate (Baker and Wiley 2009; Chapter Two). To build a more complete conceptual model of floodplain ecosystem function, guild-based analyses should incorporate these gradients, especially when comparing stream reaches that occur across diverse physical or climatic settings.

At present, guild-based assessments of riparian vegetation on many floodplains' and at large spatial scales are rare. Additionally, no published study that I am aware of, regardless of scale, has examined how streamflow and covarying environmental gradients control the distributions of riparian guilds. By testing hypotheses about how different riparian vegetation guilds relate to flow, climate, and floodplain alteration, I hope to build conceptual models of why xeric, riparian, and intermediate vegetation guilds occur at different locations on the landscape. These models can help land managers, planners, and scientists to better understand how riparian ecosystems assembled in the past and how they may change under anticipated future climate and flow alteration. Landscape-scale assessments of guilds may be particularly valuable in understanding vegetation patterns across multiple floodplains with diverse climate, flow regimes, and alteration histories.

Here, I examine landscape patterns in riparian vegetation across the western United States using two complementary frameworks, riparian guilds and riparian plant communities. I ask two sets of related questions:

1. What woody riparian plant communities occur at floodplains of the western United States? How are communities' distributed across streamflow, climate, and floodplain alteration gradients?

2. What ecologically and hydrologically distinct riparian guilds occur across the western United States? How do hydrophytic and xeric riparian guilds' abundance change as peak and base streamflow magnitude, duration, and timing are altered? As climate varies from cool and wet to dry and hot? As floodplains are increasingly altered by grazing, invasive species and channel narrowing?

By examining riparian vegetation communities' and guilds' relationships with climate, streamflow, and floodplain alteration, as well as relationships between climate and streamflow and floodplain alterations, I hope to elucidate how plant communities and guilds differ in their species composition and geographic distributions. I make this distinction because communities are a common ecological resolution at which riparian monitoring and condition assessment have historically occurred (Youngblood et al. 1985, Padgett et al. 1989, Winward et al. 2000, Coles-Ritchie 2005, Coles-Ritchie et al. 2007). Community composition, like guild abundance, changes across local and regional environmental gradients (Goebel et al. 2012, Hough-Snee et al. 2015b), although the analytical processes by which guilds and communities are identified differ. Because of similarities between community analyses and riparian guild analyses, it may be unclear how these approaches differ. A sub-objective in answering these research questions is to illustrate how community- and guild-based approaches' workflows differ, how they are similar, and how interpretation of their results complement one another.

3.2 Methods

Study region and sampling design

Between 1996 and 2002, Auble et al. (2012) surveyed woody species at 456 floodplain sites adjacent to U.S. Geological Survey gaging stations with at least a twenty year daily discharge record from 1965-1994. Because stream gages are not randomly distributed across the western U.S., floodplain Auble et al. selected reaches for sampling through a spatially weighted, random selection. This approach favored gages with few neighboring gages over gages with numerous gages nearby (Auble et al. 2012). The resulting sampling sites are located across the arid, semi-arid, and montane western conterminous United States, west of the 100th parallel and east of the Cascade Mountain crest in Washington State and Oregon, and the northern Sierra Nevada divide in California (Figure 3.1).

At each site Auble et al. mapped the 100-year floodplain over aerial photos during the site visit and then digitized in a Geographic Information System (GIS). Floodplain area ranged from < 0.01 to 4.40 km^2 and valley length ranged from 0.14 to 5.07 km. Sampled floodplains' width generally scaled to the size and discharge of the active channel. Channel areas ranged from <0.01 to 1.24 km^2. Floodplain gage selection and sampling methods are fully described in Auble et al. (2012).

Vegetation data

To determine which species occupied each floodplain, woody species >1.5 m in height were recorded in unique floodplain surface polygons within the mapped 30-year floodplain at each site (Auble et al. 2012). In some cases, conflations of two or more species in the same genus were grouped. All *Salix* species, excluding *S. amygdaloides, S. bonplandiana, S. exigua, S. gooddingii,* and *S. rubens*, were pooled into a single willow category. *Picea* species, largely *Picea pungens* and *Picea engelmannii*, and *Prunus* species, largely *Prunus virginiana* and *Prunus emarginata,* were identified only to the genus and so their species covers were pooled into *Picea* spp. and *Prunus* spp. conflations. *Tamarix ramosissima* and *Tamarix chinensis* were consolidated into a *Tamarix* species conflation. Evergreen *Tamarix aphylla* was not included in this conflation. All other unidentified woody species were classified as “other large woody species (OLW).” The full species list is available in Table 3.2 and Auble et al. (2012).

At each reach, I summed individual species’ cover across all floodplain polygons and divided by active floodplain area to calculate each species’ abundance as a percentage of the floodplain area. This floodplain area excluded the unvegetated, wetted channel, and polygons that consisted of human infrastructure like roads, bridges, or row-crop agriculture. I removed sites from the dataset where woody species cover summed to zero because the floodplain consisted predominantly of excluded and/or active channel polygons. This resulted in a final dataset of 443 floodplains.

Identifying vegetation communities from species composition

I classified floodplain sites into community types based on their woody species composition. For ease of interpretation, I chose to identify discrete communities for use as response variables in structural equation models rather than modeling reaches' full multivariate composition. I considered using ordination axes to reduce multivariate community species composition to a few composite variables (ordination axes) for modeling. However, because the riparian vegetation-flow response guild framework models groups of species (guilds) instead of trait gradients (ordination axes), I chose to model community types over composition gradients (ordination axes).

To classify floodplain sites into discrete vegetation communities, I clustered reaches based on species' abundance using hierarchical agglomerative clustering (flexible beta method; $\alpha = 0.626$, $\beta = 0.626$, $\gamma = -0.26$). I examined the resulting cluster dendrogram for between five and 13 different community types, using multilevel pattern analysis (De Caceres et al. 2010) to identify indicator species within sets of clustered reaches. Multi-level pattern analysis calculates indicator values for each species within combinations of communities based on the relative frequency and abundance of species within those combinations (De Caceres et al. 2010). Each species was allowed to serve as an indicator of at least one, but no more than four different communities (clustered groups). I set these thresholds to simplify the interpretation of vegetation communities from clustering.

I visualized communities and their relationships with environmental gradients using the first two axes of a 4-dimensional detrended correspondence analysis ordination

(DCA; four rescaling cycles; 26 segments; rare species downweighted) and fit species, riparian guilds (next section), and environmental data vectors to the final ordination solution using multiple regression (see *Environmental filter data*). Clustering used Bray-Curtis distance to distinguish similarity between reaches. I performed community analyses using R statistical software (R Core Team 2015) and the cluster, labdsv, and vegan packages (Maechler et al. 2002, Roberts 2012, Oksanen et al. 2015).

Identifying guilds using species morphological attributes and traits

I used the riparian vegetation-flow response guild framework (Merritt et al. 2010) to quantitatively determine riparian guilds from species' morphological attributes and physiological traits. I reviewed literature on functional traits of the woody species identified in the field and queried the TRY (Kattge et al. 2011), USDA PLANTS (USDA NRCS 2010) databases, and data from McCoy-Sulentic and Kolb (personal communication), and Merritt, Shafroth, Sarr and Palmquist (personal communication). I queried quantitative and categorical traits and morphological attributes for each species that reflect species' overall life history strategy within riparian environments where flooding, drying, and fluvial disturbance are common (Table 3.2). I grouped traits and morphological attributes into four categories: life form, survival and growth, resource acquisition and use, and reproductive strategy (Table 3.2; Appendix B). I did not use traits for guilding that relate to climate directly (Friedman et al. 2005, Guilbault et al. 2012), as my objective was to capture species adaptations to streamflow.

Some species lacked trait data, which led to a trade-off: exclude species with missing trait data from guild analyses or estimate trait values for these species. Excluding species due to a lack of trait data would underrepresent the resulting guilds' abundances, while estimating trait values requires the substitution of values from similar species (Mcgill et al. 2006, Violle et al. 2015). I chose to include all species and species conflations, estimating values for missing traits, so I could allocate each species to a guild. When ordinal plant traits or morphological attributes were unavailable, I used online flora and herbaria accounts to estimate plant attributes.

When species were missing quantitative traits, I determined whether similar species' trait values were appropriate for use. I did not guild "other large woody" species, but did allocate the *Salix* spp., *Prunus* spp., and *Picea* spp. conflations to guilds. I substituted *Prunus emarginata* and *Picea engelmannii* quantitative trait data and characteristics data from the USDA PLANTS database for the *Prunus* and *Picea* conflations. I estimated traits for the *Salix* spp. conflation by averaging values for all identified *Salix* species within the study area. When multiple values were available for a quantitative trait for a given species, I averaged individual plant measurements.

Because species' traits vary across environmental conditions and within and between individuals, using a single trait value for each species provides only a coarse characterization of a given species trait (Jung et al. 2010, Violle et al. 2015). While this approach to creating plant guilds is imprecise, these estimates are informative for identifying shared life history strategies within many species at the landscape scale (Cordlandwehr et al. 2013). Due to a lack of data, I did not account for species' different life stages such as seedling versus sapling versus reproductively mature tree, etc.

I used hierarchical agglomerative clustering (Ward's method; Ward 1963) on a

Gower's distance matrix of species' traits and morphological attributes to group species into guilds. Gower's distance rescales variables between zero and one, allowing me to cluster species into guilds based on categorical and continuous data. I examined the cluster dendrogram for three to six guilds. Following clustering, I visualized guilds as sets of species within a two-dimensional principal coordinates analysis (PCoA) of traits. I fit trait and morphological attribute vectors to the PCoA ordination using multiple regression, which allowed me to examine relationships between guilds, their component species and species' traits. I summarized mean trait values and attribute levels for each guild.

The guilding process was not strictly numerical, and relied on ecological knowledge of each species throughout. Root (967) felt that allocating species to guilds would always have to be subjective and rely on the expertise of the analyst to create representative guilds for answering ecological questions. In the spirit of Root's philosophy, I determined sets of guilds to be ecologically realistic if each guild consisted of species with overlapping trait syndromes that led distinct life history strategies between guilds.

Climate, streamflow, and floodplain alteration data

I summarized environmental data into three conceptual groups prior to analyses: climate, streamflow, and floodplain alteration (Table 3.1; Appendix B). I acquired climate data from 1961-1990 and calculated the study reaches' mean annual precipitation and total growing degree days (PRISM Climate Group 2012). I selected these climate variables for their direct effect on vegetation rather than their indirect effects on vegetation as mediated by streamflow. I calculated ecologically relevant flow metrics from the daily and annual streamflow record for the thirty years prior to vegetation sampling at each gage. Ecologically-relevant flow metrics are streamflow magnitude, duration, and timing, all of which influence the presence or abundance of aquatic and riparian biota through their impact on fluvial geomorphic, hydrologic, and ecological processes (Olden and Poff 2003, Olden et al. 2012).

Streamflow magnitude metrics included 25-, 10-, 5-, and 2-year recurrence flood discharge, mean, skew, and coefficient of variation of daily discharge, proportion of the growing season with no flow, ratio of the 10th percentile growing season daily flow to mean daily discharge, and the ratio of the 90th percentile growing season daily flow to mean daily discharge (Table 3.1). Streamflow timing and duration metrics included: peak flow dispersion, central tendency of the Julian day of peak flow, and central tendency of the Julian day of peak flow minus the Julian date of the last frost (Table 3.1). I fit these streamflow metrics to the community DCA ordination using multiple regression (envfit function in R).

Because streamflow magnitude, timing, and duration metrics covary, I did not treat streamflow metrics as independent predictors of vegetation in structural models. Instead, I conducted a principal components analysis (PCA) on mean standardized hydrology data to create synthetic variables (principal components) that effectively charcterize streamflow. The precedent for creating synthetic variables from correlated multi-dimensional environmental variables is discussed at length in McCune and Grace (2002) and Legendre and Legendre (2012). I used these synthetic hydrology variables as predictors of vegetation in structural equation models. I interpreted the relationships between hydrologic metrics that comprise each reach's flow regime using the PCA. The principal components elucidated how the duration, magnitude, and timing of flow varied among reaches and illustrated how flow variables relate to one another.

In addition to climate and streamflow data, I also examined Auble et al.'s (2012) categorical data on indicators of floodplain alteration that influence floodplain physical form and vegetation composition. Floodplain alteration indicators included past livestock grazing intensity, evidence of functional channel narrowing within the floodplain, and evidence that nonnative, invasive Tamarisk (*Tamarix* spp.) and Russian olive (*Elaeagnus angustifolia*) had been planted in the surrounding matrix.

Livestock grazing is a biomass-removing disturbance that selects for species that can tolerate browsing (Fleischner 1994). Functional narrowing from historic water-use and land use disconnects floodplain vegetation from groundwater and reduces flood recurrence and magnitude on floodplain landforms (Scott et al. 2000, Simon and Rinaldi 2006). Functional narrowing was identified at each reach during vegetation sampling (Auble et al. 2012; binary variable). Functional narrowing occurs when the active channel is hydrologically disconnected from the historic floodplain. It can occur through either floodplain accretion that raises floodplain elevation relative to the active channel (Manners et al. 2014) or through an increase in channel bed slope that increases unit stream power and sediment transport, lowering the streambed elevation relative to the floodplain (Schumm 1999). I use *functional narrowing* as an indicator of hydrologic disconnection between the channel and floodplain regardless of the cause. The introduction of woody invasive species in the surrounding matrix provide a vector for the establishment of invasive species that tolerate a wide range of hydrologic conditions and outcompete native riparian species following hydrologic alteration (McShane et al. 2015).

Testing hypotheses with a graph theoretic approach to structural equation models

I developed hypotheses about how streamflow, climate, and floodplain alteration might influence riparian vegetation abundance (Table 3.3). Based on these hypothesized relationships between climate, hydrology, and floodplain alteration and riparian vegetation composition, I built a structural equation metamodel to visualize the study system (Figure 3.2). I used this “graph-theoretic” approach to create, test, and evaluate hypothesis-driven structural models (Grace et al. 2010, 2012) for species composition-based community types and guild abundance.

I built structural equation models for the effects of climate, streamflow, grazing, introduction of *Elaeagnus*, and functional channel narrowing on where community types occurred on the landscape. I modeled communities as binomial presences or absences and used the WLSMV estimator for categorical endogenous variables (Rhemtulla et al. 2012). I built another model to test hypothetical relationships between guild abundance, climate, streamflow, and grazing, functional channel narrowing, and the introduction of *Elaeagnus*. The guild abundance model used the maximum likelihood estimator for continuous responses. In both models I used the first three principal components from the hydrology PCA to represent (1) mean daily flow and peak flood discharge, (2) flow variability and duration, and (3) flow timing (see hydrology PCA results below). Growing degree-days and annual precipitation represented historic climate in all models.

Evidence of past livestock grazing, evidence of *Elaeagnus* planting, and functional narrowing were used as floodplain alteration terms in both the guild and community models.

I standardized climate and disturbance variables to the mean to meet structural equation modeling assumptions, including linear relationships between variables, multivariate normality, and no dramatic outliers. I log+1 transformed guild abundance to reduce dispersion prior to modeling. I tested for significant covariance structures between the independent variables, communities or guilds. I selected models based on Grace et al.'s (2012) framework for a graph theoretic implementation of structural equation models. After creating conceptual meta models, I implemented structural equation models with terms for all hypothesized variables. I took an information-theoretic approach to comparing candidate models. I iteratively removed nonsignificant pathways, comparing models based on their fit statistics (RMSEA, χ^2, CFI, TLI), and retention of hypothesized relationships between predictor variables and response variables. I plotted each model as I removed each nonsignificant causal pathway. Over twenty models were compared as individual relationships between predictors were removed. All models were built using the Lavaan package (Rosseel 2012) for R.

3.3 Results

What woody riparian plant communities occur on floodplains of the western United States?

I identified eight riparian vegetation communities through cluster analysis and multi-level pattern analysis (Table 3.4; Figure 3.3; Appendix B) of woody species composition:

(1) A *Populus deltoides*, *Salix amygdaloides, Fraxinus pennsylvanica* mixed forest,

(2) A mixed *Salix, Alnus, Cornus sericea, Populus trichocarpa*, mixed conifer forest,

(3) A mixed *Salix, Pinus ponderosa, Cornus sericea, Artemisia tridentata* shrubland,

(4) A mixed *Salix, Cornus sericea*, *Populus trichocarpa, Pinus ponderosa, Picea engelmannii* forest,

(5) A *Populus angustifolia, Salix exigua,* mixed *Salix,* hydrophytic shrub, and mixed conifer forest,

(6) A *Populus deltoides*, *Salix exigua*, *Salix amygdaloides* gallery forest,

(7) A *Tamarix* spp*.*, *Populus fremontii*, *Elaeagnus angustifolia* forest, and

(8) A *Tamarix* spp., *Baccharis salicifolia*, *Prosopsis velutinus* shrub forest.

These communities had distinct indicator species, and often occurred in unique climatic and hydrologic settings (Figure 3.3; Figure 3.4; Table 3.4). Full indicator values for all species and communities are presented in Appendix B. I refer to communities by their numbers throughout the text.

What ecologically distinct riparian guilds occur across the western United States?

I identified four major riparian guilds: a tall, long-lived, deeply rooted evergreen tree guild (EGT), a mesoriparian, hydrophytic, hydrochorous tree guild (MRT), a mesoriparian, resprouting, wind- and water-dispersed shrub guild (MRS), and a summer-dispersed, drought-tolerant, disturbance resistant shrub and tree guild (DDT; Figure 3.5). The EGT guild consisted entirely of single stemmed, evergreen trees with long lifespans and moderate to fast growth rates (Table 3.5). This guild lacked the capacity to resprout following biomass-removing disturbance and had very limited flood, drought and salinity tolerance. The EGT guild's species grow very tall, have thick leaves, and have deep roots. These traits indicate limited adaptation to fluvial disturbance and relatively high tissue creation costs.

The MRT and MRS guilds both exhibited adaptations to the disturbance and resource gradients of the riparian environment. Both the MRT and MRS guilds' species complete their life cycle rapidly with wind and water-dispersed seed types, medium to high moisture use and anaerobic tolerance, and limited drought tolerance. Both the MRT and MRS guilds' species have thin, deciduous leaves indicative of low tissue construction costs, can resprout following disturbance and have relatively deep roots to acquire soil moisture and stabilize individuals during flooding. The MRT guild's height at maturity, single stem growth form, shade intolerance, and a lack of a mutualism with atmospheric nitrogen fixing bacteria differentiated it from the MRS guild. The MRS guild had multiple-stemmed growth forms, higher anaerobic and shade tolerance, and lower drought tolerance than the MRT guild.

The DDT guild's species had adaptations that allow them to reproduce quickly and establish under a variety of hydrologic conditions, and survive drought or intermittent flows. The DDT guild consisted of moderate-long-lived species with medium-high salt tolerance, low anaerobic tolerance, medium-high drought tolerance, and late season dispersal of seeds contained within fruits. These species had thin, leaves, moderately deep roots, and were shade intolerant, indicating a relatively fast life cycle that takes advantage of fluvial disturbance during establishment stages, and persists as environmental stress shifts from flooding to drying and salt accumulation.

When plotted into the PCoA trait space, guilds were differentiated by species' seed dispersal strategy ($R^2 = 0.68$), height at maturity ($R^2 = 0.60$), lifespan ($R^2 = 0.45$), growth rate ($R^2 = 0.39$), leaf retention ($R^2 = 0.37$), anaerobic tolerance ($R^2 = 0.34$) and moisture use ($R^2 = 0.31$; Figure 3.6). Traits are summarized for each guild in Table 3.6. Each guild was widely distributed across the study region (Figure 3.7).

Streamflow principal components analysis

Eigenvectors of the streamflow PCA showed that mean daily discharge and Q2, Q5, Q10, and Q25 flood magnitude were positively associated with the first principal component (Figure 3.8). Dispersion of peak flow, the ratio of the 10th percentile growing season daily flow to mean daily discharge, and the ratio of the 90th percentile growing season daily flow to mean daily discharge were negatively correlated to the second and third principal components. The number of days in the growing season with no flow and the coefficient of variation and skew of the daily mean flow were positively correlated to the second and third principal components. The measure of central tendency of the mean flow and the difference between mean flow and last frost were negatively correlated to the third component.

The first three principal components explained 35.4%, 23.5%, and 12.1% of the variance in the hydrology data, respectively (71% total; Eigenvalues: PC1= 5.6, PC2=

3.4, and PC3= 1.6; randomization test $p < 0.001$), and were used in causal modeling of riparian vegetation communities and guilds. I interpreted relationships between principal components and vegetation as follows: a positive correlation between guild abundance and principal component one shows that the guild is at high abundance on floodplains with high peak flood discharges and daily mean flows. Guilds that are positively correlated to the second principal component are abundant on floodplains with variable, intermittent streamflow with high summer flow variation. Guilds that are negatively correlated to the second principal component occur at high abundance in reaches with high peak flow dispersion and stable base flows (ratios of the 10% and 90% flows to the mean flow). Guilds that are positively correlated to the third principal component occur at high abundance at reaches with dispersed, late peak flows that occur long after the last frost. I interpret these relationships between PCA axes and community presence and absence in the same way.

Structural model of riparian vegetation communities - how do communities differ across streamflow, climate, and floodplain alteration gradients?

The structural model for the eight riparian vegetation communities (Figure 3.9) showed that a combination of climate, hydrology and floodplain alteration explained community distributions across the landscape while climate explained variability in hydrology. Specifically, annual precipitation and growing degree days were positively related to variable, intermittent flows (PC2), and negatively related to stable, prolonged peak and base flows. Annual precipitation was also positively related to PC3, indicating a negative relationship to flow dispersion, Julian date of flow, and the difference between timing of the year's peak flow and the year's final frost. These relationships confirmed the hypothesis that climate drives vegetation directly and indirectly as mediated through impacts on timing and duration of streamflow (Figure 3.9).

Mean annual precipitation and annual growing degree days at the sample reaches were not correlated to stream discharge and flood magnitude (PC1; $R^2<0.01$). Mean annual precipitation, while a significant predictor of vegetation guilds and communities, does not strongly relate to flood magnitude across the study reaches. This corresponds to how the mainstem channels of many large, Western rivers (e.g. the Colorado, Columbia, Missouri, etc.) occur at low elevation in dry, relatively warm environments, but have large, mountainous contributing watersheds that dictate high flow timing and magnitude. In rivers with montane headwaters, the contributing watershed's snowpack and seasonal temperatures control streamflow timing and duration rather than precipitation at a given gage station.

Across the study area, streams' water sources vary from snowmelt-driven montane streams, to groundwater-fed desert streams that experience summer monsoonal floods. Dams have also altered the timing and magnitude of floods in the mainstem Columbia and Colorado Rivers, while water diversions and withdrawals are common along tributaries of many sample reaches. Accordingly, hydrologic models of the study area require reach and basin-specific groundwater, climate, and landcover inputs. However, using this many intercorrelated predictors of flow was incongruent with the structural equation modeling framework I used to model vegetation.

When I attempted to fit models of community presence that included terms for past grazing, functional narrowing and *Elaeagnus* introduction, they did not converge after 10,000 iterations. This was due to the large number of terms in the model when incorporating causal relationships between each of the eight communities and functional narrowing, grazing, and *Elaeagnus* introduction. Accordingly, I used channel narrowing as the sole indicator of floodplain alteration in the final riparian community structural model. This was because the hydrologic decoupling of channels from floodplains was the main vegetation-floodplain relationship of interest.

Distinct riparian communities occurred at distinct climatic settings and streamflow attributes. Community one ($R^2 = 0.16$) occupied reaches with low flow magnitude. Community two ($R^2 = 0.14$) occupied cool reaches with stable base flows. Community three ($R^2 = 0.27$) occupied reaches with high discharge, late flow seasonality and cool climates. Community four ($R^2 = 0.47$) occupied reaches with late peak flows and high precipitation that had no evidence of channel narrowing. Community five ($R^2 = 0.68$) occupied cool, dry reaches with consistent late season streamflow. Community six ($R^2 = 0.05$) occupied reaches with high discharge and flood magnitude. Community seven ($R^2 = 0.56$) occupied hot, dry environments with, variable, intermittent flows, late peak flow seasonality and no evidence of channel narrowing. Community eight ($R^2 = 0.42$) occupied reaches with low flow magnitude and late-season high flows, and positively correlated to growing degree-days. Structural model statistics indicated a well-parameterized model for the data (Figure 3.9).

Structural model of riparian vegetation guilds - how do guilds' abundance differ across streamflow, climate, and floodplain alteration gradients?

The structural model for riparian guilds, hydrology, climate, and floodplain alteration showed that flood magnitude was highest at warm reaches and flow variability and duration was highest in warm reaches with high precipitation (Figure 3.9). The evergreen tree guild was abundant at wet, cool reaches with variable flow and limited evidence of grazing and *Elaeagnus* planting. The mesoriparian tree guild was most abundant at cool reaches with high daily flow and flood magnitude, perennial streamflow, limited livestock grazing, and evidence of channel narrowing and *Elaeagnus* planting. The mesoriparian shrub guild was abundant at cool reaches with stable flows and limited evidence of grazing and *Elaeagnus* planting. The drought and disturbance tolerant shrub guild was most abundant at hot, dry reaches with low flood and daily flow magnitude, and early peak flow seasonality.

The drought- and disturbance-tolerant shrub guild included *Tamarix* and *Elaeagnus* species, both of which are known to colonize floodplains at high flow and persist under subsequent dry streamflow conditions (Friedman and Lee 2002). Species within this guild can also facilitate channel narrowing through floodplain accretion (Manners et al. 2014). I found reaches with abundant drought and disturbance tolerant guild species are likely to show evidence of functional narrowing (Figure 3.9). The drought and disturbance tolerant shrub guild was rare at wet reaches with dispersed, late-summer peak flows. The drought and disturbance tolerant guild was negatively related to planted *Elaeagnus*. This may be because planted *Elaeagnus* did not increase the abundance of all non-*Elaeagnus* species that occurred within the drought and disturbance tolerant shrub guild. The final model for guild abundance fit the data well (Figure 3.9).

3.4 Discussion

My objective was to examine how floodplain plant communities and flow response guilds relate to climate, streamflow, and floodplain alteration. I identified eight vegetation communities and four riparian vegetation-flow response guilds from 48 woody plants of the western United States. Communities ranged from high-elevation, mixed conifer forests to gallery cottonwood and mesic shrub forests to *Tamarisk* and *Elaeagnus*-dominated floodplain shrublands. Guilds included long-lived, evergreen trees that do not require riparian hydrology and disturbance (EGT guild), obligate riparian trees (MRT guild) and shrubs (MRS guild) with high soil moisture needs, wind and water-based dispersal, and flooding tolerance, and plastic species that tolerate riparian stressors like salinity and drought, and can disperse under altered flow regimes (DDT guild).

I enumerated how streamflow magnitude, duration, and seasonality shape riparian vegetation communities and guilds alongside geographic patterns in climate and floodplain alteration across the western United States. Communities with abundant drought and disturbance tolerant species (DDT guild) occurred at locations with brief peak flow duration, higher proportions of no-flow days, and floods that are only marginally higher than the average flow. These flow regimes vary from the natural flow regime of many western rivers and support species with adaptations that allow them to persist following reductions in base flow and peak flow magnitude and duration. Streams with snowmelt pulse flow regimes had abundant mesoriparian shrubs that require floods for dispersal and to disturb floodplains, creating growing space. Evergreen trees (EGT guild) were also abundant in these snowmelt driven montane streams although these species are not obligate riparian species.

My analysis differs from many North American riparian vegetation studies in that, rather than simplifying floodplain plant communities to dominant native and nonnative species (e.g. *Populus* and *Tamarix;* Sher et al. 2002, Stromberg et al. 2007, Dewine and Cooper 2008), I have identified communities based on woody species composition and trait-based riparian plant guilds. Furthermore, I linked these communities to streamflow, climate, and floodplain alteration. This expands upon individual reach and watershed studies that identify how a few dominant species relate to hydrology and disturbance (Scott et al. 2000, Shafroth et al. 2002, etc.). The landscape scale across which I performed my analyses, highlights that the processes controlling riparian vegetation distributions across the western U.S. vary over large biophysical gradients as well as the local processes that have been documented at individual reaches.

Relating communities and guilds to streamflow

Plant establishment, growth and persistence relate to streamflow magnitude, timing, and duration at a variety of scales (Greet et al. 2011), but landscape-scale studies that link streamflow to riparian vegetation are rare. Across the American West, numerous studies have identified how individual species' distributions (Reynolds et al. 2014, McShane et al. 2015) or physiological performance relate to streamflow (Mahoney and Rood 1998, Rood et al. 2003, Hultine et al. 2010). These studies often compare how streamflow shapes the performance or distributions of non-native invaders like *Tamarisk* and *Elaeagnus* relative to native riparian species like *Acer negundo*, *Platanus wrightii*, *Populus* species, *Salix* species (Sher et al. 2002, Friedman et al. 2005, Mortenson and Weisberg 2010, Reynolds et al. 2014, McShane et al. 2015). These studies link plant physiology to hydrology at small scales or examine a few species' distributions at broad scales. I identified riparian vegetation-flow response guilds from species adaptations to fluvial environments where streamflow creates resource, stress, and disturbance gradients, which allowed us to assess relationships between streamflow and plant functional groups at a heretofore unprecedented spatial scale.

I assessed vegetation guilds alongside communities to identify how functionally similar taxa (guilds) relate to flow within geographically distinct communities of co-occurring species. For example, communities 1-2 and 4-7 had indicator species that included one of four cottonwood species (*P. deltoides, P. angustifolia, P. trichocarpa,* and *P. fremontii*) whose gallery forests were historically common along free-flowing western rivers (Braatne et al. 1996). These communities corresponded to stable flow regimes with dispersed peak flows (Figure 3.8; Figure 3.9) that support the recruitment and growth of cottonwood, regardless of climate (Mahoney and Rood 1998). Cottonwood species were allocated to the mesoriparian tree guild based on their deep roots, rapid life cycles, and need for wind and water to disperse seeds to bare alluvial substrates where individuals germinate and grow to track receding spring floods (Mahoney and Rood 1998). This overlay of guilds to communities shows which dominant life history strategies occur within each community, and how that strategy relates to flow beyond a single community in which it occurs.

Reductions in flood recurrence, magnitude, and/or duration can shift floodplain species dominance from hydrophytic riparian vegetation to drought tolerant species (Johnson 1998). While I did not examine streamflow and vegetation over time to see whether flow alteration changed vegetation composition, streamflow was the only variable that differed between some floodplain communities. Community seven consisted of the mesoriparian tree, *Populus fremontii* (7.7% cover) and drought and disturbance tolerant *Elaeagnus angustifolia* (2.1% cover) and *Tamarix* species (13.5% cover), while community eight had < 1% *Populus fremontii* cover and was dominated by *Tamarix* species (60.1% cover). These communities occurred in similar climates, but average daily streamflow was 15 times greater in community seven than in community eight. Low discharge and variable flow duration may allow *Tamarix* to outcompete *Populus* species that need consistent flow to disperse, establish, and grow to reproductive maturity (Shafroth et al. 2000, Merritt and Poff 2010). To test for the mechanisms behind these observed patterns in discharge and vegetation, I suggest assessing hydrologic and successional dynamics over time. While the patterns I observed are informative, I cannot disentangle whether individual flow events that disturb floodplains, or longer-term flow regimes whose water support plant photosynthesis and growth are responsible for community composition and persistence over time.

Relating communities and guilds to climate

I anticipated that climate would drive riparian vegetation communities' distributions as climatic thresholds limit many riparian species' ranges (Friedman et al. 2005, Ikeda et al. 2014), and isolate populations that evolve into new species over time (Eckenwalder 1996). Communities' distributions were related to the climatic niches of indicator species within each community (Figure 3.3; Figure 3.7; Figure 3.9). While I identified riparian guilds based on their adaptations to streamflow, guilds' growing degree-days and mean annual precipitation influenced guild abundance directly and indirectly, as mediated through streamflow (Figure 3.9).

When modeling changes in riparian guilds at large spatial scales, climate should be considered a direct driver of vegetation alongside flow as watershed precipitation and temperature directly correspond to streamflow duration and timing (Whited et al. 2007). Precipitation, temperature, and streamflow also correspond to species' larger distributions as these attributes often shape plant physiological performance and/or phenology at the edge of their ranges (Morin et al. 2007, Kearney and Porter 2009, Angert 2009). At the edge of a species' range, extremes in climate or hydrology may cause more pronounced asynchrony between dispersal, establishment, and/or growth than at the center of their bioclimatic ranges. Based on these complex interactions, studies of how either climate or hydrology alone influence riparian species or guilds' distributions (e.g. Ikeda et al. 2014) are informative, but likely incomplete.

Hydrology and climate – considerations for future models

I considered how decadal-scale trends in mean annual precipitation and growing degree days influence riparian vegetation directly and as mediated through streamflow. The models found limited connections between climate and hydrology. This may be because the climate trends that I anticipated to correspond to woody vegetation guilds and community distributions do not relate to hydrology as well as climate in the contributing area upstream of that reach. While average watershed precipitation or temperature may be better predictors of hydrology than the same measurements at a single reach, climate data based on decadal averages may be insufficient to predict future change in plant distributions.

Studies that model riparian species' distributions should include climate as a biological driver of plant performance (temperature, precipitation) and climate as it contributes to flow (watershed precipitation timing and form) to more realistically capture the processes that govern species' distributions. Climate data, while viable for identifying relationships between vegetation and precipitation and temperature, was a poor predictor of the composite streamflow variables (PCA ordination axes). Future models could merge numerous climate variables into composite variables, much as I used PCA ordination to represent multiple streamflow metrics. Process-based models (e.g. variable infiltration capacity; Wenger et al. 2010a) may do a better job of incorporating how precipitation type, duration, and quantity translate to streamflow than empirical relationships between climate and streamflow metrics. Future research should be undertaken to explore climate variables that are both biologically and hydrologically meaningful when attempting to decouple the direct and indirect effects of climate on riparian vegetation.

Climate extremes and their associated high-magnitude floods should also be incorporated into future landscape models of riparian vegetation. Anomalous floods and droughts will become more frequent in the future (Hirabayashi et al. 2008), especially across the western U.S. as snow-dominated watersheds' precipitation shifts to winter rainfall (Barnett et al. 2005). These events have a disproportionate capacity to alter floodplain ecosystems as large floods transport large amounts of sediment and water, reworking entire floodplains and valley bottoms. These high magnitude events’ duration and recurrence should be considered in models of floodplain vegetation that project future vegetation distributions. Ideally, future models of riparian vegetation will link individual streamflow and climate events to decadal scale trends in streamflow and climate to assess how short and long-term patterns shape floodplain habitats.

Guilds and floodplain alteration

Riparian vegetation-flow response guilds are grouped based on their flow-related traits and may not be informative groups from which to examine biomass-removing disturbances like wildfire or ungulate grazing. The evergreen tree and mesoriparian shrub and tree guilds all occurred at lower densities in areas with high historic grazing. Grazing directly limits the recruitment of woody seedlings (Fleischner 1994) and reduces mature shrub and tree vigor selecting for species that are more adapted to biomass-removing disturbance than streamflow (Holland et al. 2005). Using the same data that I have here, McShane et al. (2015) found that grazing was only weakly tied to individual species presence and abundance. This difference in my results indicates that multi-species models of guilds or communities may better capture the effects of landscape or floodplain alteration on riparian vegetation diversity than individual species models.

Grazing can also reduce floodplain-channel connectivity, increasing the recurrence time between floods on floodplain landforms and dewatering riparian vegetation (Scott et al. 2003). Within the guild structural model, grazed sites were also sites where functional narrowing had occurred. Additionally, species like *Tamarix* and

Elaeagnus species (drought and disturbance tolerant guild) may cause functional narrowing as their canopy architecture or stem densities lead to floodplain accretion that narrows the active channel and reduces competing hydrophytic guilds' fitness in that environment (Manners et al. 2014).

Communities and guilds – how are these approaches complementary?

Biological communities have been historically viewed as both organism-like (Clements 1916), and individualistically (Gleason 1926). The idea that communities arise based on their individual species' environmental tolerances (Gleason 1926), popularized the use of individual species as indicators of environmental condition. For example, species distribution models predict where a species is likely to occur on a landscape based on that species' climatic niche. However, while floodplain plant species are modeled individually (Ikeda et al. 2014, McShane et al. 2015), they do not usually occur in isolation, but alongside other species with which they interact.

Classifying floodplain vegetation into communities or guilds reduces the complexity of these ecosystems to their representative pieces. Riparian communities and guilds can be used to communicate *what* representative groups of species exist within an ecosystem, and ideally, how those groups relate to the environment. When used to guide land management, ecological communities and their component guilds or species can serve as indicators of environmental change, including grazing (Hough-Snee et al. 2013), hydrologic alteration (Merritt and Cooper 2000), or climate (McDowell and Allen 2015, McDowell et al. 2015). In many management applications, riparian plant community composition is already explained based on individual species' adaptations to streamflow

(Auble et al. 1994), the dominant environmental gradient alongside rivers. Guild-based approaches build on this, by considering species' traits that relate to streamflow earlier in the analytical process.

The guild framework groups species based on their adaptations to streamflow *a priori*. Grouping species into riparian vegetation-flow response guilds allows managers and scientists to explicitly link groups of similar species to hydrology, regardless of which communities they occur in. Across landscapes with large floras, where many species' ranges may not overlap, species with similar hydrologic niches can be modeled against streamflow to better understand or predict the distributions of different riparian plant strategies (Merritt et al. 2010). When examined as assemblages of multiple guilds, riparian guilds can be assessed as meta-communities of the different guilds that occur in different combinations based on streamflow and other disturbances.

While community-based studies can be undertaken from species composition data alone, guild based studies require biological trait data, or ecological trait information about each species. Trait data, while increasingly available in trait databases (Mcgill et al. 2006, Kattge et al. 2011) and presented in ecological contexts (Mcgill et al. 2006), may be unavailable for some species. Missing trait data and limited understandings of species' environmental tolerances may preclude identifying guilds of species with similar responses to flow. In areas that lack species trait data, comparisons of species based on communities and/or dominant species may be less logistically challenging and easier to interpret than guild studies. Additionally, where hydrology interacts with additional disturbances or climatic gradients, models of riparian trait-based guilds may be inaccurate unless they incorporate other environmental filters within that community.

3.5 Conclusion

Communities of co-occurring species and riparian vegetation-flow response guilds are shaped by climate, streamflow, and floodplain alteration across the American West. Communities with abundant drought and disturbance tolerant species occurred at locations with short flood pulses, higher proportions of no-flow days, and floods that are only marginally higher than the average flow. These are flow regimes indicative of hydrologic alteration from the natural flow regime. Montane ecosystems with natural snowmelt pulse flow regimes were more likely to exhibit communities that had mesoriparian shrubs and large, evergreen trees that do not require flood disturbance to complete their lifecycles. The mesoriparian tree guild, which includes *Populus* species that have declined from range-wide flow modification, occurred at reaches with long-duration spring floods that allow them to complete their lifecycle. As climate change and water development alter streamflow in the future, I anticipate that environmental conditions may not support mesoriparian guilds at their historic levels. Guild and community-based analyses should be considered in tandem when land managers attempt to identify whether streamflow alteration has changed floodplain ecosystem composition.

3.6 Acknowledgments

I thank Greg Auble, Jonathan Friedman, Pat Shafroth, Mike Merigliano, and Mike Scott for making data available and reading early drafts of this work. I thank Wally MacFarlane, David Merritt, Emily Palmquist, Barb Ralston, and Alex Walker for meaningful discussions regarding this work and/or reviews of drafts. I was supported in part by STAR Fellowship Assistance Agreement no. 91768201 – 0 awarded by the U.S. Environmental Protection Agency (EPA). This research has not been formally reviewed by the EPA. The views expressed herein are solely those of the authors. EPA does not endorse any products or commercial services mentioned in this publication.

3.6 Tables and Figures

Table 3.1. Summary of environmental variables considered for inclusion in models describing relationships between climate, streamflow and riparian vegetation communities and guilds.

Environmental variable type	Environmental variable (abbreviation in figures)	Units	Median	Mean	Range	
					Min.	Max.
Climate	Growing degree days	°C days	2391.0	2833.0	352.0	8540.0
	Mean annual precipitation	mm	357.0	394.8	75.0	2175.0
Streamflow timing	Peak flow dispersion (r)	Circular scale: 0-1	0.74	0.71	0.07	0.99
	Central tendency of peak flow (d)	Julian date	153.7	153.8	5.5	363.8
	Central tendency Julian date of peak flow minus Julian date of last frost (diff)	Difference in days	4.4	8.7	-176.7	181.0
Streamflow magnitude and variability	2-year recurrence flood discharge (PQ.5)	$m^3 s^{-1}$	44.3	148.9	0.21	6793.2
	5-year recurrence flood discharge (PQ.2)	$m^3 s^{-1}$	93.4	248.5	0.55	8982.1
	10-year recurrence flood discharge (PQ.1)	$m^3 s^{-1}$	140.1	342.9	0.87	10451.8
	25-year recurrence flood discharge (PQ.04)	$m^3 s^{-1}$	196.8	516.9	1.4	12337.7
	Proportion growing season with no flow (NOFLOWG)	Proportion : 0-1	0	0.06	0	0.96
	Mean daily discharge (GDMEAN)	$m^3 s^{-1}$	4.4	37.7	0	3205.0
	Coefficient of variation in daily flow (QDCV)	$m^3 s^{-1}$	4.7	8.2	0.2	8.3
	Skew of daily flow (QDSKEW)	Skew coefficient	0.13	0.30	0.00	2.22
	10% percentile growing season daily flow/grand mean daily (Q10RG)	Dimension-less	0.15	0.22	0.00	7.20
	90% percentile growing season daily flow/grand mean daily (Q90RG)	Dimension-less	2.4	2.5	0.00	1.5

Table 3.1 (cont.)

Environmental variable type	Environmental variable (abbreviation in figures)	Units	Median	Mean	Range	
					Min.	Max.
Disturbance	Past grazing intensity	Ordinal: 1-4	1=297	2=102	3=31	4=13
	Elaeagnus introduction	Binary: 0-1	0=321		1=122	
	Evidence of channel narrowing	Binary: 0-1	0=332		1=111	

Table 3.2. Full species list, abbreviations for species used in figures and tables, frequency of species, and completion of trait availability.

Species abbreviation	Species	Family	Frequency	Traits complete, replaced, or estimated?
ABICON	*Abies concolor*	Pinaceae	2	Complete
ABILAS	*Abies lasiocarpa*	Pinaceae	6	Complete
ACENEG	*Acer negundo*	Aceraceae	78	Complete
ALNINC	*Alnus incana*	Betulaceae	33	Complete
ALNOBL	*Alnus oblongifolia*	Betulaceae	5	Replaced
ALNSIN	*Alnus sinuata*	Betulaceae	21	Complete
ARTTRI	*Artemisia tridentata*	Asteraceae	27	Complete
ATRCAN	*Atriplex canescens*	Chenopodiaceae	3	Complete
BACSAL	*Baccharis salicifolia*	Asteraceae	51	Complete
BETOCC	*Betula occidentalis*	Betulaceae	29	Complete
CELOCC	*Celtis occidentalis*	Ulmaceae	5	Complete
CELRET	*Celtis laevigata* var. *reticulata*	Ulmaceae	21	Complete
CORSER	*Cornus sericea*	Cornaceae	77	Complete
ELAANG	*Elaeagnus angustifolia*	Elaeagnaceae	93	Complete
ELACOM	*Elaeagnus commutata*	Elaeagnaceae	5	Complete
FORNEO	*Forestiera neomexicana*	Oleaceae	10	Replaced
FRAPEN	*Fraxinus pennsylvanica*	Oleaceae	53	Complete
FRAVEL	*Fraxinus velutina*	Oleaceae	19	Replaced
HYMMON	*Hymonclea monogyra*	Asteraceae	12	Complete
JUGMAJ	*Juglans major* / *J. microcarpa*	Juglandaceae	14	Complete
PICSPE	*Picea* species	Pinaceae	18	Replaced
PINPON	*Pinus ponderosa*	Pinaceae	32	Complete
PLAWRI	*Platanus wrightii*	Platanaceae	11	Complete
PLUSER	*Pluchea sericea*	Asteraceae	17	Complete
POPANG	*Populus angustifolia*	Salicaceae	75	Complete
POPDEL	*Populus deltoides*	Salicaceae	88	Complete
POPFRE	*Populus fremontii*	Salicaceae	69	Complete
POPTRE	*Populus tremuloides*	Salicaceae	18	Complete
POPTRI	*Populus trichocarpa*	Salicaceae	47	Complete
PROVEL	*Prosopis velutina*	Fabaceae	39	Replaced
PRUSPE	*Prunus* species	Rosaceae	47	Replaced
PSEMEN	*Pseudotsuga menziesii*	Pinaceae	11	Complete
QUEGAM	*Quercus gambellii*	Fagaceae	6	Complete

Table 3.2. (cont.)

Species abbreviation	Species	Family	Frequency	Traits complete, replaced, or estimated?
QUEMAC	*Quercus macrocarpa*	Fagaceae	5	Complete
RHUTRI	*Rhus trilobata*	Anacardiaceae	23	Complete
ROBNEO	*Robinia neomexicana*	Fabaceae	4	Complete
SALAMY	*Salix amygdaloides*	Salicaceae	93	Complete
SALBON	*Salix bonplandiana*	Salicaceae	2	Complete
SALEXI	*Salix exigua*	Salicaceae	265	Complete
SALGOO	*Salix goodingii*	Salicaceae	49	Complete
SALRUB	*Salix rubens* [*alba* x *fragilis*]	Salicaceae	8	Estimated/ replaced
SALSPP	*Salix* species	Salicaceae	160	Estimated
SHEARG	*Shepherdia argentea*	Elaeagnaceae	37	Complete
TAMAPH	*Tamarix aphylla*	Tamaricaceae	4	Complete
TAMSPP	*Tamarix ramosissima* and *T. chinensis*	Tamaricaceae	124	Complete
THUPLI	*Thuja plicata*	Cupressaceae	4	Complete
ULMAME	*Ulmus americana*	Ulmaceae	17	Complete
ULMPUM	*Ulmus pumilla*	Ulmaceae	28	Complete

Table 3.3. Initial functional and morphological attributes used in the determination of riparian vegetation-flow response guilds. Species' functional and morphological attribute levels and values were acquired from various databases, herbaria records, and flora (USDA NRCS 2010, Kattge et al. 2011). Attributes are grouped by four coarse life history stages: life form, persistence and growth, reproduction, and resource use.

Functional and morphological attributes	Variable type	Dominant life history category	Plant-environment associations in the riparian environment
Growth form	Categorical	Life form	Reflects species' overbank flooding response, canopy spread and light acquisition, asexual reproduction, etc.
Growth habit	Categorical		Indicator of species size and space occupied
Lifespan	Categorical		Indicator of reproduction strategy and stress response
Growth rate	Categorical	Survival and growth	Rate of growth corresponds to water use efficiency and ability to outgrow fluvial disturbance
Anaerobic tolerance	Categorical		Depth, duration and timing of soil saturation from overbank flooding
Salinity tolerance	Categorical		Soil salinization is a common stressor that plants must respond to in dewatered and desert riparian environments
Drought tolerance	Categorical		Species response to seasonal soil drying or moisture deficit
Height at maturity	Continuous		Ability to acquire atmospheric light and CO_2 and resistance to flooding, fluvial shear stress, etc.
Leaf retention	Categorical		Maintenance and construction costs of photosynthetic tissues; evergreen leaves are generally thicker and require a greater investment for construction
Specific leaf area	Continuous		Allocation investment in thick, long-lived, photosynthetically efficient, *costly* leaves or thin, short-lived, *cheap* leaves. Plants likely to be disturbed by floods, often invest less in tissues that can be regrown following biomass removing disturbance
Resprout capacity	Categorical		Regrowth response to fluvial disturbance, flooding, sediment deposition, etc.
Shade tolerance	Categorical		Potential to meet cellular respiration demands by gaining carbon in shaded environments like forest understories
Seed dispersal	Categorical	Reproduct-ion	The mechanism by which a seed disperses (e.g. wind, animals, water) is tied to seed morphology or type
Seed/fruit timing	Categorical		Timing of flowering in response to environmental cues such as spring flooding, etc.
Moisture use	Categorical	Resource use	Required moisture to support transpiration and maintain whole plant water balance
Root depth	Continuous		Potential to acquire soil resources, including deep moisture, nutrients, etc.
Nitrogen fixation	Categorical		Symbiotic relationships with atmospheric nitrogen-fixing bacteria in plant roots allows nitrogen acquisition in nutrient-poor alluvial substrates

Table 3.4. Structural hypotheses between climate and hydrology, and climate, hydrology, and floodplain alteration and riparian vegetation.

Causal pathway group	Hypotheses	References
1. Climate influences stream hydrology.	Precipitation influences the magnitude, duration, and timing of streamflow by providing water through rain and snowfall. As growing degree days increase, stream evaporation and plant transpiration increase. Wet, cool locales have higher daily and peak flood discharges, less variable flow, longer flow duration, and few no-flow days. Hot, dry locations lower daily and peak flood discharges, variable flow, short flow duration, and a greater proportion of days without flow.	Wenger et al. (2010b), Coopersmith et al. (2014), Dhungel et al. (2016)
2. Streamflow influences riparian vegetation communities and riparian flow guilds.	High streamflow magnitude, long peak flow duration, and later peak flow timing are positively correlated to communities with riparian species that have synchronized their dispersal and growth with streamflow.	Auble et al. (1994, 2005), Merritt and Poff (2010), Caskey et al. (2015)
	Low flow, variable flow duration and late peak flow timing will correspond to communities with opportunistic species (guilds), and/or species that can establish following riparian flood disturbance and persist under altered flow regimes (e.g. *Elaeagnus*, *Tamarix*).	
3. Climate influences riparian vegetation communities and guilds.	Cool and wet climates' riparian communities will have more species (guilds) with life history strategies that do not require typical riparian hydrology or disturbance for reproduction or growth.	Sarr and Hibbs (2006), Baker and Wiley (2009), Ikeda et al. (2014), McShane et al. (2015), Hough-Snee et al. (2015b)
	Dry, hot climates' communities will exhibit hydrophytic species (guilds) that require stream hydrology for dispersal and growth due to the difference in floodplains and uplands' hydrology.	
	Where climate and streamflow are correlated, climates that correspond to distinct flow regimes should also predict guilds that correspond to distinct flow regimes.	
4. Floodplain alteration influences vegetation communities and guilds	Anthropogenic land use, including livestock grazing (biomass-removing disturbance), planting of invasive *Elaeagnus* (introduction of a drought-plastic invader), and channel narrowing from dewatering and/or vegetation will correspond to communities with species within guilds that are tolerant of these stressors.	Kauffman et al. (1997), Birken and Cooper (2006), Hough-Snee et al. (2015b)

Table 3.5. Woody plant communities determined through cluster analysis and indicator species analysis. Indicator species for each community cluster were determined using multi-level pattern analysis (De Caceres 2008; α of $p < 0.05$) and are listed from strongest indicator (100) to weakest in each community (0).

Community		Species				
Community 1: *P. deltoides*, *S. amygdaloides*, mixed shrub forest (n = 51)	Sp.	POPDEL	SALAMY	FRAPEN	ACENEG	ELAANG
	IV	90.0	67.9	66.8	60.2	58.7
	Sp.	ULMAME	PRUSPE	QUEMAC	CELOCC	
	IV	44.8	38.9	27.5	27.3	
Community 2: Mixed *Salix*, *Alnus*, *P. trichocarpa*, mixed conifer forest (n = 121)	Sp.	SALSPP	OLW	CORSER	POPTRI	ALNINC
	IV	76.2	70.1	50.9	47.3	38.9
	Sp.	BETOCC	ALNSIN	PINPON	ARTTRI	FRAVEL
	IV	37.5	36.6	33.6	32.4	29.9
	Sp.	PICSPE	PSEMEN			
	IV	29.7	26.3			
Community 3: Mixed *Salix*, *P. ponderosa*, *A. tridentata* shrubland (n = 54)	Sp.	SALEXI	SALSPP	OLW	CORSER	PINPON
	IV	87.6	76.2	70.1	50.9	33.6
	Sp.	ARTTRI				
	IV	32.4				
Community 4: Mixed *Salix*, *C. sericea*, *P. trichocarpa* (n = 42)	Sp.	SALSPP	OLW	CORSER	POPTRI	PRUSPE
	IV	76.2	70.1	50.9	47.3	38.9
	Sp.	PINPON	PICSPE			
	IV	33.6	29.7			
Community 5: *P. angustifolia*, *S. exigua*, mixed *Salix*, mixed shrub and conifer forest (n = 38)	Sp.	POPANG	SALEXI	SALSPP	OLW	CORSER
	IV	93.3	87.6	76.2	70.1	50.9
	Sp.	ALNINC	PRUSPE	RHUTRI	BETOCC	PINPON
	IV	38.9	38.9	37.6	37.5	33.6
	Sp.	ARTTRI	PSEMEN			
	IV	32.4	26.3			
Community 6: *P. deltoides*, *S. exigua*, *S. amygdaloides* gallery forest (n = 41)	Sp.	POPDEL	SALEXI	SALAMY	FRAPEN	ELAANG
	IV	90.0	87.6	67.9	66.8	58.7
	Sp.	PRUSPE	RHUTRI			
	IV	38.9	37.6			
Community 7: *Tamarix*, *P. fremontii*, *Elaeagnus* mixed forest (n = 79)	Sp.	TAMSPP	POPFRE	ELAANG	BACSAL	PROVEL
	IV	92.6	66.5	58.7	57.5	56.7
	Sp.	SALGOO	PLUSER	HYMMON	FRAVEL	
	IV	43.4	38.4	35.8	29.9	
Community 8: *Tamarix*, *Baccharis*, *Prosopsis* forest (n = 17)	Sp.	TAMSPP	BACSAL	PROVEL	SALGOO	
	IV	92.6	57.5	56.7	43.4	

Table 3.6. Summary of morphological attributes and traits by guild. Counts are provided for categorical attributes and means are presented ± standard error for continuous traits.

Dominant life history category	Species' functional and morphological attributes	Levels	Guild (abbreviation)			
			Tall, deeply-rooted evergreen tree guild (EGT guild; n = 6)	Mesoriparian water-dispersed tree guild (MRT guild; n = 11)	Mesoriparian hydrophytic shrub guild (MRS guild; n = 14)	Drought and stress tolerant, deeply rooted, shrub-tree guild (DDT guild; n = 17)
Life form	Growth form	Multiple stem	0	1	11	8
		Rhizomatous	0	0	1	1
		Single stem	6	9	1	7
		Thicket forming	0	1	1	1
	Growth habit	Shrub	0	1	0	7
		Tree	6	9	3	1
		Shrub/small tree	0	1	11	9
	Lifespan	Long	6	0	1	10
		Moderate	0	5	9	5
		Short	0	6	4	2
Survival and growth	Growth rate	Rapid	0	11	12	6
		Moderate	2	0	1	4
		Slow	4	0	1	7
	An-aerobic tolerance	High	0	0	7	0
		Medium	0	7	2	5
		Low	1	3	3	4
		None	5	1	2	8
	Salinity tolerance	High	0	1	2	5
		Medium	1	4	0	5
		Low	1	3	4	3
		None	4	3	8	4
	Drought tolerance	High	1	4	0	9
		Medium	1	4	7	4
		Low	4	3	7	4
	Height at maturity (m)		45.9 ± 6.4	21.6 ± 2.7	7.4 ± 1.1	10.7 ± 2.1
	Leaf retention	Yes	6	0	0	3
		No	0	11	14	14
	Specific leaf area (cm^2/g)		50.3 ± 8.3	139.4 ± 13.1	151.2 ± 15.4	150.2 ± 11.2

Table 3.6. (cont.)

Dominant life history category	Species' functional and morph-ological attributes	Levels	Guild (abbreviation)			
			Tall, deeply-rooted evergreen tree guild (EGT guild; n =6)	Mesoriparian water-dispersed tree guild (MRT guild; n =11)	Mesoriparian hydrophytic shrub guild (MRS guild; n = 14)	Drought and stress tolerant, deeply rooted, shrub-tree guild (DDT guild; n =17)
Survival and growth	Resprout capacity	Yes	0	10	11	15
		No	6	1	3	2
	Shade tolerance	Tolerant	3	2	0	2
		Intermediate	2	1	7	3
		Intolerant	1	8	7	12
Reproduction	Seed dispersal	Achene	0	0	0	2
		Catkin	0	0	4	0
		Cone	6	0	0	0
		Animal dispersed fruit	0	0	2	11
		Hairy	0	5	6	2
		Pod	0	0	2	0
		Small seed	0	0	0	1
		Winged	0	6	0	1
	Seed/fruit timing	Spring	0	9	8	2
		Summer	6	2	6	15
Resource use	Moisture use	High	0	6	10	2
		Medium	6	5	4	9
		Low	0	0	0	6
	Root depth (cm)		74.4 ± 9.4	69.3 ± 8.9	57.2 ± 4.1	58.4 ± 5.3
	Nitrogen fixation	High	0	0	0	1
		Low	0	0	3	0
		Medium	0	0	3	1
		None	6	11	8	15

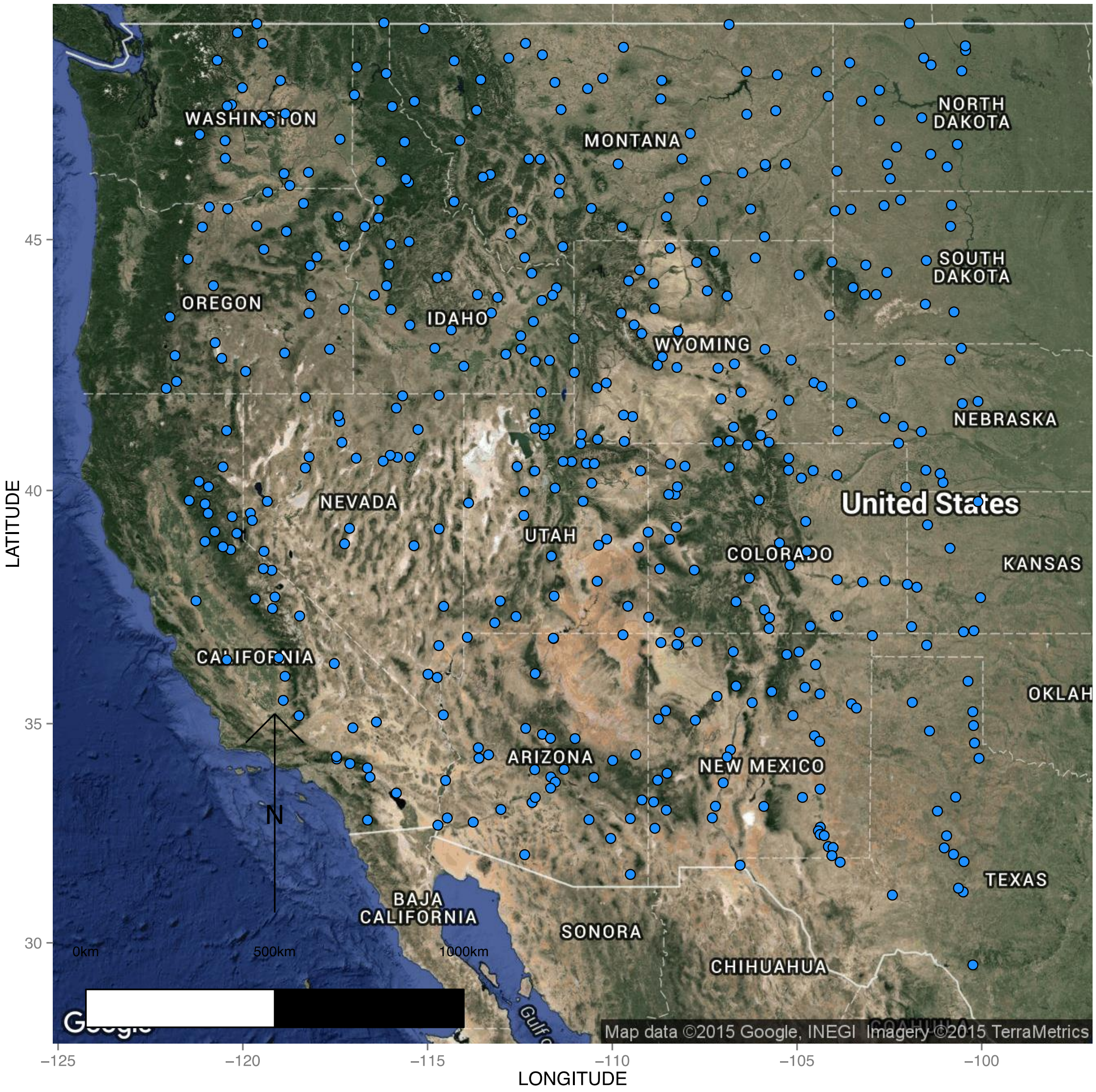

Fig. 3.1. A map of the study area, showing stream gages where floodplain vegetation was sampled between 1997-2002. Daily discharge records existed for at least twenty years at each gage. Watershed boundaries are outlined for the Columbia, Missouri, Arkansas, Texas-Gulf, Rio Grande, Colorado, Great Basin, and California regions of the U.S. Of the 456 sampled reaches only 443 were used in community analyses due to a lack of woody vegetation

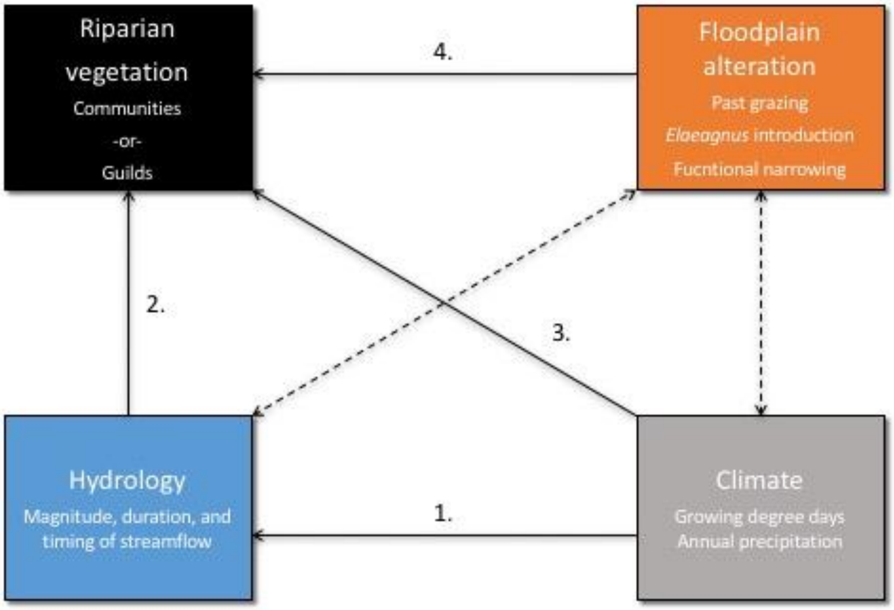

Fig. 3.2. Structural metamodel of hypotheses tested using causal models. Models are for the relationships between (1) climate and hydrology (2) hydrology and vegetation, (3) climate and vegetation, (4) disturbance and vegetation, and (5) biotic interactions within guilds. Diagrams are for floodplain riparian plant communities (top), and between climate, hydrology, disturbance and riparian vegetation guilds (bottom).

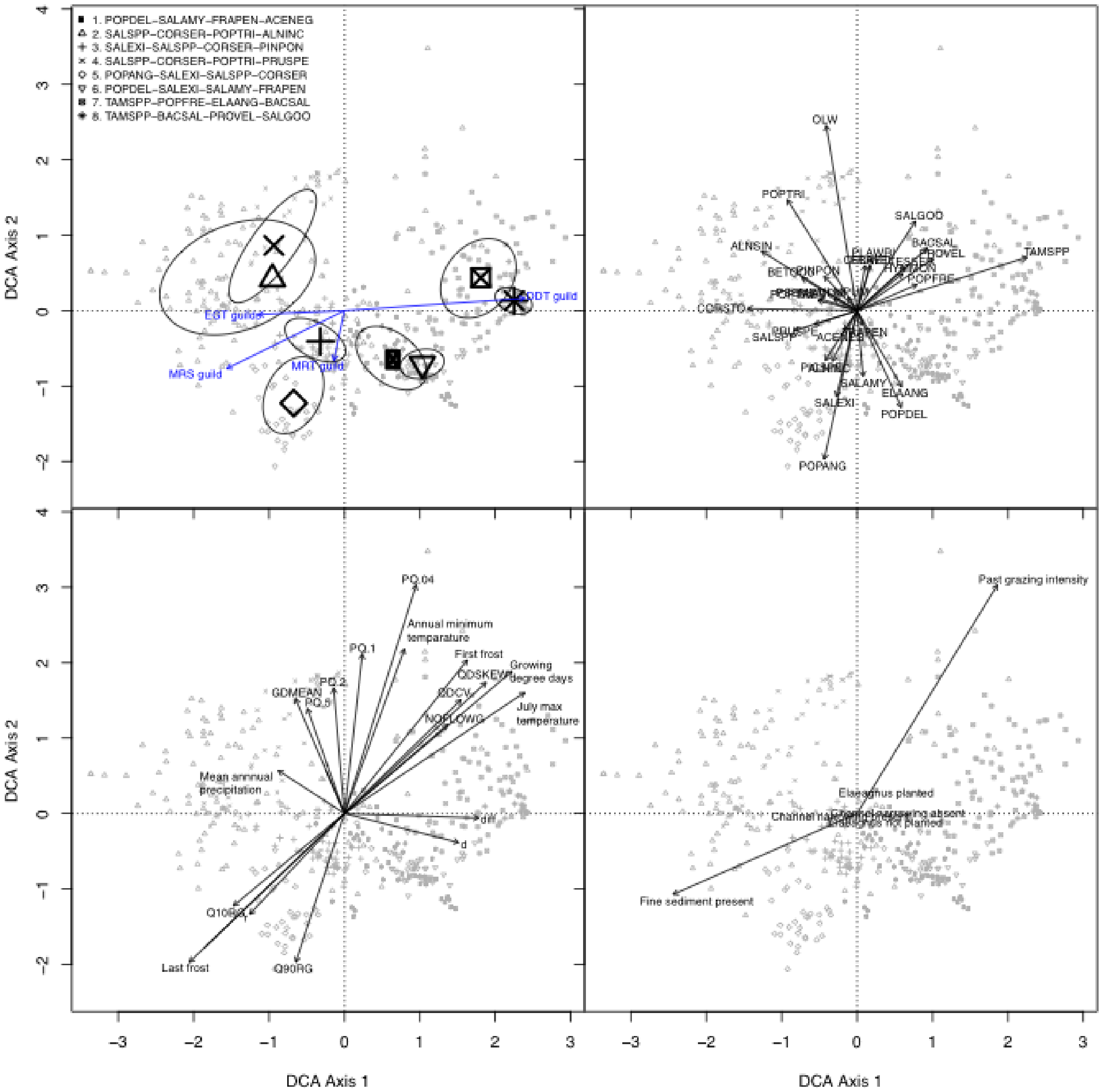

Fig. 3.3. Communities displayed in the first two axes of a detrended correspondence analysis ordination of individual reaches' species composition (grey points) and community centroids (black shapes in top left panel) and their correlations to (top left panel) guilds (blue vectors), (top right) species, (bottom left) hydrology and climate, and (bottom right) disturbance indicators. Polygon hulls in the top left panel indicate standard deviation of clustered communities.

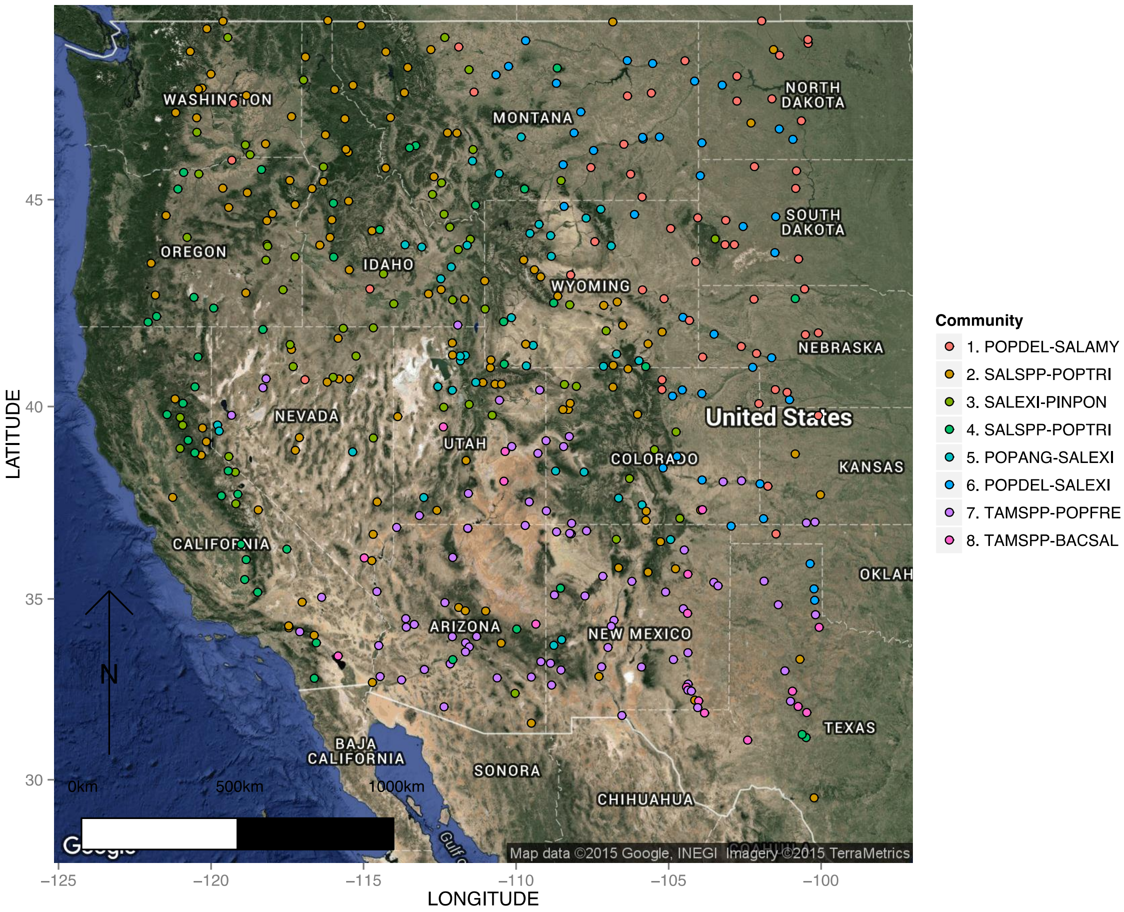

Fig. 3.4. Distributions of the eight identified riparian vegetation communities across the western United States showed strong geographic grouping that corresponded to climate, hydrology and disturbance.

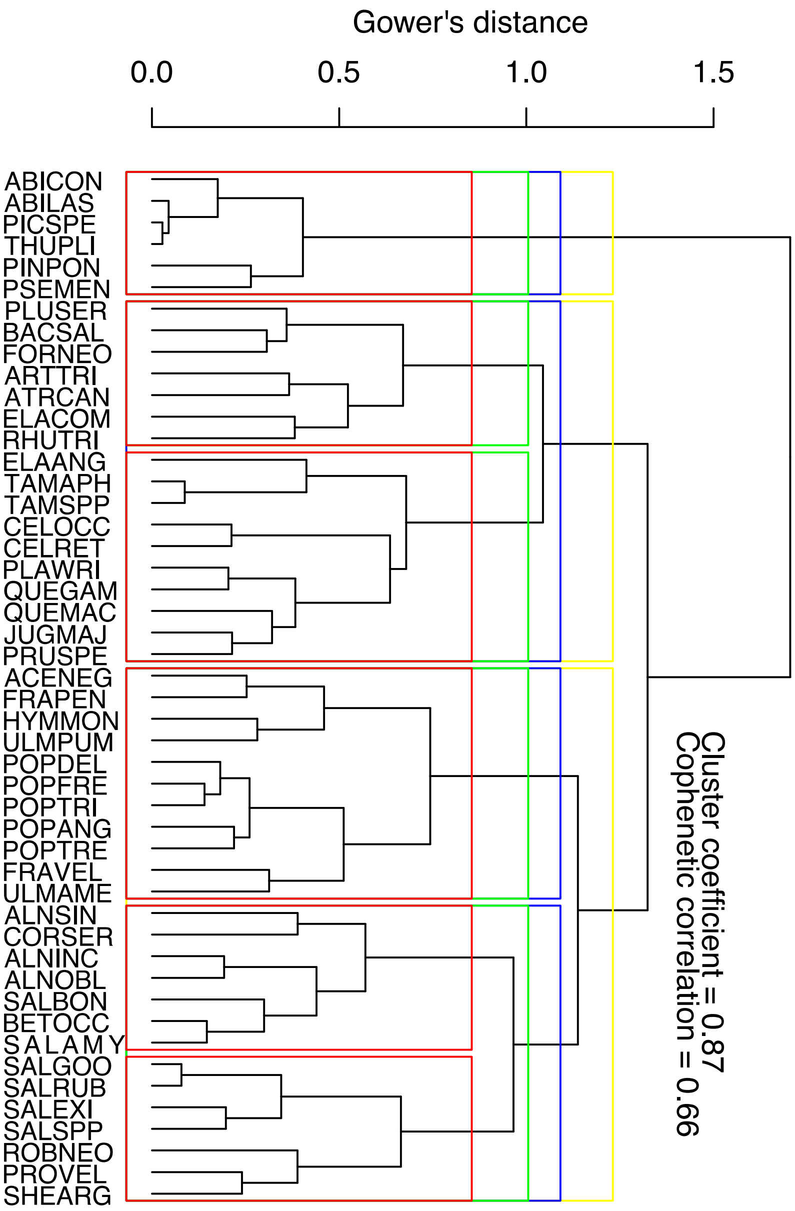

Fig. 3.5. Riparian vegetation guilds were identified using cluster analysis of species by traits and morphological attributes (Gower's distance; Ward's method for clustering). Boxes correspond to three (yellow), four (blue), five (green) and six (red) guilds. Four guilds were used in analyses (from left to right): a tall, long-lived, deeply rooted evergreen tree guild, a summer-dispersed, drought-tolerant, disturbance resistant shrub and tree guild, a mesoriparian, hydrophytic, hydrochorous tree guild, and a mesoriparian resprouting, wind and water dispersed shrub guild.

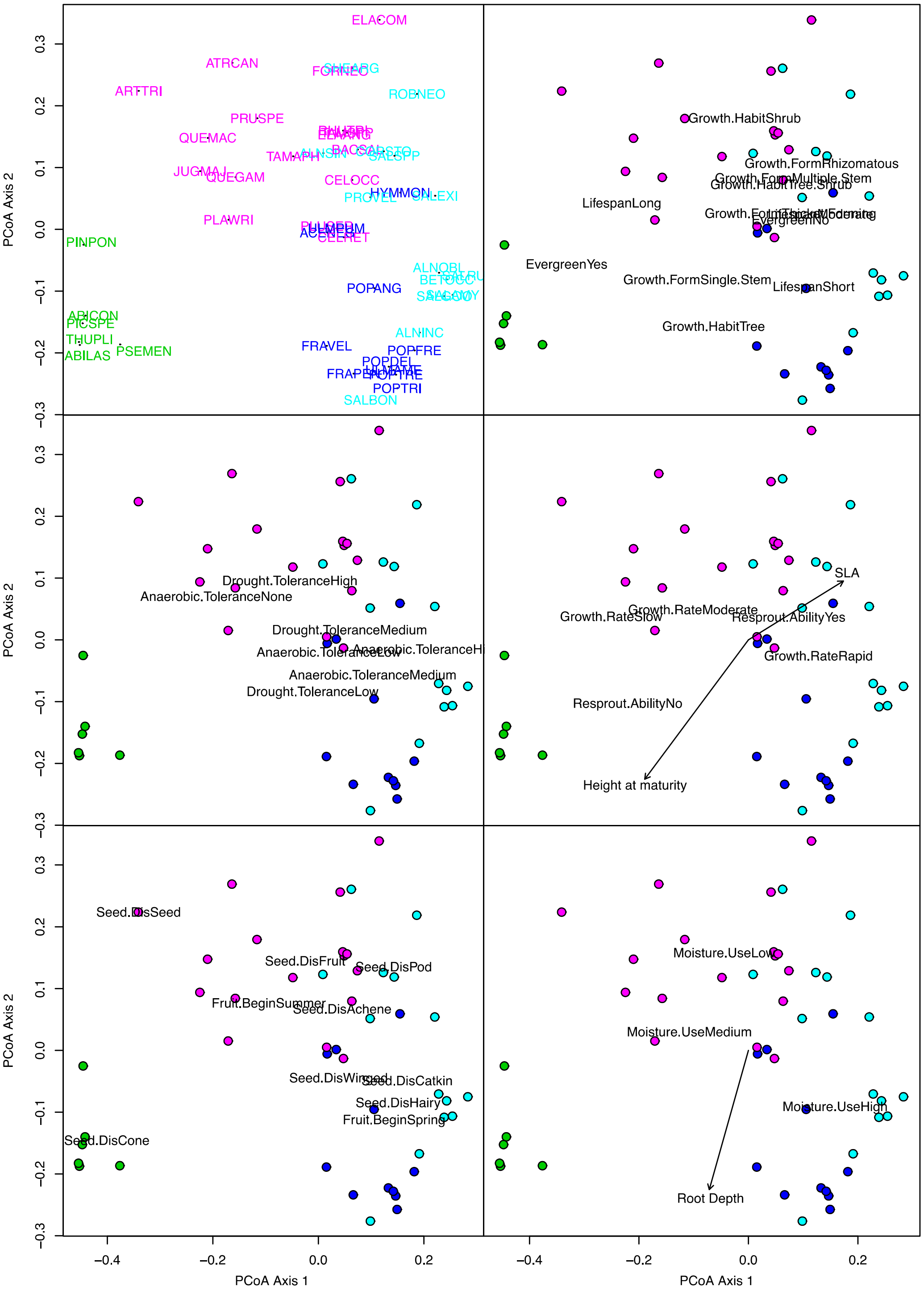

Fig. 3.6. Principal coordinates analysis of plant species clustered into riparian vegetation-flow response guilds based on their morphological attributes and physiological traits. Panels correspond to (a) species, traits in the (b) life form, (c and d) survival and growth, (e) reproduction, and (f) resource use groups.

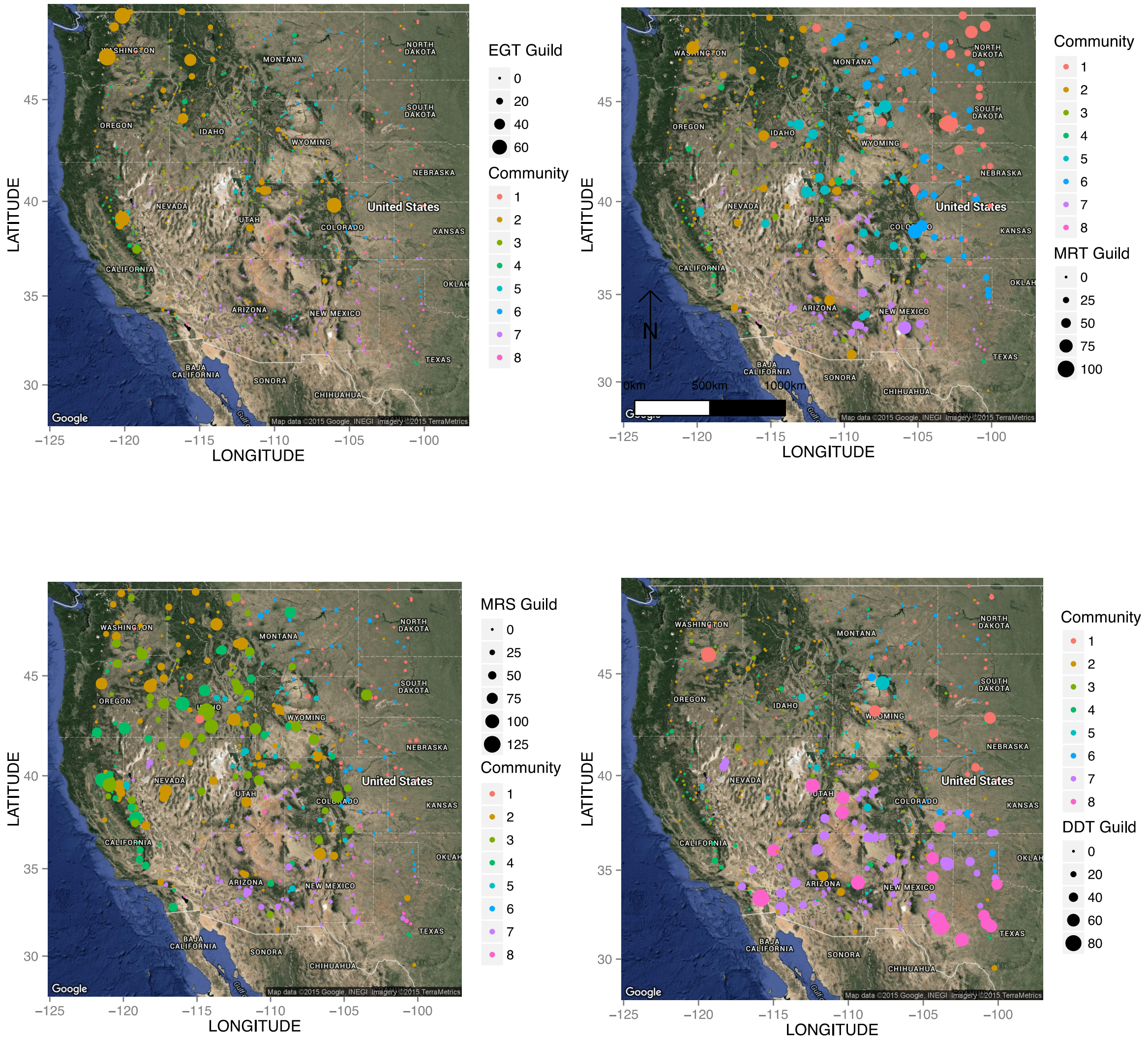

Fig. 3.7. The distributions of identified riparian vegetation communities (point colors), overlain with point size corresponding to guild relative abundance at a given reach: (a) large, evergreen tree guild, (b) mesoriparian tree guild, (c) mesoriparian shrub guild, and (d) drought and disturbance tolerant tree and shrub guild. Note that point size scales to guild relative cover for each map. Scale differs between guilds.

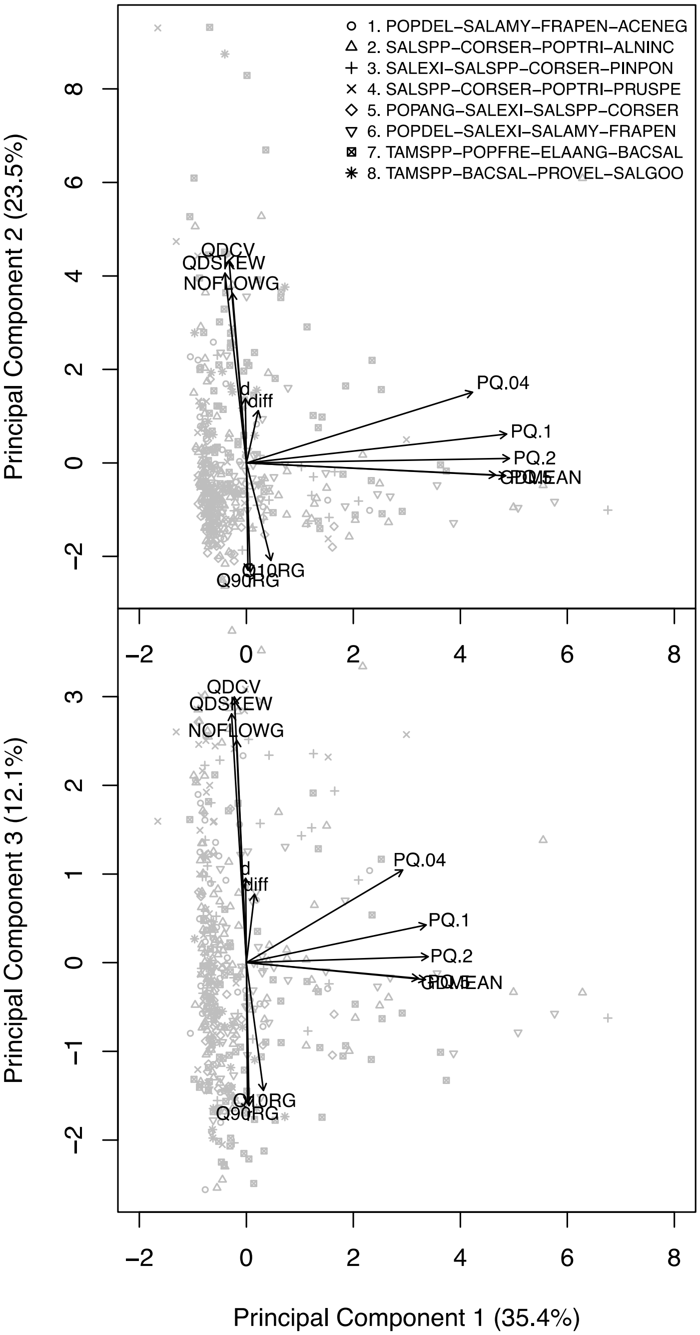

Fig. 3.8. Principal component analysis of streamflow variables showed that the first three principal components corresponded to (1) mean daily flow and peak flood discharge, (2) flow variability and duration, and (3) flow timing. These principal components represented stream hydrology in structural equation models of vegetation.

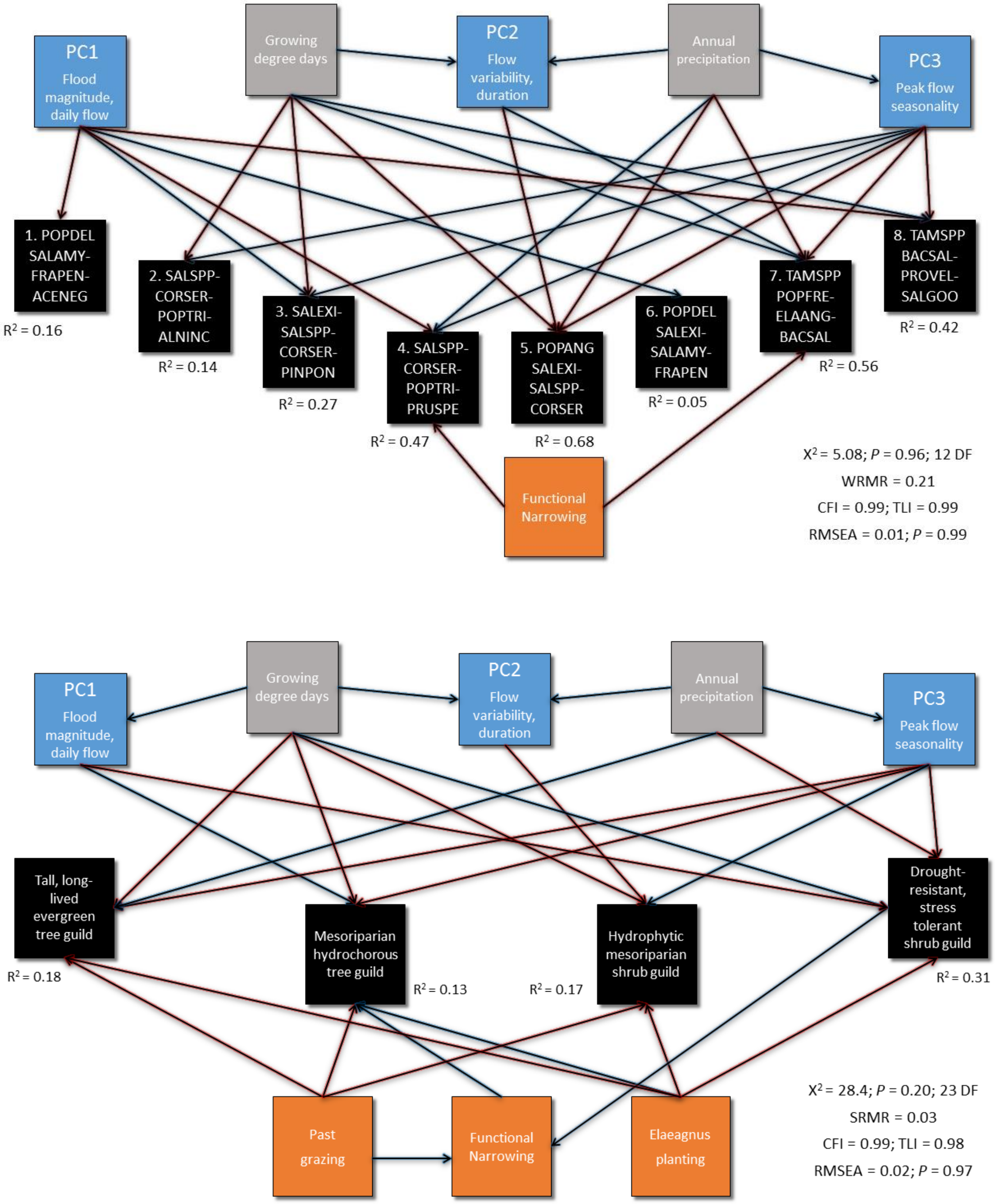

Fig. 3.9. Causal models explaining (top) the relationships between climate, hydrology, disturbance and riparian communities, and (bottom) the relationships between climate, hydrology, disturbance, and guilds, and guilds on channel downcutting. Blue and red arrows indicate significant (α of $P < 0.1$) positive and negative pathways respectively.

CHAPTER 4

SUMMARY, FUTURE APPLICATIONS, AND CONCLUSIONS

4.1. Guilds and ecological inference across the western United States

Guild-based analyses allow scientists to aggregate species from within a given flora into distinct groups based on their responses to environmental resources, stress, and disturbance. Guilds allow scientists to make inference at a resolution that is distinct from individual species, groups of closely phylogenetically related taxa, and communities of species that coexist on the landscape (Simberloff and Dayan 1991). Here I identified guilds of floodplain woody species based on their environmental tolerances and physiological and morphological attributes that allow them to persist amid flooding, drying, and disturbance. These guilds were then placed into landscape and community contexts to understand how riparian plants' life history strategies are distributed across the landscape and within which communities they occur.

In Chapter Two, I examined how guilds occupy distinct bioclimatic niches across the interior Columbia and upper Missouri River basins and documented guild assemblages' environmental correlates. Previously, I studied the same riparian vegetation communities, using indicator species (Dufrêne and Legendre 1997) to make inference about which species are most common within each community (Hough-Snee et al. 2015b). By explaining individual species' niches within a community, I discussed how community composition shifted across landscape and watershed environmental gradients. However, this approach required *post hoc* interpretation of why species occurred where they did. It also failed to mechanistically tie species' traits to important resource and disturbance gradients. By linking trait-based guilds to the environment, species' suites of traits can be linked to environmental stress and resources that dictate the ranges of some life history strategies.

In Chapter Three, I found that when examined at sub-continental scales, guilds aggregated many closely-related species. These included the genera *Salix* within the mesoriparian shrub guild, and *Populus* within the mesoriparian tree guild, and coniferous, evergreen gymnosperms in the large, evergreen tree guild (largely within Pineaceae). These guilds' species evolved to occupy distinct hydroclimatic niches across western North America. The species within these guilds are, in many cases, both phylogenetically and functionally similar. This implies that, for certain groups of taxa with distinct niches, phylogenetic relatedness may be an acceptable proxy for functional relatedness of species. Within riparian ecology, *Salix* and *Populus* have often been grouped together for studies of stream condition or landscape change, as they often respond similarly to changes in hydrology and disturbance (Dwire et al. 2004, Booth et al. 2012, Hough-Snee et al. 2013). Aggregating these species may be acceptable at broad, landscape scales, or when comparing riparian species to xeric upland species (e.g. *Juniperus* spp., *Artemisia* spp., etc.). However aggregating species by genus or family may be too coarse to be informative when studying individual floodplains where closely related species with similar hydroclimatic niches are separated by small resource and disturbance gradients (Rossell et al. 2009, Biederman and Whisenant 2011, Hough-Snee et al. 2011).

4.2. Limitations to determining guilds

The guild concept was introduced prior to modern computing in ecology (Root 1967), and provides a conceptual frame from which to study many species based on their functional similarity (Simberloff and Dayan 1991). Historic limitations to defining guilds of species included a lack of computing power and effective multivariate methods for quantitatively defining guilds. These limitations encouraged ecologists to groups species into guilds based not on quantitative traits, but general ecological strategies (e.g. foraging strategy, beak or seed type) or coarse descriptors of species' life history strategies (Simberloff and Dayan 1991). While advances in statistical methods and a growth in trait data have overcome these early limitations, subjectivity still permeates the process of defining guilds, much as Root argued that it should (Root 1967). For example, which traits are used to allocate species into guilds, which statistical methods are used to separate guilds, or how species' relative tolerances are defined (i.e. "low," "medium," "high"), all require considerable statistical, botanical, and ecological expertise. Within analyses like cluster analysis or ordination, which groups are treated as guilds is sensitive to what trait information is available and included, and what similarity measure and distance criteria are used to aggregate groups of species.

Ecologists identifying riparian flow-response guilds are often limited by a lack of species' trait data that reflect water balance, dispersal, or growth and energy balances as related to streamflow (Merritt et al. 2010). Quantitative traits, measured plant morphological or physiological attributes within an individual, have been collected for many species, and increasingly these measurements have been aggregated into large databases (e.g. Kattge et al. 2011, Aguiar et al. 2014). In many cases, these databases include common species, common traits, or both, limiting how many species can be allocated into guilds and which traits can be used to do this. This may lead to guilds being based on incomplete trait data or sets of species, or both. In Chapter Two, a lack of herbaceous species data for most species actually precluded the use of non-woody species guilds. In both Chapters Two and Three, categorical proxies for water balance traits were used because this data was largely unavailable. These categorical proxies are subjective and introduce bias based on the expertise of the individuals ranking ordinal ecological traits. In many cases, these categorical proxies may be the dominant performance attributes available for rare species.

While some species lack trait data for a given metric, other species have a wide range of values for one or more traits. This is not unanticipated, as any measured physiological or morphological parameter should, when measured in multiple populations and environmental conditions, reflect the genotypic and phenotypic diversity of that species. Incorporating this trait plasticity into guilds, as well as allocating species life stages into different guilds, are critical steps in effectively capturing how flow shapes riparian vegetation. Additionally, in many cases, it is not well known which trait or a family of traits, are most responsible for a species or guilds' persistence over the lifetime of the organism.

For example, the flow regimes required for *Populus* species to establish as seeds and grow as seedlings, versus the flows required to sustain transpiration costs from photosynthesis in mature trees may differ widely. In this way, a week-old individual of one species should probably not be considered in the same guild as a decadent, mature individual of the same species. Dispersal, growth, and reproduction are all important components to an individual plants' passing of genes onward over time, but vary in importance at different life history stages. Incorporating time into models of guilds' growth and reproduction may capture the establishment, growth, and mortality of individuals within a given guild at a given life stage. Incorporating transitions between life stages into guild-based models may be difficult, as structured population models of riparian species are still rare (Lytle and Merritt 2004) as the traits and vital rates of many riparian species are not well known.

4.3. Future application and opportunities

When proposed by Merritt et al. (2009, 2010), the riparian vegetation-flow response guild concept was presented as a decision-support tool in which land managers or natural resource scientists could group species based on their adaptations to stream flow, probabilistically modeling their presence and abundance within a floodplain (Merritt et al. 2009, 2010). By identifying how flow alteration changes the abundance of specific guilds, land managers can make informed decisions about how flow allocation may change the shifting floodplain mosaic (Kattge et al. 2011). For example, as flows are reduced, mesoriparian shrub or tree guilds (Chapter Three) may decline while the drought and disturbance tolerant guild increases in abundance as suitable, dewatered habitat expands.

These analyses inform the probable trajectories of floodplain surfaces in response to hydrologic change. By assessing flow and vegetation concurrently over time, more complete inference can be made about how groups of species' distributions will change in response to climatic and/or streamflow modification. Reach-scale structured population models, individual-based models, or mechanistic models of how spatially-explicit processes like flooding and drying influence community dynamics within a floodplain, have potential to provide insights into streamflow driven floodplain competition and succession. Additionally, coupling guilds' size and stem and root architecture with hydrology and sediment transport may provide insight into how sediment is eroded and deposited on floodplains (Manners et al. 2014) during succession. These two-way interactions between flow and vegetation can be modeled spatially through multiple floods to look at how flood events shape populations of organisms, landform evolution, and community development.

4.4. Conclusions

I determined that multiple vegetation guilds occur on the landscape as a product of distinct hydrology, climate, disturbance, and biotic interactions. Guilds ranged from small-statured, shade tolerant plants that coexist with overstory trees, to obligate hydrophytes that specialize at tolerating floods and distributing propagules during floods. These guilds had similar hydrologic and climatic niches, but the way these species respond to floodplain alteration and upland disturbance gradients differed. These studies allowed me to make inference about how climate, hydrology, and disturbance shape guild assemblages and communities across western North America. The guild framework allows for a flexible framework to explore how plant species that occur in floodplains respond to environmental gradients. By modeling these relationships under anticipated climate or disturbance regimes, informed hypotheses can be created about how riparian ecosystems might change over time as climate and land use change. Riparian guilds provide a unifying starting point for making inference about how groups of riparian plant species may change as climate, streamflow and disturbance regimes do.

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APPENDICES

APPENDIX A

SUPPLEMENTS TO CHAPTER TWO

Table S.2.1. Summary of the categorical, morphological and physical attributes by guild. Counts of each attribute level are presented for each guild.

Life history and morphological attributes	Levels	Guild				
		Evergreen tree	Upland disturbance shrub	Mesic shrub	Meso-riparian tree and shrub	Understory shrub
Growth form	Multiple stem	0	4	5	6	2
	Rhizomatous	0	3	1	1	3
	Single stem	7	0	0	1	2
	Thicket forming	0	2	3	0	2
Lifespan	Long	7	1	2	1	6
	Moderate	0	8	5	6	1
	Short	0	0	2	1	2
Adapted to coarse textured soils	No	2	0	4	1	5
	Yes	5	9	5	7	4
Adapted to fine textured soils	No	5	9	1	0	5
	Yes	2	0	8	8	4
Adapted to medium textured soils	No	0	0	0	0	2
	Yes	7	9	9	8	7
Anaerobic tolerance	High	0	3	1	1	1
	Low	3	3	5	1	3
	Medium	0	2	2	5	2
	None	4	1	1	1	3
Drought tolerance	High	1	0	0	0	2
	Low	5	0	7	6	6
	Medium	1	8	1	1	1
	None	0	1	1	1	0
Growth rate	Moderate	3	5	1	3	6
	Rapid	1	4	8	5	2
	Slow	3	0	0	0	1
Leaf retention	No	0	8	9	8	8
	Yes	7	1	0	0	1
Resprout ability	No	7	0	2	0	1
	Yes	0	9	7	8	8
Shade tolerance	Intermediate	2	5	6	1	1
	Intolerant	1	2	0	6	1
	Tolerant	4	2	3	1	7

Table S.2.1 (cont.)

Life history and morphological attributes	Levels	Guild				
		Evergreen tree	Upland disturb-ance shrub	Mesic shrub	Meso-riparian tree and shrub	Understory shrub
Vegetative spread rate	Moderate	0	6	3	4	2
	None	7	1	2	0	4
	Rapid	0	0	1	1	2
	Slow	0	2	3	3	1
Bloom period	ESpring	0	1	1	0	1
	ESummer	0	2	1	2	2
	LSpring	3	3	2	2	3
	MSpring	3	0	1	1	1
	MSummer	1	1	0	0	0
	Spring	0	0	4	1	1
	Summer	0	2	0	2	1
Fruit/seed abundance	High	4	4	4	6	0
	Low	0	1	3	1	2
	Medium	3	4	2	0	7
	None	0	0	0	1	0
Fruit/seed period begin	Spring	0	1	9	1	2
	Summer	7	8	0	7	7
Fruit /seed persistence	No	6	9	7	8	3
	Yes	1	0	2	0	6
C:N ratio	High	7	7	3	4	2
	Low	0	0	0	1	1
	Medium	0	2	6	3	6
Moisture use	High	0	4	8	7	4
	Low	0	4	1	0	0
	Medium	7	1	0	1	5
Live staking	Excellent	0	0	0	2	0
	Fair	0	2	2	2	5
	Fair-good	0	1	0	2	0
	Good	0	1	0	0	1
	None	7	5	5	0	3
	Very good	0	0	2	2	0
Nitrogen fixation	Medium	0	1	1	0	0
	None	7	8	8	8	9
Fire tolerance	High	2	6	9	4	3
	Low	5	2	0	0	1
	Medium	0	1	0	4	5

Table S.2.2. Correlations between species' life history traits and the principal coordinate analysis ordination.

Primary trait group	Trait	R^2	*P*
Life form	Growth form	0.32	0.0001
	Lifespan	0.27	0.0001
Persistence and growth	Adapted coarse textured soils	0.16	0.0001
	Adapted fine textured soils	0.21	0.0001
	Adapted medium textured soils	0.08	0.0235
	Anaerobic tolerance	0.15	0.0289
	Drought tolerance	0.24	0.0003
	Fire tolerance	0.28	0.0001
	Growth rate	0.32	0.0001
	C:N ratio	0.21	0.0001
	Height at maturity	0.70	0.0001
	Leaf retention	0.36	0.0001
	Resprout ability	0.25	0.0001
	Shade tolerance	0.16	0.0032
	Vegetative spread rate	0.27	0.0001
Reproduction	Bloom period	0.26	0.1950
	Fruit seed abundance	0.14	0.0367
	Fruit seed period begin	0.12	0.0031
	Fruit seed persistence	0.09	0.0102
	Live staking	0.23	0.0160
Resource use	Moisture use	0.36	0.0001
	Root depth	0.45	0.0001
	Nitrogen fixation	0.03	0.3175

Table S.2.3. Goodness-of-fit statistics for environmental filters and riparian guilds fit to the NMDS ordination solution for guild assemblages. These filters and guilds are plotted to the ordination solution in Figure 2.3. Filters followed by ^ were not used in conditional inference trees or generalized linear models due to collinearity with other variables or a lack of initial hypotheses on how the filter would correlate to riparian guild distributions.

Scale	Variable	R^2	*P*
Landscape-scale filters	AnnPrecip	0.04	0.0001
	AvgPrecip^	0.05	0.0001
	AvgTemp	0.03	0.0001
	MeanElev^	0.08	0.0001
	MinElev	0.12	0.0001
	MaxElev^	0.08	0.0001
Watershed- and buffer-scale filters	StreamDens^	0.01	0.1793
	BufRoads	0.03	0.0004
	BufForested	0.06	0.0001
	BufSlope	0.15	0.0001
	BufGrazed	0.04	0.0001
	Watershed Area	0.03	0.0003
	Watershed Burned	<0.01	0.6537
	AvgWaterTable	0.01	0.0221
	AvgSoilThick	0.01	0.0480
Stream-scale filters	BankStability^	0.02	0.0078
	Gradient	0.08	0.0001
	Sinuosity	0.09	0.0001
	BFWidth	0.04	0.0001
	Hydraulic Radius	0.02	0.0041
	Bank Angle	0.02	0.0123
	WetWDRatio	0.02	0.0053
	UndercutBank	0.01	0.0174
Riparian guilds	Evergreen tree	0.06	0.0001
	Upland disturbance	0.35	0.0001
	Mesic shrub	0.09	0.0001
	Understory shrub	0.32	0.0001
	Mesoriparian shrub and tree	0.33	0.0001

Table S.2.4. Alternative plausible generalized linear models as determined by AIC.

Guild (short guild name)	Final model terms (effect)	AIC	Δ AIC	Log-likelihood	Pseudo R^2	
					Cragg and Uhler	Max. likelihood
Long-lived, deeply-rooted, tall, shade tolerant, evergreen trees (evergreen tree guild)	WatershedArea (-0.01) AvgTemp (-0.10) AnnPrecip (1.04) BufForested (0.06) WatershedBurned (-0.01) BufRoads (0.17) BufSlope (-0.05) WetWDRatio (0.03) Sinuosity (-0.95) Gradient (0.18) AvgWaterTable (-0.97) UD (0.61) US (0.88) MR (-0.51)	591.59	3.83	-280.80	0.42	0.28
	WatershedArea (-) AvgTemp (-) AnnPrecip (+) MinElev (-) BufForested (+) WatershedBurned (-) BufRoads (+) BufSlope (-) WetWDRatio (+) Sinuosity (-) Gradient (+) AvgWaterTable (-) UD (+) US (+) MR (-)	593.06	5.3	-280.53	0.42	0.28
	WatershedArea (-) AvgTemp (+) AnnPrecip (+) MinElev (-) BufForested (+) WatershedBurned (-) BufRoads (+) BufSlope (-) WetWDRatio (+) Sinuosity (-) Gradient (+) AvgWaterTable (-) UD (+) US (+) MR (-) AvgTemp:AnnPrecip (-) AvgTemp:MinElev (+) AnnPrecip:MinElev (+) AvgTemp:MinElev:AnnPrecip (-)	589.31	1.55	-274.65	0.44	0.30
	WatershedArea (-) AvgTemp (-) AnnPrecip (-) MinElev (-) BufForested (+) WatershedBurned (-) BufRoads (+) BufSlope (-) WetWDRatio (+) Sinuosity (+) Gradient (+) AvgWaterTable (-) UD (+) US (+) MR (-) AnnPrecip:MinElev (+)	587.76	0	-276.88	0.43	0.29

Table S.2.4. (cont.)

Guild (short guild name)	Final model terms (effect)	AIC	Δ AIC	Log-likelihood	Pseudo R^2	
					Cragg and Uhler	Max. likelihood
Rapidly growing, multi-stemmed, rhizomatous and thicket-forming, drought-plastic, shrub guild (upland disturbance guild)	WatershedArea (-0.00) AvgTemp (0.11) BufForested (0.01) BufSlope (-0.10) BankAngle (-0.05) BfWidth (0.20) WetWDRatio (0.02) Gradient (0.40) AvgWaterTable (-0.83) BufSlope:BankAngle (0.00) BfWidth:WetWDRatio (-0.00) ET (0.57)	760.70	0	-367.34	0.23	0.16
	WatershedArea (-) AvgTemp (+) BufForested (+) BufSlope (-) BankAngle (-) BfWidth (+) WetWDRatio (+) Gradient (+) AvgWaterTable (-) BufSlope:BankAngle (+) BfWidth:WetWDRatio (-) ET (+) MR (+)	760.77	0.07	-366.39	0.24	0.17
	WatershedArea (-) AvgTemp (+) BufForested (+) BufSlope (-) BankAngle (-) BfWidth (+) WetWDRatio (+) Gradient (+) AvgWaterTable (-) BufSlope:BankAngle (+) BfWidth:WetWDRatio (-) ET (+) AvgSoilThick (+)	761.43	0.73	-366.72	0.23	0.17

Table S.2.4. (cont.)

Guild (short guild name)	Final model terms (effect)	AIC	Δ AIC	Log-like-lihood	Pseudo R^2	
					Cragg and Uhler	Max. like-lihood
Low-stature, hydrophytic, multi-stemmed thicket forming shrubs (mesic shrub guild)	WatershedArea (-0.00) AvgTemp (-0.39) AnnPrecip (-0.80) MinElev (-0.00) BufSlope (0.28) BankAngle (0.04) BfWidth (0.17) WetWDRatio (-0.00) Sinuosity (-0.56) BfWidth:WetWDRatio (-0.00) BufSlope:BankAngle (-0.00) US (0.63) MR (0.74)	376.25	0	-174.13	0.31	0.15
	WatershedArea (-) AvgTemp (-) AnnPrecip (-) MinElev (-) BufSlope (+) BankAngle (+) BfWidth (+) WetWDRatio (-) Sinuosity (-) BfWidth:WetWDRatio (-) BufSlope:BankAngle (-) US (+) MR (+)AvgWaterTable (+) AvgSoilThick (-)	377.16	1.96	-173.02	0.31	0.15
	WatershedArea (-) AvgTemp (-) AnnPrecip (-) MinElev (-) BufSlope (+) BankAngle (+) BfWidth (+) WetWDRatio (-) Sinuosity (-) BfWidth:WetWDRatio (-) BufSlope:BankAngle (-) US (+) MR (+) AvgWaterTable: AvgSoilThick (+)	379.12	2.87	-172.56	0.31	0.15

Table S.2.4. (cont.)

Guild (short guild name)	Final model terms (effect)	AIC	Δ AIC	Log-like-lihood	Pseudo R^2	
					Cragg and Uhler	Max. like-lihood
Medium-deeply rooted, vegetatively reproducing shrubs and trees (meso-riparian shrub and tree guild)	AvgTemp (-0.43) AnnPrecip (-0.66) MinElev (-0.00) BufGrazing (0.01) BufRoads (0.12) BufSlope (0.05) BfWidth (0.12) Gradient (0.18) AvgSoilThick (1.73) ET (-0.51) MS (0.67) US (0.68)	657.50	0	-315.73	0.26	0.17
	AvgTemp (-) AnnPrecip (-) MinElev (-) BufGrazing (+) BufRoads (+) BufSlope (+) BfWidth (+) Gradient (+) AvgSoilThick (+) ET (-) MS (+) US (+) AvgWaterTable (+)	659.31	1.81	-315.65	0.26	0.17
	AvgTemp (-) AnnPrecip (-) MinElev (-) BufGrazing (+) BufRoads (+) BufSlope (+) BfWidth (+) Gradient (+) AvgSoilThick (+) ET (-) MS (+) US (+) Sinuosity (-)	659.42	1.92	-315.72	0.26	0.17
Short-statured, shade-tolerant, water stress and flooding intolerant understory shrubs (understory guild)	WatershedArea (-0.00) AvgTemp (-0.23) AnnPrecip (-4.12) MinElev (-0.01) BufForested (-0.01) BufRoads (0.16) BufSlope (0.04) BankAngle (-0.01) Gradient (0.48) AnnPrecip:Elev (0.00) ET (0.87) MS (0.68) MR (0.83)	581.67	0	-276.83	0.33	0.21
	WatershedArea (-) AvgTemp (-) AnnPrecip (-) MinElev (-) BufForested (-) BufRoads (+) BufSlope (+) BankAngle (-) Gradient (+) AnnPrecip:Elev (+) ET (+) MS (+) MR (+) AvgSoilThick (+)	583.31	1.64	-276.65	0.33	0.22
	WatershedArea (-) AvgTemp (-) AnnPrecip (-) MinElev (-) BufForested (-) BufRoads (+) BufSlope (+) BankAngle (-) Gradient (+) AnnPrecip:Elev (+) ET (+) MS (+) MR (+) AvgWaterTable (-)	583.63	1.96	-276.81	0.33	0.21

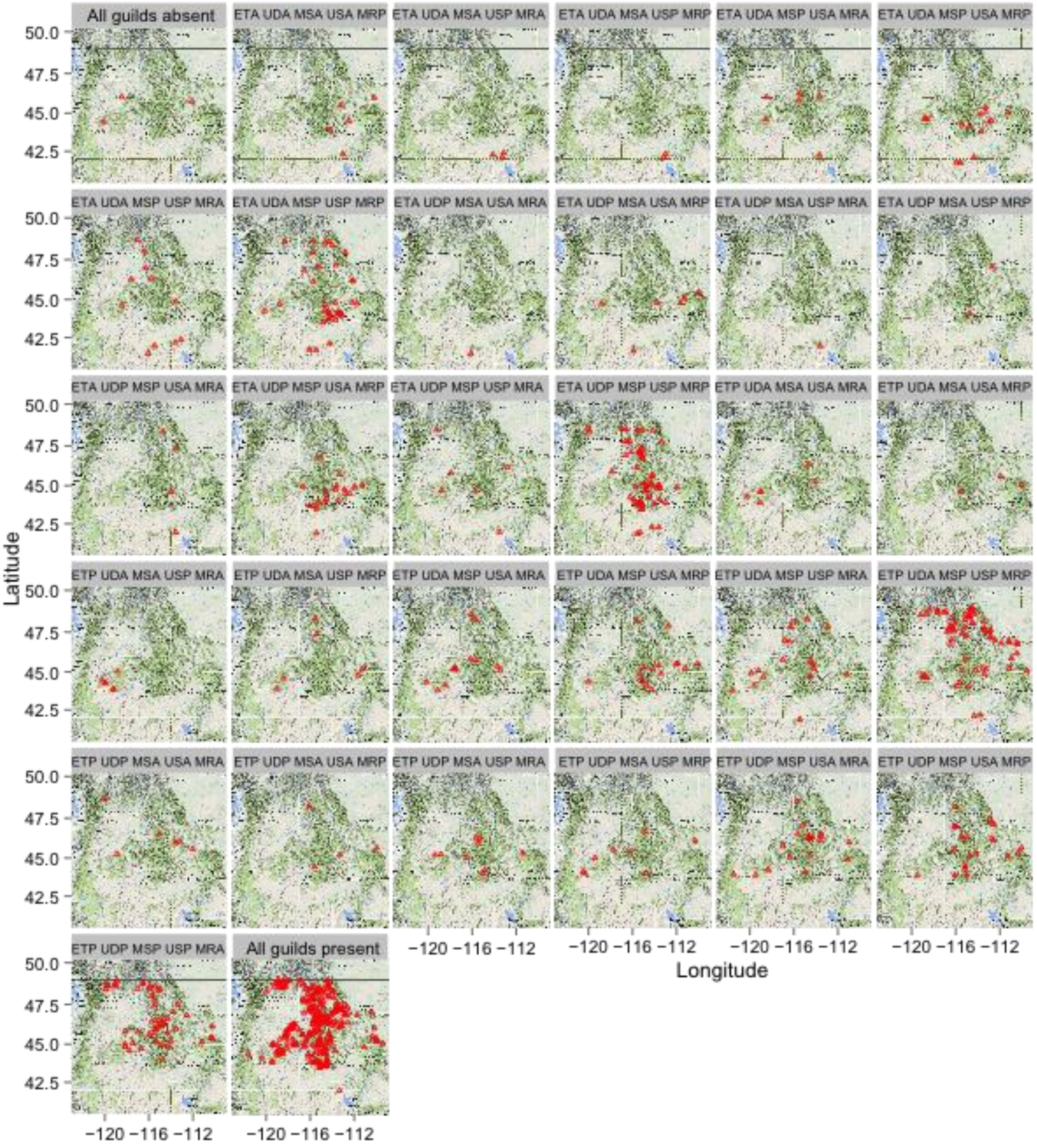

Fig. S.2.1. Map of combinations of guild assemblages across the Columbia and Missouri River basins showed that a majority of reaches contained all possible guilds. Only a few reaches were absent of all woody guilds. Map labels consist of guild initials and "P" for guild presence and "A" for guild absence. For example, UDP corresponds to *upland disturbance present* while ETA corresponds to *evergreen tree absent,* etc.

APPENDIX B

SUPPLEMENTS TO CHAPTER THREE

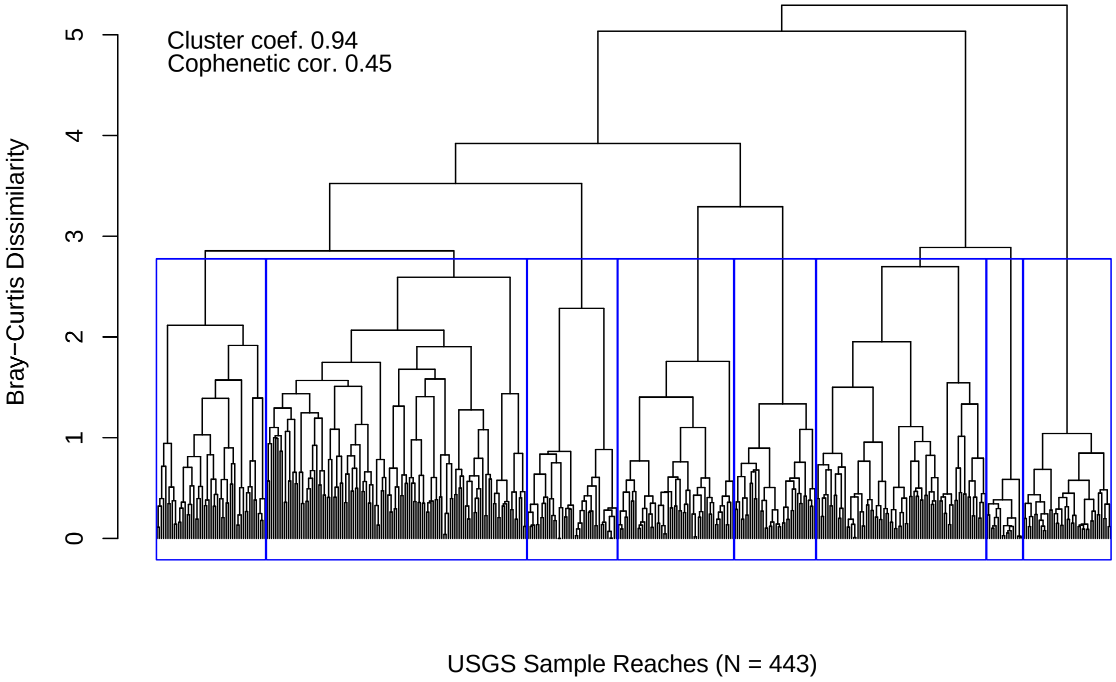

Fig. S.3.1. Eight riparian vegetation communities were identified by cluster analysis of floodplain reaches by floodplain woody plant species abundance.

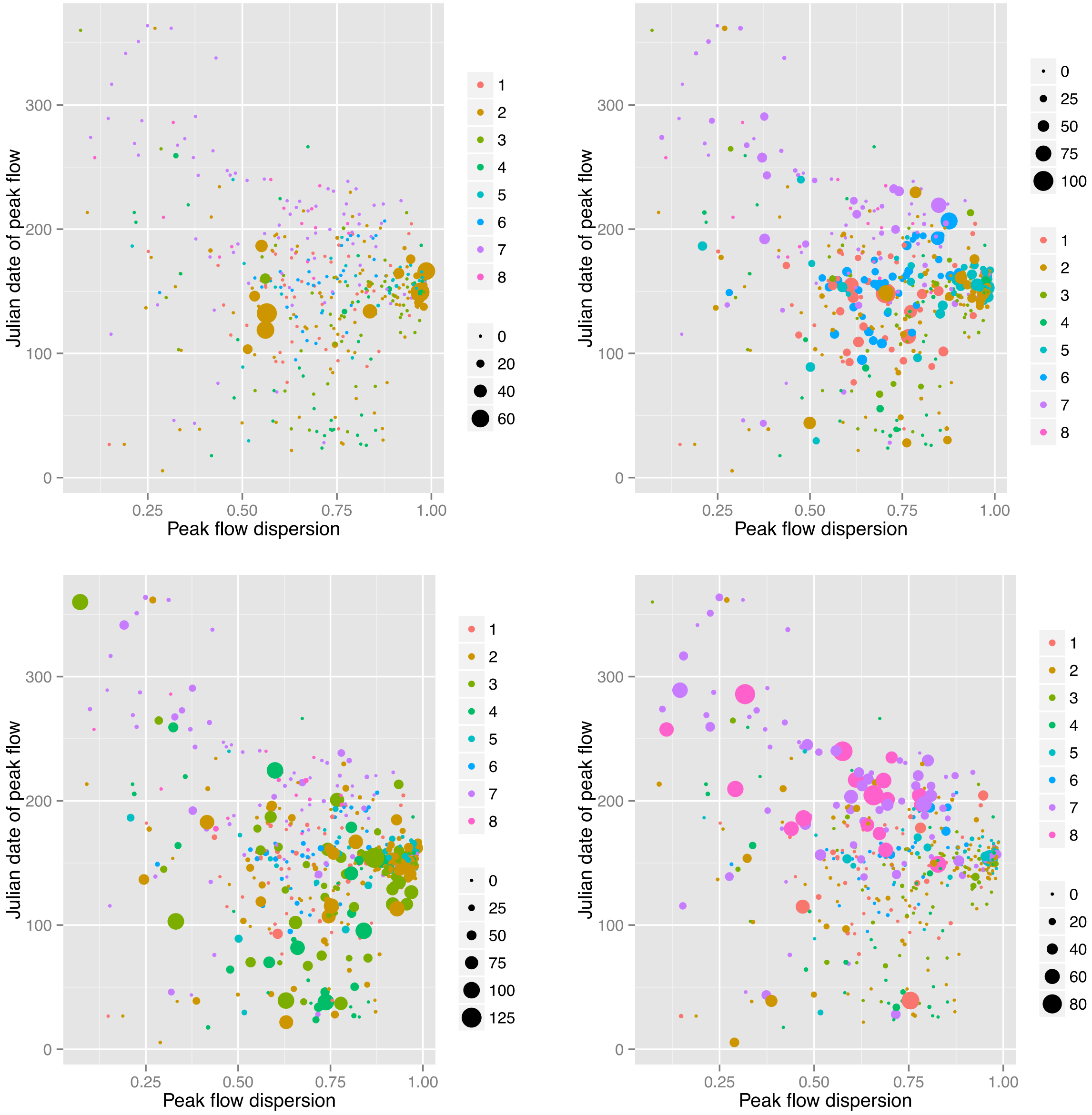

Fig. S.3.2. Relationships between date of peak flow, flow dispersion, community type and guild abundance showed that both communities and individual riparian vegetation guilds were linked to the timing of streamflow. The EGT guild and communities seven and eight occurred at reaches with later peak flows and low to moderate peak flow dispersion. The hydrophytic MRT and MRS guilds occurred at highest abundance at reaches with early peak flows and high peak flow dispersion.

Table S.3.1. Full environmental summary of the 433 study reaches across the western United States. Not all variables were used to describe guilds and communities in structural models due to correlation between variables or a lack of *a priori* hypotheses about how variables related to guilds or communities.

Environmental filter type	Environmental filter (units)	Median	Range	
Physical setting	Latitude	40.99	29.48	49.00
	Longitude	-110.30	-122.10	-100.0
	Gradient (%)	< 0.01	<0.01	0.14
	Channel width (m)	18.4	0.91	433.80
	Elevation (m)	1213.0	-70.0	2804.0
Climate	Growing degree days (C days)	2391.0	352.0	8540.0
	Mean annual minimum extreme temperature (C * 10)	-235.0	-376.0	-14.0
	Mean annual total precipitation (mm)	357.0	75.0	2175.0
	Mean maximum July temperature (C * 10)	308.0	179.0	436
	Median Julian date of last spring frost	137	17	196
	Median Julian date of first fall frost	267	227	359
Flow timing	Peak flow dispersion (0-1)	0.74	0.07	0.99
	Central tendency Julian day of peak flow	153.73	5.53	363.82
	Central tendency Julian day of peak flow – Julian date of last frost	4.38	-176.73	181.01
Flow variables	2-year recurrence flood discharge ($m^3 s^{-1}$)	44.32	0.21	6793.21
	5-year recurrence flood discharge ($m^3 s^{-1}$)	93.42	0.55	8982.10
	10-year recurrence flood discharge ($m^3 s^{-1}$)	140.11	0.87	10451.75
	25-year recurrence flood discharge ($m^3 s^{-1}$)	196.77	1.38	12337.65
	Proportion growing season with no flow	0	0	0.96
	Mean daily discharge ($m^3 s^{-1}$)	4.38	0.00	3205.00
	Coefficient of variation in daily flow	4.70	0.22	8.25
	Skew of daily flow	0.13	0.00	2.22
	10% percentile growing season daily flow/grand mean daily, dimensionless	0.15	0.00	7.20
	90% percentile growing season daily flow/grand mean daily, dimensionless	2.42	0.00	1.50
	Unit stream power for 2-year recurrence flood (Watts)	63.27	0.17	4915.83

Table S.3.1 (cont.)

Disturbance and alteration	Fine sediment (%)	23	1.00	50.00	
	Past grazing intensity (1-4) NA =4	1=293	2=102	3=31	4=13
	Salinity indicators (0,1)	0 = 400	1 = 43		
	Downcutting	0=332	1=111		
	Tamarisk planting	0=435	1=8		
	Elaeagnus planting	0=321	1=122		

Table S.3.2. Full multi-level pattern analysis results for the eight communities identified through cluster analysis. A perfect indicator equals one, and a non-indicator equals zero for any community or set of communities. *P*-values for each indicator are calculated from 9999 Monte Carlo simulations using the “indicspecies” package in R.

Species	Community								*P*
	1	2	3	4	5	6	7	8	
ABICON	0	0.13	0	0	0	0	0	0	0.745
ABILAS	0	0.19	0	0.19	0	0	0	0	0.265
ACENEG	0.60	0	0	0	0	0	0	0	0.005
ALNINC	0	0.39	0	0	0.39	0	0	0	0.015
ALNOBL	0	0.15	0	0	0.15	0	0	0	0.605
ALNSIN	0	0.37	0	0	0	0	0	0	0.015
ARTTRI	0	0.32	0.32	0	0.32	0	0	0	0.010
ATRCAN	0	0.13	0.13	0	0	0	0	0	0.820
BACSAL	0	0	0	0	0	0	0.57	0.57	0.005
BETOCC	0	0.37	0	0	0.37	0	0	0	0.005
CELOCC	0.27	0	0	0	0	0	0	0	0.005
CELRET	0	0.23	0.23	0	0	0	0.23	0.23	0.675
CORSER	0	0.51	0.51	0.51	0.51	0	0	0	0.005
ELAANG	0.59	0	0	0	0	0.59	0.59	0	0.005
ELACOM	0	0.18	0	0	0	0	0	0	0.270
FORNEO	0	0	0	0	0.26	0	0.26	0.26	0.055
FRAPEN	0.67	0	0	0	0	0.67	0	0	0.005
FRAVEL	0	0.30	0	0	0	0	0.30	0	0.025
HYMMON	0	0	0	0	0	0	0.36	0	0.005
JUGMAJ	0	0.18	0.18	0.18	0	0	0	0.18	0.935
OLW	0	0.70	0.70	0.70	0.70	0	0	0	0.005
PICSPE	0	0.30	0	0.30	0	0	0	0	0.025
PINPON	0	0.34	0.34	0.34	0.34	0	0	0	0.035
PLAWRI	0	0.23	0	0	0	0	0.23	0	0.115
POPANG	0	0	0	0	0.93	0	0	0	0.005

Table S.3.2 (cont.)

Species	Community								*P*
	1	2	3	4	5	6	7	8	
POPDEL	0.90	0	0	0	0	0.90	0	0	0.005
POPFRE	0	0	0	0	0	0	0.67	0	0.005
POPTRE	0	0.25	0.25	0.25	0.25	0	0	0	0.100
POPTRI	0	0.47	0	0.47	0	0	0	0	0.005
PROVEL	0	0	0	0	0	0	0.57	0.57	0.005
PRUSPE	0.39	0	0	0.39	0.39	0.39	0	0	0.005
PSEMEN	0	0.26	0	0	0.26	0	0	0	0.040
QUEGAM	0	0	0	0	0.20	0	0	0	0.135
QUEMAC	0.28	0	0	0	0	0	0	0	0.005
RHUTRI	0	0	0	0	0.38	0.38	0	0	0.005
ROBNEO	0	0	0.14	0	0	0	0	0	0.770
SALAMY	0.68	0	0	0	0	0.68	0	0	0.005
SALBON	0	0.10	0	0	0	0	0.10	0	1.000
SALEXI	0	0	0.88	0	0.88	0.88	0	0	0.005
SALGOO	0	0	0	0	0	0	0.43	0.43	0.005
SALRUB	0	0.17	0.17	0	0.17	0.17	0	0	0.795
SALSPP	0	0.76	0.76	0.76	0.76	0	0	0	0.005
SHEARG	0.29	0	0.29	0	0.29	0.29	0	0	0.495
TAMAPH	0	0	0	0	0	0	0.18	0	0.210
TAMSPP	0	0	0	0	0	0	0.93	0.93	0.005
PLUSER	0	0	0	0	0	0	0.38	0	0.005
THUPLI	0	0.18	0	0	0	0	0	0	0.185
ULMAME	0.45	0	0	0	0	0	0	0	0.005
ULMPUM	0.24	0	0.24	0	0.24	0.24	0	0	0.780

Table S.3.3. Species functional and morphological attributes used in determining guilds.

Species	Morphological attributes								
	Nitrogen fixation	Resprout capacity	Anaerobic tolerance	Drought tolerance	Moisture use	Salinity tolerance	Shade tolerance	Seed dispersal	Fruit period begin
ABICON	None	No	None	Medium	Medium	None	Intermediate	Cone	Summer
ABILAS	None	No	None	Low	Medium	None	Tolerant	Cone	Summer
ACENEG	None	Yes	Medium	High	Medium	Medium	Tolerant	Winged	Summer
ALNINC	Medium	No	High	Low	High	None	Intermediate	Catkin	Spring
ALNOBL	Medium	No	High	Low	High	None	Intolerant	Catkin	Spring
ALNSIN	Low	Yes	Low	Low	High	None	Intermediate	Catkin	Summer
ARTTRI	None	No	None	High	Medium	Medium	Intolerant	Seed	Summer
ATRCAN	None	Yes	None	High	Low	High	Intermediate	Winged	Summer
BACSAL	None	Yes	Low	Low	Medium	High	Intolerant	Achene	Summer
BETOCC	None	Yes	Medium	Low	High	None	Intermediate	Catkin	Spring
CELOCC	None	Yes	Medium	High	Low	Low	Tolerant	Fruit	Summer
CELRET	None	Yes	Medium	Low	High	Low	Tolerant	Fruit	Summer
CORSTO	None	Yes	High	Low	High	None	Intolerant	Fruit	Summer
ELAANG	High	Yes	Low	High	High	High	Intolerant	Fruit	Summer
ELACOM	Medium	Yes	None	High	Low	Medium	Intolerant	Fruit	Summer
FORNEO	None	Yes	Low	Medium	Medium	Medium	Intolerant	Fruit	Summer
FRAPEN	None	Yes	Medium	Medium	Medium	Low	Tolerant	Winged	Spring
FRAVEL	None	No	Low	Medium	Medium	None	Intolerant	Winged	Spring
HYMMON	None	Yes	Medium	High	Medium	High	Intolerant	Winged	Spring
JUGMAJ	None	No	None	Medium	Medium	None	Intolerant	Fruit	Summer
PICSPE	None	No	None	Low	Medium	None	Tolerant	Cone	Summer
PINPON	None	No	None	High	Medium	Medium	Intolerant	Cone	Summer
PLAWRI	None	Yes	Low	High	Low	None	Intolerant	Fruit	Summer
PLUSER	None	Yes	Medium	Low	Medium	Medium	Intolerant	Achene	Spring
POPANG	None	Yes	Medium	Low	High	Medium	Intolerant	Hairy	Summer
POPDEL	None	Yes	Medium	High	High	None	Intolerant	Hairy	Spring

Table S.3.3. (cont.)

Species	Morphological attributes								
	Nitrogen fixation	Resprout capacity	Anaerobic tolerance	Drought tolerance	Moisture use	Salinity tolerance	Shade tolerance	Seed dispersal	Fruit period begin
POPFRE	None	Yes	Medium	Medium	High	Low	Intolerant	Hairy	Spring
POPTRE	None	Yes	Low	Low	High	Medium	Intolerant	Hairy	Spring
POPTRI	None	Yes	Medium	Low	High	None	Intolerant	Hairy	Spring
PROVEL	Low	Yes	None	Medium	Medium	High	Intermediate	Pod	Spring
PRUSPE	None	Yes	None	Medium	Medium	None	Intolerant	Fruit	Summer
PSEMEN	None	No	Low	Low	Medium	Low	Intermediate	Cone	Summer
QUEGAM	None	Yes	None	Low	Low	None	Intolerant	Fruit	Summer
QUEMAC	None	Yes	None	High	Medium	Low	Intermediate	Fruit	Summer
RHUTRI	None	Yes	None	Medium	Low	Medium	Intermediate	Fruit	Spring
ROBNEO	Low	Yes	Low	Medium	Medium	Low	Intolerant	Pod	Summer
SALAMY	None	Yes	Medium	Low	High	None	Intolerant	Hairy	Spring
SALBON	None	No	Low	Low	High	None	Intermediate	Hairy	Spring
SALEXI	None	Yes	High	Medium	High	Low	Intermediate	Hairy	Summer
SALGOO	None	Yes	High	Medium	High	None	Intolerant	Hairy	Spring
SALRUB	None	Yes	High	Medium	High	Low	Intolerant	Hairy	Spring
SALSPP	None	Yes	High	Medium	Medium	Low	Intolerant	Hairy	Summer
SHEARG	Medium	Yes	None	Medium	Medium	High	Intermediate	Fruit	Summer
TAMAPH	None	Yes	Medium	High	Medium	High	Intolerant	Hairy	Summer
TAMSPP	None	Yes	Medium	High	Medium	High	Intolerant	Hairy	Summer
THUPLI	None	No	None	Low	Medium	None	Tolerant	Cone	Summer
ULMAME	None	Yes	Low	Medium	High	Low	Intermediate	Winged	Spring
ULMPUM	None	Yes	None	High	Medium	Medium	Intolerant	Winged	Spring

Table S.3.3. (cont.)

Species	Traits							
	Specific leaf area ($cm^2\ g^{-1}$)	Height at maturity (m)	Root depth (cm)	Growth habit	Growth form	Growth rate	Leaf retention	Lifespan
ABICON	51.4	36.6	101.6	Tree	Single stem	Slow	Yes	Long
ABILAS	39.5	27.4	101.6	Tree	Single stem	Slow	Yes	Long
ACENEG	232	18.3	101.6	Tree	Multiple stem	Rapid	No	Short
ALNINC	201.2	7.6	61.0	Tree/shrub	Thicket forming	Rapid	No	Short
ALNOBL	144.3	9.1	61.0	Tree/shrub	Multiple stem	Rapid	No	Moderate
ALNSIN	259.8	4.9	25.4	Tree/shrub	Multiple stem	Slow	No	Long
ARTTRI	88.7	1.2	50.8	Shrub	Multiple stem	Slow	Yes	Long
ATRCAN	39.7	1.8	50.8	Shrub	Multiple stem	Slow	No	Long
BACSAL	105	3.0	30.5	Shrub	Multiple stem	Rapid	No	Short
BETOCC	161.6	7.6	50.8	Tree/shrub	Multiple stem	Rapid	No	Short
CELOCC	167.2	15.2	91.4	Tree/shrub	Single stem	Rapid	No	Moderate
CELRET	190.3	24.4	61.0	Tree/shrub	Single stem	Moderate	No	Moderate
CORSTO	194.2	3.7	50.8	Tree/shrub	Multiple stem	Moderate	No	Moderate
ELAANG	124	10.7	50.8	Tree/shrub	Single stem	Rapid	No	Long
ELACOM	201.49	3.7	45.7	Shrub	Multiple stem	Rapid	No	Moderate
FORNEO	152.31	2.4	30.5	Shrub	Multiple stem	Moderate	No	Moderate
FRAPEN	184.2	24.4	101.6	Tree	Single stem	Rapid	No	Short
FRAVEL	135	15.2	30.5	Tree	Single stem	Rapid	No	Moderate
HYMMON	73.3	2.4	30.5	Shrub	Thicket forming	Rapid	No	Short
JUGMAJ	163.9	6.1	61.0	Tree/shrub	Single stem	Slow	No	Long
PICSPE	34.5	36.6	50.8	Tree	Single stem	Slow	Yes	Long
PINPON	45.04	68.0	50.8	Tree	Single stem	Moderate	Yes	Long
PLAWRI	203.5	24.4	91.4	Tree	Single stem	Slow	No	Long
PLUSER	125.48	18.3	50.8	Shrub	Multiple stem	Moderate	Yes	Short
POPANG	133.4	25.9	30.5	Tree	Single stem	Rapid	No	Moderate

Table S.3.3. (cont.)

Species	Traits							
	Specific leaf area (cm^2 g^{-1})	Height at maturity (m)	Root depth (cm)	Growth habit	Growth form	Growth rate	Leaf retention	Lifespan
POPDEL	128	27.4	61.0	Tree	Single stem	Rapid	No	Short
POPFRE	105.3	19.8	81.3	Tree	Single stem	Rapid	No	Moderate
POPTRE	151.9	30.5	81.3	Tree	Single stem	Rapid	No	Short
POPTRI	167.6	7.6	76.2	Tree	Single stem	Rapid	No	Moderate
PROVEL	82.01	24.4	61.0	Tree/shrub	Single sStem	Rapid	No	Moderate
PRUSPE	218	61.0	50.8	Tree/shrub	Thicket forming	Moderate	No	Long
PSEMEN	90	12.2	66.0	Tree	Single stem	Moderate	Yes	Long
QUEGAM	138.9	30.5	91.4	Tree/shrub	Single stem	Slow	No	Long
QUEMAC	167.5	1.2	71.1	Tree/shrub	Single stem	Slow	No	Long
RHUTRI	142.2	7.6	30.5	Shrub	Rhizomatous	Slow	No	Moderate
ROBNEO	230.4	18.3	30.5	Tree/shrub	Multiple stem	Rapid	No	Moderate
SALAMY	157.7	7.3	76.2	Tree/shrub	Multiple stem	Rapid	No	Short
SALBON	82.51	3.0	61.0	Tree	Multiple stem	Rapid	No	Short
SALEXI	134	12.2	50.8	Tree/shrub	Rhizomatous	Rapid	No	Moderate
SALGOO	133	6.1	71.1	Tree	Multiple stem	Rapid	No	Moderate
SALRUB	175	3.7	76.2	Tree	Multiple stem	Rapid	No	Moderate
SALSPP	90	4.6	63.5	Tree/shrub	Multiple stem	Rapid	No	Moderate
SHEARG	71.435	12.2	61.0	Tree/shrub	Multiple stem	Rapid	No	Moderate
TAMAPH	134	9.1	91.4	Tree/shrub	Multiple stem	Rapid	Yes	Long
TAMSPP	191.67	0.9	76.2	Tree/shrub	Multiple stem	Rapid	No	Long
THUPLI	41.57	45.7	76.2	Tree	Single stem	Slow	Yes	Long
ULMAME	120.2	36.6	106.7	Tree	Single stem	Rapid	No	Moderate
ULMPUM	102.3	21.3	61.0	Tree/shrub	Single stem	Rapid	No	Short

APPENDIX C

PERMISSION-TO-USE LETTERS FOR CHAPTER TWO

UtahStateUniversity
ECOGEOMORPHOLOGY & TOPOGRAPHIC
ANALYSIS LABORATORY

Nate Hough-Snee
Department of Watershed Sciences
5210 Old Main Hill
Logan, UT 84322-5210

November 14, 2015

Dr. Brian G. Laub
Department of Watershed Sciences
5210 Old Main Hill
Logan, UT 84322-5210

Re: Permission to use request

Dear Brian,

I am in the process of preparing my dissertation in the Watershed Science Department at Utah State University. I am requesting your permission to include the manuscript we coauthored, *Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds* that recently appeared in *Ecosphere* (full citation below).

Please indicate your approval of this request by signing in the space provided below. If you have any questions, please do not hesitate to contact me.

Thanks,

Nate Hough-Snee

nate@natehough-snee.org; 1.435.535.5085

I hereby give permission to Nate Hough-Snee to reprint the following material in his dissertation:

Hough-Snee, N., B. G. Laub, D. M. Merritt, A. L. Long, L. L. Nackley, B. B. Roper, and J. M. Wheaton. 2015. Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds. Ecosphere 6(10):173. http://dx.doi.org/10.1890/ES15-00064.1

Signed _ Brian G Laub
____

Date ____11/13/2015____

5210 Old Main Hill Logan, UT 84322-5210 PH: (435) 797-9189 FAX: (435) 797-1781 www.cnr.usu.edu/wats

UtahStateUniversity
ECOGEOMORPHOLOGY & TOPOGRAPHIC
ANALYSIS LABORATORY

Nate Hough-Snee
Department of Watershed Sciences
5210 Old Main Hill
Logan, UT 84322-5210

November 14, 2015

Dr. David M. Merritt
USDA Forest Service
National Stream and Aquatic Ecology Center
Rocky Mountain Research Station
2150 Centre Ave, Bldg. A, Suite 368
Fort Collins, CO 80526

Re: Permission to use request

Dear Dave,

I am in the process of preparing my dissertation in the Watershed Science Department at Utah State University. I am requesting your permission to include the manuscript we coauthored, *Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds* that recently appeared in *Ecosphere* (full citation below).

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Signed David M. Merritt

Date 11/13/2015

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Nate Hough-Snee
Department of Watershed Sciences
5210 Old Main Hill
Logan, UT 84322-5210

November 16, 2015

Ms. A. Lexine Long
U.S. Geological Survey
Colorado Plateau Research Station
Northern Arizona University
525 S. Beaver St. #5614
Flagstaff, AZ 86011

Re: Permission to use request

Dear Dave,

I am in the process of preparing my dissertation in the Watershed Science Department at Utah State University. I am requesting your permission to include the manuscript we coauthored, *Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds* that recently appeared in *Ecosphere* (full citation below).

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Signed __ ____

Date ____11/16/15____

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Nate Hough-Snee
Department of Watershed Sciences
5210 Old Main Hill
Logan, UT 84322-5210

November 13, 2015

Dr. Lloyd L. Nackley
University of California Cooperative Extension
Department of Plant Sciences, MS6
University of California
One Shields Avenue
Davis, CA 95616-8780

Re: Permission to use request

Dear Lloyd,

I am in the process of preparing my dissertation in the Watershed Science Department at Utah State University. I am requesting your permission to include the manuscript we coauthored, *Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds* that recently appeared in *Ecosphere* (full citation below).

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Signed ____

Date _____11/12/2015____

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Logan, UT 84322-5210

November 13, 2015

Dr. Brett B. Roper
USDA Forest Service
Rocky Mountain Research Station
Forestry Sciences Lab
860 North 1200 East
Logan UT 84321

Re: Permission to use request

Dear Dave,

I am in the process of preparing my dissertation in the Watershed Science Department at Utah State University. I am requesting your permission to include the manuscript we coauthored, *Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds* that recently appeared in *Ecosphere* (full citation below).

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Signed ____________________

Date November 12 - 2015

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Nate Hough-Snee
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Logan, UT 84322-5210

November 13, 2015

Dr. Joseph M. Wheaton
Department of Watershed Sciences
Utah State University
5210 Old Main Hill
Logan, UT 84322-5210

Re: Permission to use request

Dear Joe,

I am in the process of preparing my dissertation in the Watershed Science Department at Utah State University. I am requesting your permission to include the manuscript we coauthored, *Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds* that recently appeared in *Ecosphere* (full citation below).

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Signed ______________________ Digitally signed by Joe Wheaton
Date: 2015.11.13 17:45:33 -07'00'

Date ______________________

VITA

Nate Hough-Snee
http://www.natehough-snee.org

Education

Utah State University – Logan, UT:
Ph.D. in Ecology: Ecology Center and Department of Watershed Sciences, 2016
Dissertation: Relationships between riparian vegetation, hydrology, climate and disturbance across the western United States.
Graduate Certificate: National Environmental Policy Act

University of Washington – Seattle, WA:
M.S. in Ecosystem Analysis: School of Forest Resources, 2010
Thesis: The effects of flooding, fertilization, and initial plant size on the growth and biomass allocation of *Carex obnupta* and *Carex stipata*.

B.A. in Environmental Studies (with distinction): Program on the Environment, 2008
Thesis: Prioritizing for riparian restoration surrounding a eutrophied lake: a pre-restoration analysis of riparian buffer potential and implications for the restoration of New Zealand's Lake Omapere.
Certificate: Restoration Ecology

Publications

Macfarlane W.W., J.M. Wheaton, N. Bouwes, M. Jensen, J. Gilbert, N. Hough-Snee, J. Shivik. *In Press*. Modeling the capacity of riverscapes to support beaver dams. *Geomorphology*. DOI: 10.1016/j.geomorph.2015.11.019

Hough-Snee, N., A. Kasprak, R.K. Rossi, N. Bouwes, B.B. Roper, J.M. Wheaton. *In Press*. Hydrogeomorphic and biotic drivers of instream wood differ across sub-basins of the Columbia River Basin, USA. *River Research and Applications*. DOI: 10.1002/rra.2968

Kasprak A., N. Hough-Snee, T. Beechie, N. Bouwes, G.J. Brierley, R. Camp, K.A. Fryirs, H. Imaki, M.L. Jensen, G. O'Brien, D.L. Rosgen, J.M. Wheaton. 2016. The blurred line between form and process: a comparison of stream channel classification frameworks. *PLoS ONE*. DOI: 10.1371/journal.pone.0150293.

Hough-Snee, N., B.B. Roper, J.M. Wheaton, R.L. Lokteff. 2015. Riparian vegetation communities of the American Pacific Northwest are tied to multi-scale environmental filters. *River Research and Applications* 31(9): 1151-1165. DOI: 10.1002/rra.2815.

Hough-Snee, N., B.G. Laub, D.M. Merritt, A.L. Long, L.L. Nackley, Brett B. Roper, J.M. Wheaton. 2015. Multi-scale environmental filters and niche partitioning shape the distributions of riparian vegetation guilds. *Ecosphere* 6: art173.

Hough-Snee, N., L.L. Nackley, S-H. Kim, K. Ewing. 2015. Life history strategies explain plant performance under environmental stress: the effects of flooding and fertilization on the growth and allocation of two wetland sedges. *Aquatic Botany* 120B: 151–159.

Hough-Snee, N., R.L. Pond. 2014. Amending impaired soils increases seedling growth but reduces seedling survival at a retired gravel mine. *Ecological Restoration* 32 (3): 231-235.

Hough-Snee, N., A.K. Kasprak, B.B. Roper, C.S. Meredith. 2014. Decoupling geomorphic, climate, disturbance and riparian vegetation effects on instream wood in the interior Pacific Northwest, USA. *Riparian Ecology and Conservation* 2 (1): 14-34.

Hough-Snee, N., B.B. Roper, J.M. Wheaton, P. Budy, R.L. Lokteff. 2013. Riparian vegetation communities change rapidly following passive restoration at a northern Utah stream. *Ecological Engineering* 58: 371-377.

Hough-Snee, N., A.L. Long, R.L. Pond. 2012. Passive soil manipulation influences the successional trajectories of forest communities at a denuded former campsite. *Ecological Restoration* 30 (1): 9-12.

Hough-Snee, N., A.L. Long, L. Jeroue, K. Ewing. 2011. Mounding alters environmental filters that drive plant community development in a novel grassland. *Ecological Engineering* 37 (11): 1932-1936.

Hough-Snee, N., D.D. Cooper. 2011. The effect of perigynia removal on the germination of awl-fruit sedge, *Carex stipata* Muhl. Ex Willd (Cyperaceae). *Native Plants Journal* 12 (1): 41-43.

Hough-Snee, N., J.D. Bakker, K. Ewing. 2011. The long-term effects of initial site treatment on fescue abundance in a novel grassland. *Ecological Restoration* 29 (1-2): 14-17.

Professional Ecology Experience

Biological scientist: PIBO Effectiveness Monitoring Program, USDA Forest Service, Logan, UT, 3/2012 – 5/2013.

Restoration ecologist: Snoqualmie Indian Tribe, Snoqualmie, WA, 9/2006 – 8/2008.

From 2007-2011, I held numerous seasonal wetland, stream, and forest biologist positions with Small Hydro Enterprises (Kerikeri, New Zealand), David Evans and Associates (Bellevue, WA), Snohomish County Surface Water Management (Everett, WA), The Center for Environmental Management of Military Lands (Fairbanks, AK), and Sustainable Resource Group International Inc. (Kailua, HI).

Academic Research and Teaching Experience

Utah State University:
Research assistant: Dept. of Watershed Sciences, Logan, UT, 6/2011 – 12/2015.

University of Washington:
Research assistant: Pack Forest Center for Sustainable Forestry, Eatonville, WA, Union Bay Natural Area, Seattle, WA, 9/2008 – 12/2010, Expedition to the Arctic National Wildlife Refuge, Kaktoviak and Fairbanks, AK, 7/2006 – 8/2006.

Teaching assistant: BIO 424/ESRM 478, Plant Ecophysiology; SFR 501, Forest Community Ecology; BIO 180, Introduction to Ecology and Evolution; ESRM 411, Plant Propagation. Six quarters 3/2007 – 12/2009.

Cleveland State University, Cleveland, OH:
Research assistant: Dr. John P. Holcomb, Department of Mathematics. Revision of Daniel, W.W. 2004. Biostatistics: A Foundation for Analysis in the Health Sciences, 8th Edition. Wiley and Sons. 9/2003 – 4/2004.

<u>Published Abstracts and Conference Proceedings (since 2011)</u>
Hough-Snee, N. 2015. Riparian functional guilds, disturbance, and biotic interactions in the Columbia River Basin, USA. Society of Wetland Scientists, Providence, RI.

Hough-Snee, N. 2015. Brand management for early-career scientists: using social media and online content to expand your professional footprint. Society of Wetland Scientists, Providence, RI.

Hough-Snee, N., et al. (ten co-authors). 2015. Beaver emulation and facilitation to restore incised streams: cases from the semi-arid West. Society of Wetland Scientists Rocky Mountain, Golden, CO.

Hough-Snee, N., B.G. Laub, D.M. Merritt, B.B. Roper, A.L. Long, L.L. Nackley, J.M. Wheaton. 2014. Riparian vegetation guilds: applications to small streams of the interior Pacific Northwest. Restoring the West, Managing for Resilient Riparian Corridors. Logan, UT.

Kasprak, A.K., N. Hough-Snee, et al. (seven co-authors). 2014. Comparing channel classification frameworks to better inform watershed management? Restoring the West, Managing for Resilient Riparian Corridors, Logan, UT.

Sarr, D., N. Hough-Snee. 2014. Riverscapes and mindscapes: using inventory, monitoring, and biogeography to explore riparian management domains in the West. Restoring the West, Managing for Resilient Riparian Corridors, Logan, UT.

Hough-Snee, N., A. Kasprak, J.M. Wheaton, N. Bouwes, B.B. Roper, C.S. Meredith. 2014. Direct and indirect drivers of instream wood: cases from the interior Pacific Northwest. Joint Aquatic Sciences Meeting, Portland, OR.

Hough-Snee, N. et al. (eight co-authors). 2014. Riparian vegetation and instream wood dynamics in streams of the interior Columbia River basin. Society of American Foresters Intermountain Meeting, Logan, UT.

Hough-Snee, N., B.B. Roper, J.M Wheaton. 2013. Riparian degradation and restoration: cases from the interior Pacific Northwest. Society of Wetland Scientists, Duluth, MN.

Hough-Snee, N., B.B. Roper, J.M Wheaton. 2013. Multi-scale drivers of riparian vegetation: a case from the upper Columbia and Missouri River basins. Utah State University Spring Runoff Conference, Logan, UT.

Hough-Snee, N., B.B. Roper, J.M Wheaton. 2013. Riparian Vegetation Composition Recovers Rapidly From Disturbance Following Grazing Retirement at a Northern Utah Headwater Stream. River Restoration Northwest, Stevenson, WA.

Hough-Snee, N., A. Van Wagenen B.B. Roper. 2012. Multi-scale drivers of riparian vegetation: a case from the upper Columbia and Missouri River basins. Society of Wetland Scientists Pacific Northwest, Boise, ID.

Pond, R.L., A.L. Long, N. Hough-Snee. 2012. Passive Soil Manipulation Influences the Successional Trajectories of Forest Communities at a Denuded Former Campsite. Restoration 2012: Beyond Borders. Victoria, BC.

Select Professional Service and Leadership

Ad hoc manuscript reviewer: *AoB Plants, Ecohydrology, Ecological Applications, Ecological Engineering, Ecological Restoration, Environmental and Experimental Botany, Forests, Hydrology and Earth Systems Science, Journal of Hydrology, Native Plants Journal, Northeastern Naturalist, Restoration Ecology, Riparian Ecology and Conservation, Wetland Science and Practice, Wetlands.*

President: Society of Wetland Scientists Pacific Northwest Chapter. 10/2014 – 3/2016.
Executive vice-president: Society of Wetland Scientists Pacific Northwest Chapter. 9/2012 – 9/2014.

Grants and Awards – $121,175 to date (5/2016) – select awards below

Society of Wetland Scientists Student Research Grant – $1,000	2015
U.S. EPA, Science to Achieve Results Fellowship – $84,000	2014-16
Utah State University, Ecology Center Research Grant – $2,400	2014
Utah State University, Presidential Fellowship – $12,000	2011-12

Professional Societies

Ecological Society of America, Society for Ecological Restoration, Society of Wetland Scientists, Northwest Scientific Association, Xi Sigma Pi