

Running head: Environmental filtering, niche partitioning, and riparian guilds

Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds.

Nate Hough-Snee^{1*}, Brian G. Laub¹, David M. Merritt^{2,3}, A. Lexine Long^{1,4}, Lloyd L. Nackley⁵, Brett B. Roper^{1,6}, Joseph M. Wheaton¹

¹Department of Watershed Sciences and Ecology Center, Utah State University, Logan, UT, 84322-5210, USA

²USDA Forest Service, National Stream and Aquatic Ecology Center, Natural Resource Research Center, Fort Collins, CO 80526, USA

³Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80526, USA

⁴United States Geological Survey, Southwest Biological Science Center, Flagstaff, AZ, 86011, USA

⁵University of California Davis, Department of Plant Sciences, Davis, CA, 95616, USA

⁶USDA Forest Service, National Stream and Aquatic Ecology Center, Forest Sciences Laboratory, Logan, UT 84321, USA

*Corresponding author: nate@natehough-snee.org; +1.435.535.5085

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. Identifying the environmental filters that exert selective pressures on specific riparian vegetation guilds is a critical step in setting baseline expectations for how riverscapes may respond to the environmental conditions anticipated under future global change scenarios. In this study, we 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) 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. We clustered species into guilds by morphological characteristics and attributes related to environmental tolerances, modeling these guilds' distributions as a product of abiotic environmental filters – regional climate, watershed hydrogeomorphic characteristics, and stream channel form – and guild co-existence. We 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. We 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 response guilds framework is to be used as a decision-support tool framework at large spatial extents.

Key words: riparian vegetation; riparian guilds; functional diversity; community assembly; environmental filtering; niche partitioning; global change; riparian management; Columbia River basin; Missouri River basin.

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). With the degradation of riparian vegetation comes the decline of vegetation-mediated ecosystem processes including allocthonous energy subsidies to aquatic ecosystems (Delong and Brusven 1994), contribution of large wood to stream networks (Hough-Snee et al. 2014a), temperature regulation by mature overstory vegetation (Pollock et al. 2009), and valuable terrestrial wildlife habitat (Bateman and Merritt 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). These synergies 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?

To answer this question, ecologists have suggested that by aggregating individual species into groups based on common life history strategies, 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 plant functional approach to riparian community assembly, determination of riparian vegetation guilds or riparian vegetation "flow-response guilds" *sensu* Merritt et al. (2010), 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. 2014b), the most commonly studied environmental drivers of riparian vegetation are 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 depth, 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, Perry et al. 2013). 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. One such knowledge gap is how riparian vegetation assembles in unregulated, low-order streams – especially across expansive landscapes.

While headwaters make up disproportionate amounts of stream area within watersheds, the environmental filters that control riparian plant functional diversity in low-order streams have

101 rarely been elucidated at broad spatial scales (Hough-Snee et al. 2014b). Many riparian
 102 ecosystems, especially those in low-order, headwater streams, are tightly linked to more than just
 103 reach-level hydrogeomorphic gradients (Richardson and Danehy 2007), including biotic
 104 interactions (Whigham et al. 2012) and landscape to local-scale processes including climate, land
 105 management, and fluvial disturbance (Dunn et al. 2011, Hough-Snee et al. 2014b). Riparian plant
 106 communities assemble in response to both biotic and abiotic environmental filters that limit
 107 which species and functional traits can occur at a given location within a stream network (Díaz et
 108 al. 1998). These filters, whether they originate from stream or upland processes, select for sets of
 109 traits, both within and between species, which allow those species and guilds with shared life
 110 history strategies to successfully grow, reproduce, and maintain populations. While riparian
 111 environmental filters may occur at multiple spatial and temporal scales within a given
 112 environment, filtering can select for comparable sets of traits or guilds with shared life history
 113 strategies regardless of the dominant processes at work.

114
 115 Identifying trait-based plant assemblages provides a novel approach for assessing plant
 116 functional diversity where numerous species with similar realized niches and corresponding life
 117 history strategies may occur (Grime 1977, Merritt et al. 2010). Within riparian ecosystems,
 118 guild-based approaches have been used to identify how functional riparian vegetation
 119 assemblages respond to flow regulation (Bejarano et al. 2012, 2013). However, riparian guild
 120 determination, or “riparian guilding,” may also provide insights into the broad environmental
 121 filters that shape riparian plant functional diversity across landscapes. Riparian guilding allows
 122 for the identification of groups of species with shared functional traits, morphological
 123 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 (e.g. Catford and Jansson 2014). 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 traits syndromes to coexist. That is, multiple life history strategies and guilds may co-exist in comparable environments due to their different strategies for tolerating environmental stress, responding to disturbance, and acquiring nutrients and water (Grime 1977, Catford and Jansson 2014). By identifying environmental filters that shape riparian community assembly and the coexistence of trait-based plant guilds, inference can be made on the filters that most strongly influence riparian plant functional diversity that mediates ecosystem function. This functional diversity-based approach to riparian ecology may also provide insight into the environmental gradients across which vegetation change may occur under future climate and land management scenarios.

To investigate relationships between riparian functional plant diversity and environmental filtering, we investigate two sets of questions in this paper:

1. Can riparian woody plant guilds be identified based on species' shared morphological and life history attributes? If so, 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 all guilds present at a given site, across landscapes?

Methods

Study Sites

We selected 703 low-order stream reaches within the interior Columbia and upper Missouri River basins (Figure 1) for inclusion in the study. These reaches are part of an existing stream monitoring program and were sampled under a spatially balanced, probabilistic sampling design (Kershner et al. 2004). All reaches were low-gradient ($\approx 3\text{--}4\%$) and occur within subwatersheds (USGS 6th order hydrologic unit code) 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 base flow conditions during the growing season (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 plant cover was measured for all species in a lower vegetation layer (< 1m in height) and an upper woody species layer (> 1m in height). Cover was estimated in classes: ≥ 5 -15%, ≥ 15 -25%, ≥ 25 -38%, ≥ 38 -50%, ≥ 50 -75%, ≥ 75 -95%, and ≥ 95 -100%. Due to the possibility of overestimating guild cover by using data from both layers or underestimating guild cover by only using one of the layers, species presence and absence were derived. 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

We identified functional groups by allocating species to groups based on life history strategies as a product of their shared functional and morphological attributes (Merritt et al. 2010), selecting attributes based on their importance in maintaining individual plants and populations within a riparian environment along a typical, low-order stream. 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 landscape processes (climate, etc.). Accordingly, the plant attributes we selected for guilding aligned with multiple environmental filters across the study landscape (Table 1). We 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 1) in the riparian environment. 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 1).

For example, adaptation to different soil textures and sizes illustrates the capacity for a plant to persist and grow in an environment where interannual differences in deposition and erosion may deposit diverse 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 persist, photosynthesize, and grow amid interannual and intrannual hydrologic variability. The timing and duration of flowering, seed set and the duration of seed 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).

We 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, whereas many of our species attributes were categorizations and not empirical measurements. It is worth noting that of the small number of attributes selected for guilding here, many often covary with other traits. A limited number of attributes (or when available, measured traits) may be used in such guilding 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).

215

216 *Environmental metrics*

217 Stream gradient, bankfull width, bank stability, channel sinuosity, bank angle, median particle
 218 size, wood frequency, wetted width-depth ratio, residual pool depth, hydraulic radius, and
 219 percent undercut banks were field measured at each reach using standardized protocols (Table 2;
 220 (PIBO EM 2012b). We identified a 30m buffer surrounding each stream in GIS and calculated
 221 the proportion of each buffer polygon that was grazed by livestock in the last 30-years using
 222 USFS grazing allotment data. Because forest patchess serve as corridors for propagule dispersal
 223 following disturbance and tree canopies shape understory light and humidity, we identified the
 224 proportion of each watershed and reach covered by overstory forest vegetation using
 225 LANDFIRE (USGS 2012). We also used LANDFIRE data to estimate the proportion of each
 226 watershed that had burned between 1997 and 2007. We calculated road density (km/km²) within
 227 each buffer and watershed because roads serve as plant dispersal vectors and alter local
 228 hydrology. We used 10m digital elevation models to define watershed boundaries and calculate
 229 watershed area, stream density and the average slope of the watershed and buffer surrounding
 230 each reach. An erosivity index – a unitless, continuous measure of the uniaxial compressive
 231 strength of lithology types – was calculated to estimate the relative erosion potential at each
 232 reach (Cao et al. 2007). Average soil thickness and depth to the seasonal high water table,
 233 indicators of hydric soils, were estimated at each reach (NRCS 2012). All landscape and
 234 watershed-scale filters were summarized for the watershed area upstream of each reach (Table
 235 2).

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237 *Riparian guild identification*

We identified riparian life history strategy guilds by clustering species based on their morphological and physical attributes (Table 1). We 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. We 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. We visualized the resulting guilds and the attributes that differentiated them using a three-dimensional principal coordinate analysis (PCoA). Guild fidelity was tested using permutational 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. 2013). We determined guild presence by creating lists of woody species that occurred at each reach. If any species from a given guild was field identified as present at the reach, then that guild was categorized as present. 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 we performed NMDS ordination 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 we correlated environmental filters to the final NMDS solution using multiple

regression. 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). Prior to model building we removed environmental variables with correlations > 0.65 to avoid collinearity. We 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. We used a systematic stepwise model selection, removing variable and interaction terms at each step of model comparison. This approach was taken to minimize the AIC and negative log-likelihood for each model, while maintaining an information theoretic approach that retained key hydrologic and climatic variables that were thought to have meaningful biological relationships with the life history strategies and their component attributes identified through guilding.

To further explore how guild distributions were related to co-occurring guilds and environmental filters, we 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. We assessed conditional inference tree

performance by fitting our 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.

Results

Riparian guilds

We identified five riparian guilds comprised of 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, drought-plastic 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 3, Figures 2 and 3). Guilds were given abbreviate names for simplicity of presentation: (1) evergreen tree, (2) upland disturbance, (3) mesic shrub, (4) mesoriparian shrub and tree, and (5) understory shrub (Table 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 (Figures 2 and 4; Appendices A, B, C). Guilded species' composite 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 (Figures 3 and 4,

Appendix B). Surprisingly, 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

Riparian guild assemblages occurred in 32 different combinations at the 703 study reaches, from reaches with no woody riparian guilds present to reaches where all identified woody riparian guilds were present (Figure 5, Appendix E). 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 filters (Figure 5, Table 4, Appendices C and D). 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 5A, 5B, 5C, Appendix D). The guilds assemblages within the NMDS ordination space (Figure 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 5; Appendix D). These guild assemblage - individual guild correlations were two to three-times stronger than any of the correlations between environmental filters and the ordination (Appendix D), indicating strong relationships between individual guilds and 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 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 4). The final evergreen tree guild GLM contained numerous environmental filters and riparian guilds. Hydrologic variables that negatively correlated to evergreen tree guild presence were watershed area and average water table depth while the channel-form variables, sinuosity and buffer slope, were also negatively correlated to conifer 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 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 5; 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 4, Appendix E). 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 5).

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 and absence 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 5). 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 5). This CIT correctly classified 78.2% of reaches.

Discussion

We identified riparian plant guilds based on component species' divergent life history strategies that reflect each guild's resource use, reproduction, persistence, and growth in the riparian environment. Specific 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. Specific life history strategies were tied to species' canopy height and root depth that allow for persistence and growth in competitive aboveground and stressful 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 stressors like fire or herbivory (e.g. upland disturbance). 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.

We found that guild distributions can be predicted by multiple environmental gradients that filter life history strategies from individual reaches. Our results build on previous research that showed riparian forest regeneration strategies are tied to multiple environmental gradients and biotic interactions (Sarr et al. 2011) and that functional guilds that respond to such gradients are informative. The occurrence of each guild was strongly associated with environmental conditions at landscape (e.g., elevation, precipitation, temperature), watershed-buffer (e.g., fire, grazing), and local scale hydrogeomorphic variables (e.g. water table, sinuosity, gradient). Functional guilds' distributions suggest 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 effects, and climate patterns that vary across large watersheds. For example, parameters such as stream width, gradient, and sinuosity were predictors of multiple guilds, suggesting that hydrogeomorphic processes exert control on 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. 2014b).

In addition to identifying environmental filters that predict guild distributions, multiple guilds coexist at the same reach due to complementary life history strategies. Individual guilds were consistently found either to be complementary to, or mutually exclusive with other guilds,

suggesting that in some cases 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 less disturbance adapted 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, preventing 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 and 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 and predicting the occurrence of riparian guilds has focused primarily on limited environmental filters, namely flow modification, at the scale of a few reaches within a stream network (Bejarano et al. 2011, 2012). This work has limited utility when considering riparian functional plant diversity across large watersheds with diverse climatic and hydrogeomorphic settings and widely varying upland and fluvial disturbance regimes. We 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, we showed that riparian guilds were structured directly by channel-forming, flow-related metrics, and that many guilds with upland life-history strategies were linked to upland disturbances and bioclimatic factors that influence species' broad environmental tolerances.

To extend the concept of riparian guilds as a useful tool for understanding how riparian communities are structured across landscapes, species' traits for guilding must be selected for multiple disturbances, life history stages (dispersal, establishment, persistence) and limiting resources (soil moisture, nutrition, light). For example, in low-order streams where riparia blend into uplands, traits that comprise versatile non-riparian life history strategies will be important in identifying distinct 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 both within and between stream reaches.

By extending the guild concept, our 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 communities. 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 multi-tiered guild models that account for both flow-related habitat creation and upland disturbances that will change under probable land-use and climatic scenarios.

The utility of the riparian guild framework is developing rapidly and will improve as increased 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 hydraulic models that differentiate landforms' hydrogeomorphic settings along a reach. Because riparian plants respond to micro-site differences in environmental parameters such as groundwater elevations, exceedance probabilities and patchy soil nutrient availability, guilding's utility will increase as fine-scale geomorphic and vegetation data are paired with carefully selected landscape variables relevant to specific catchments. Thus, future research should, whenever possible, incorporate spatially explicit, reach-scale hydrogeomorphic diversity with broader bioclimatic environmental filter data. Future research can also build guilds using measured plant trait data, incorporating phenotypic plasticity into functional riparian guilds. Using average trait values for guilding may render environmental filters too narrowly, missing sub-optimal trait levels indicative of reduced plant performance (Cooper and Merritt 2012). 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 watershed to local scales, but also influences the operation of such processes through feedback mechanisms (Merritt 2013). For example, large wood accumulation alters local hydraulics and the subsequent deposition of sediment that forms islands that provide suitable germination sites for new riparian communities that 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 these key guilds are predictors of habitat types, this could provide information for predicting changes in aquatic and riparian habitat quality. In watersheds like the Columbia, where endangered salmonid habitat condition is a national management priority, the ability to predict habitat processes or habitat condition based on occurrence of riparian guilds could explicitly link riparian ecology to aquatic conservation (*sensu* Kominoski et al. 2011, Hough-Snee et al. 2014a).

Understanding how plant functional diversity is structured and is likely to respond to global change will be critical for managing and maintaining the ecosystem services provided by riparian plant communities. The guilding approach presented here elucidates how life history strategy-based guilds are related to multi-scale environmental filters and niche partitioning between guilds. Accordingly, the selection of life history attributes for guilding should be matched to temporally and regionally relevant environmental filters of interest. Adopting this guilding approach in explanatory and predictive capacities will allow for the development of generalizable theories on functional plant ecology that can be broadly applied to riparian management.

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Statement of author contributions

NH-S, DMM, and BBR conceptualized the project and workflows. NH-S, BGL, ALL, and LLN assembled species and trait information and built a riparian guild database. NH-S performed database work, statistical analyses, and created figures and tables. NH-S, BGL, DMM, ALL, LLN, BBR, and JMW wrote the manuscript.

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

Riparian guild – 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 (*sensu* Grime 1977). Species' measured functional traits, or categorized/estimated functional or morphological attributes are all used to describe species life history strategies. Here we 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). We 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. Guild 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. Here we assess only perennial woody vegetation and so this life history stage is largely homogeneous.

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.

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Table 1. Initial 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.

Table 2. Summaries (mean, standard deviation, minimum and maximum) of environmental filters used to predict riparian guild presence and absence. 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.

Table 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.

Table 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 the Cragg and Uhler (1970) and maximum likelihood methods. Model AIC, Δ AIC, log-likelihood Alternative models are presented in Appendix E.

714 Table 1.

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 ₂ O, 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
Bloom period	Categorical	Reproduction	Flowering timing in response to environmental cues (flooding, 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

Filtering, niche partitioning, and riparian guilds

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: moisture, nutrients, etc.
Nitrogen fixation	Categorical		Symbiotic relationships with atmospheric nitrogen-fixing bacteria in plant roots allows nitrogen acquisition in nutrient-poor alluvial substrates

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716 Table 2.

Variable scale	Environmental variable	Abbreviation in figures	Data source	Mean	SD	Min	Max
Landscape	Elevation (m)	MinElev	USGS NED	1429.32	455.89	186.00	2714.00
	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	LANDFIRE	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	LANDFIRE	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
Hydrogeomorphic (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

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719 Table 3.

Guild name (Short name)	Guild description	Guild species
Long-lived, deeply-rooted, shade tolerant, evergreen tree (Evergreen tree guild; n = 7)	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.	<i>Abies grandis</i>
		<i>Abies lasiocarpa</i>
		<i>Picea engelmannii</i>
		<i>Pinus contorta</i>
		<i>Pinus ponderosa</i>
		<i>Pseudotsuga menziesii</i>
		<i>Thuja plicata</i>
Rapidly growing, multi-stemmed, rhizomatous and thicket-forming, drought-plastic shrub guild (Upland disturbance shrub guild; n = 9)	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.	<i>Acer glabrum</i>
		<i>Alnus viridis</i>
		<i>Dasiphora fruticosa</i>
		<i>Menziesia ferruginea</i>
		<i>Philadelphus lewisii</i>
		<i>Ribes hudsonianum</i>
		<i>Salix exigua</i>
		<i>Spiraea douglasii</i>
		<i>Vaccinium scoparium</i>
Low-moderate stature, hydrophytic, multi-stemmed thicket forming shrubs (Mesic shrub guild; n = 9)	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.	<i>Alnus incana</i>
		<i>Betula occidentalis</i>
		<i>Rosa acicularis</i>
		<i>Rosa nutkana</i>
		<i>Rubus parviflorus</i>
		<i>Salix drummondiana</i>
		<i>Salix geyeriana</i>
		<i>Salix lucida</i>
		<i>Vaccinium membranaceum</i>
Medium-deeply rooted, vegetatively reproducing, alluvial substrate preferring shrubs and trees (Mesoriparian shrub and tree guild; n = 8)	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	<i>Amelanchier alnifolia</i>
		<i>Cornus sericea</i>
		<i>Populus balsamifera</i>
		<i>Salix bebbiana</i>
		<i>Salix boothii</i>
		<i>Salix melanopsis</i>
		<i>Salix sitchensis</i>
		<i>Salix wolfii</i>
Short-statured, shade-tolerant, water stress and flooding intolerant understory shrubs (Understory shrub guild; n = 9)	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.	<i>Cornus canadensis</i>
		<i>Lonicera involucrata</i>
		<i>Rhamnus alnifolia</i>
		<i>Ribes inerme</i>
		<i>Ribes lacustre</i>
		<i>Rosa woodsii</i>
		<i>Rubus idaeus</i>
		<i>Spiraea betulifolia</i>
		<i>Symphoricarpos albus</i>

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721 Table 4.

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		
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	Landscape	AvgTemp	-0.43	0.10	0.26	0.17

Filtering, niche partitioning, and riparian guilds

rooted, vegetatively reproducing, alluvial substrate preferring shrubs and trees (Mesoriparian shrub and tree guild)		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		
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		

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Figure legends

Figure 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.

Figure 2. The final dendrogram of species clustered by their traits using Gower's dissimilarity.

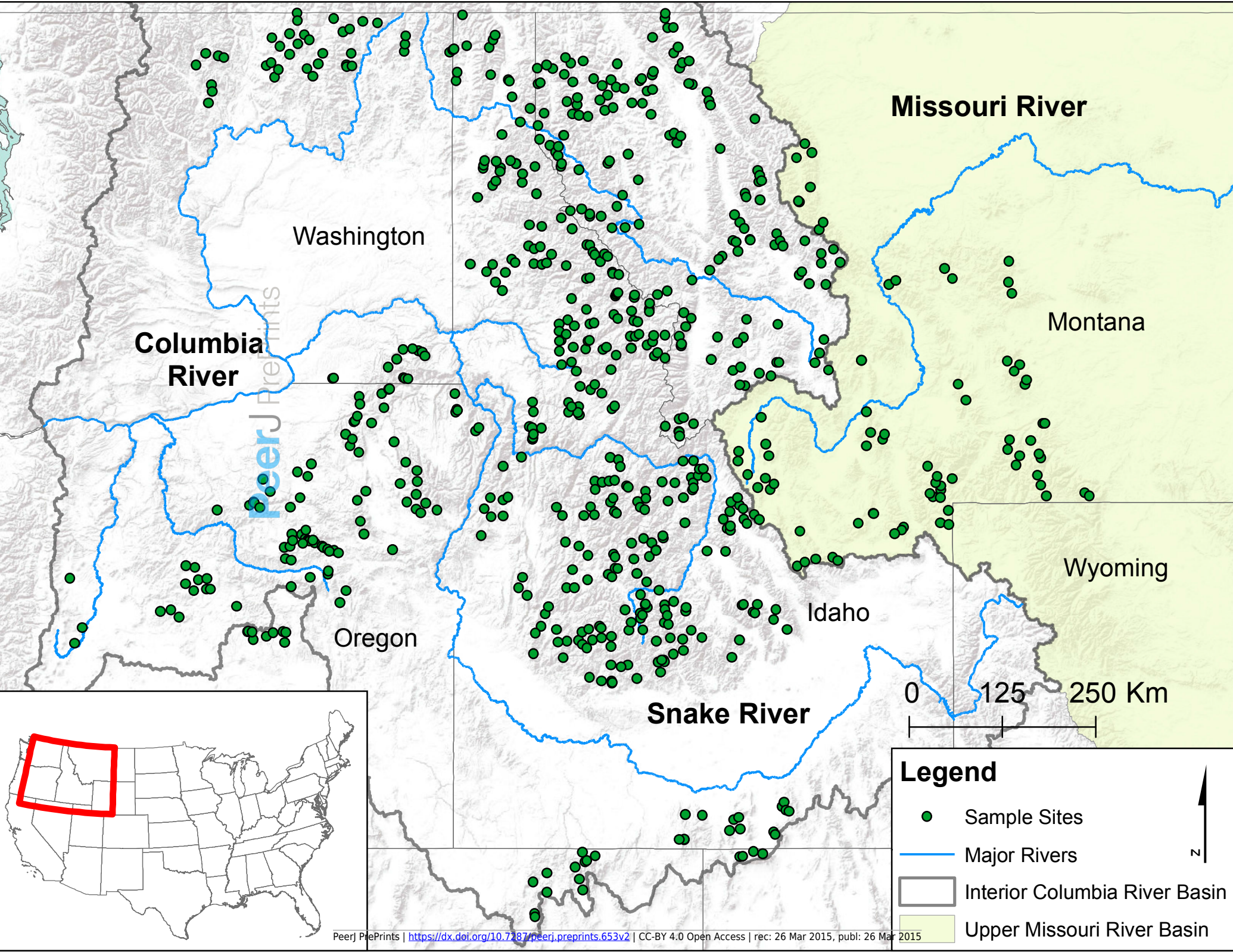
Colored bands indicate sets of three (yellow), four (blue), five (green) and six (red) guilds that were examined *post-hoc*. Five guilds were selected based on their observed ecological niches and guild fidelity using PERMANOVA: (ET) evergreen tree guild, (UD) upland disturbance guild, (MS) mesic shrub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

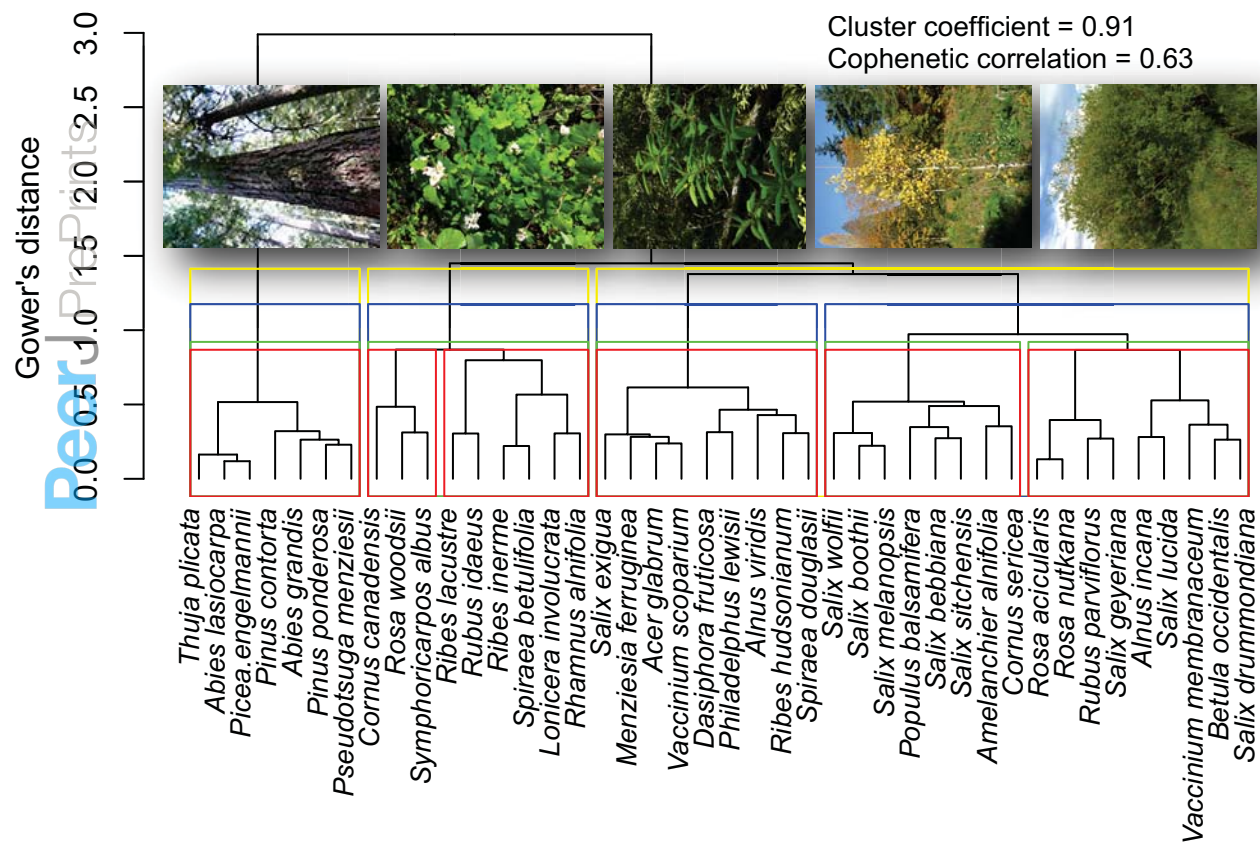
Figure 3. Principal coordinates analysis (PCoA) of species clustered by traits into guilds showed that guilds have distinct life history strategies. Figure 2A shows the individual species by their guild membership: evergreen tree guild (black), upland disturbance guild (red), mesic shrub guild (green), 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.

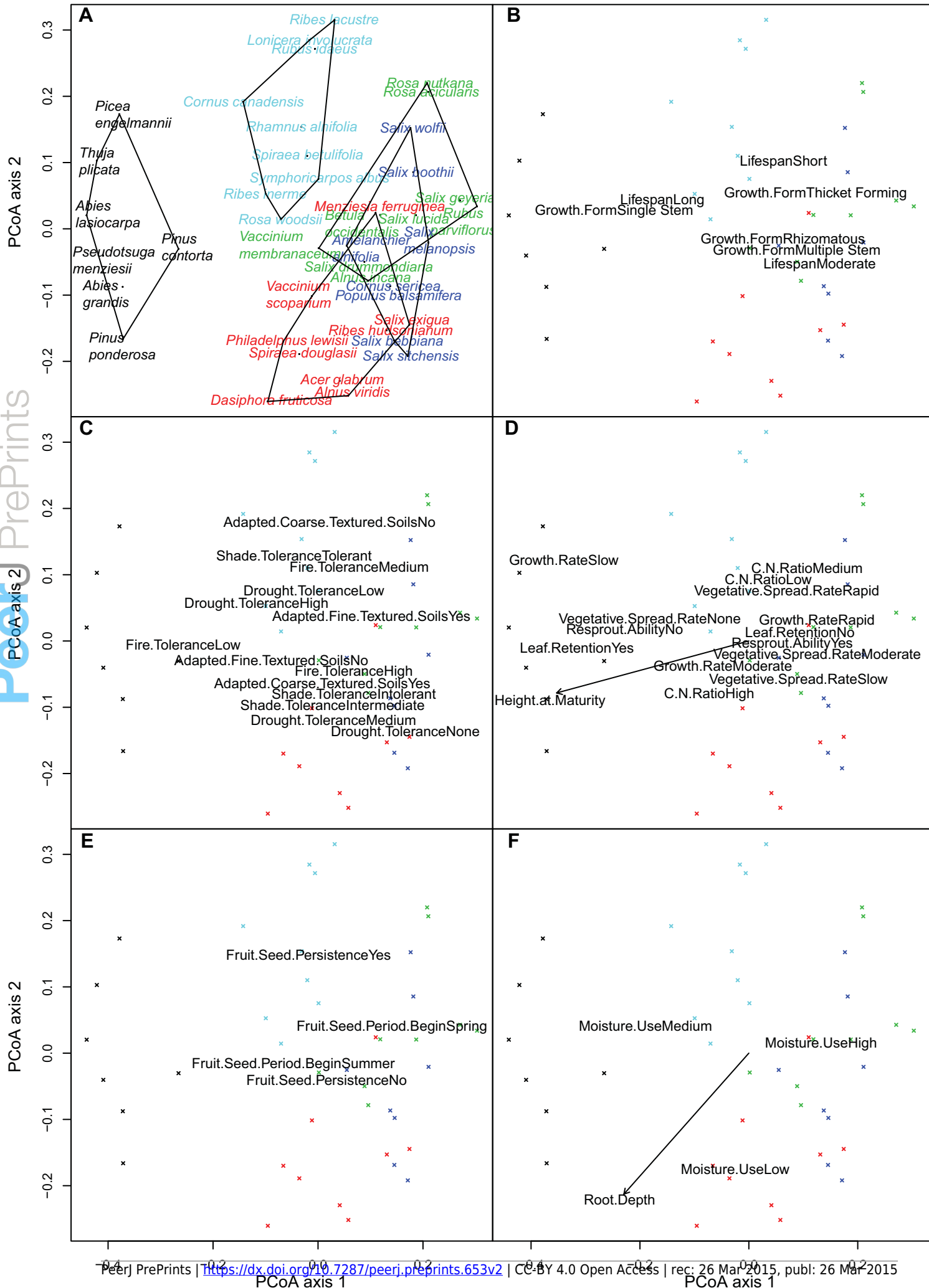
Figure 4. Summaries of the six morphological and physical attributes most strongly correlated to the principal coordinates analysis of clustered species and guilds showed different life history strategies for each guild. Guilds along the horizontal axis are from left to right, (ET) evergreen tree guild, (UD) upland disturbance guild, (MS) mesic shrub guild, (MR) mesoriparian shrub and tree guild, and (US) understory shrub guild. Rooting depth and height at maturity are presented as box and quartile plots while categorical variables are presented as histograms of levels.

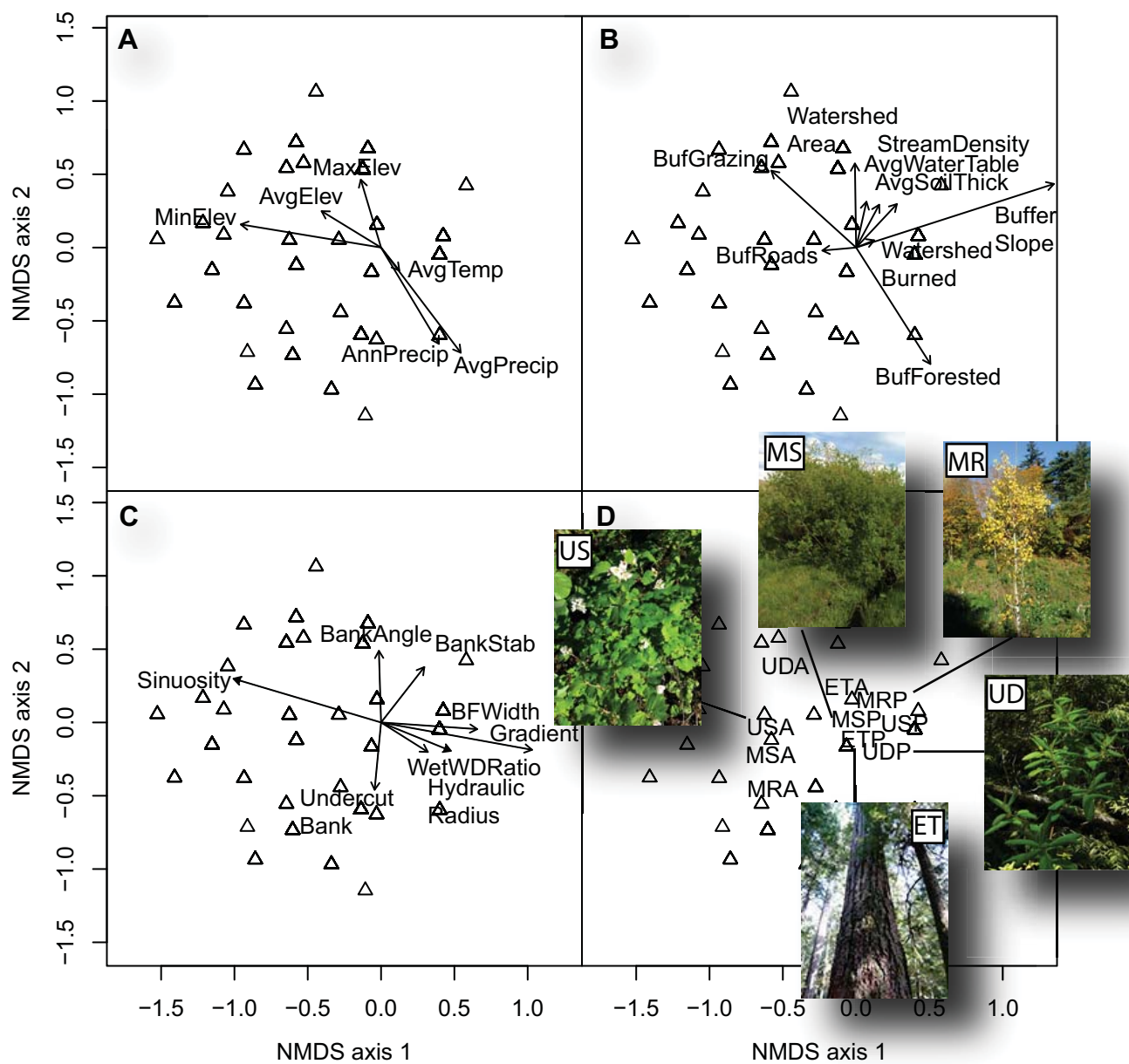
Figure 5. Fitting of environmental vectors to the final nonmetric multi-dimensional scaling (NMDS) solution for trait assemblages at each reach showed that landscape (A), watershed and stream buffer (B) and stream (C) scale environmental filters were all correlated to guild assemblage composition. The 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 study reaches. Darker points reflect more frequently occurring guild assemblages than lighter points

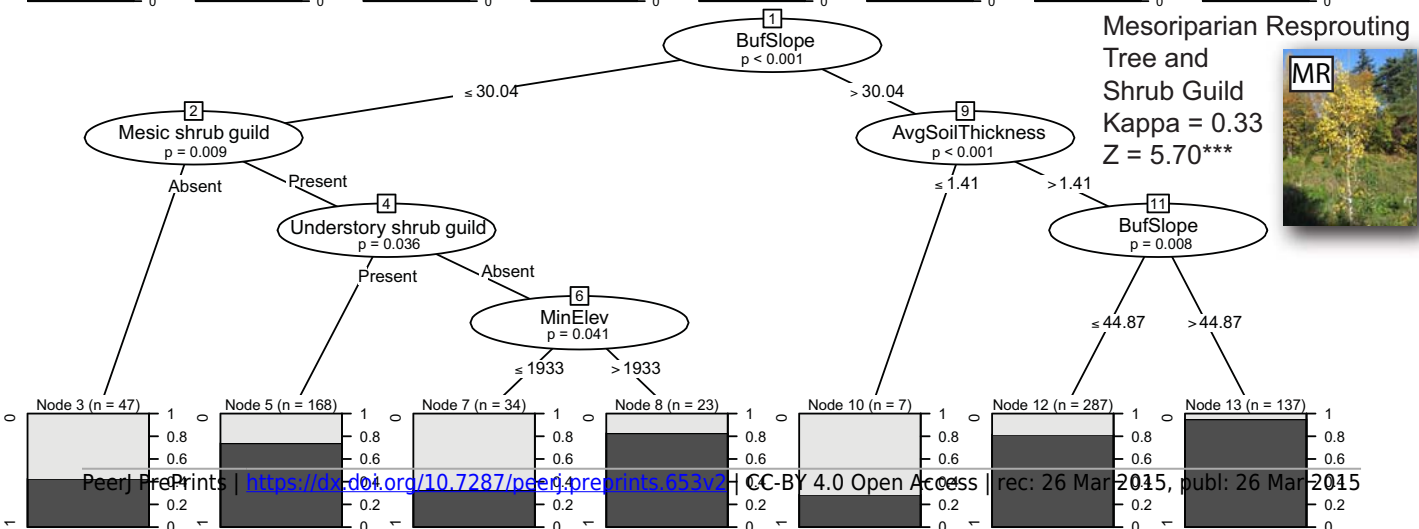
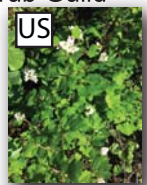
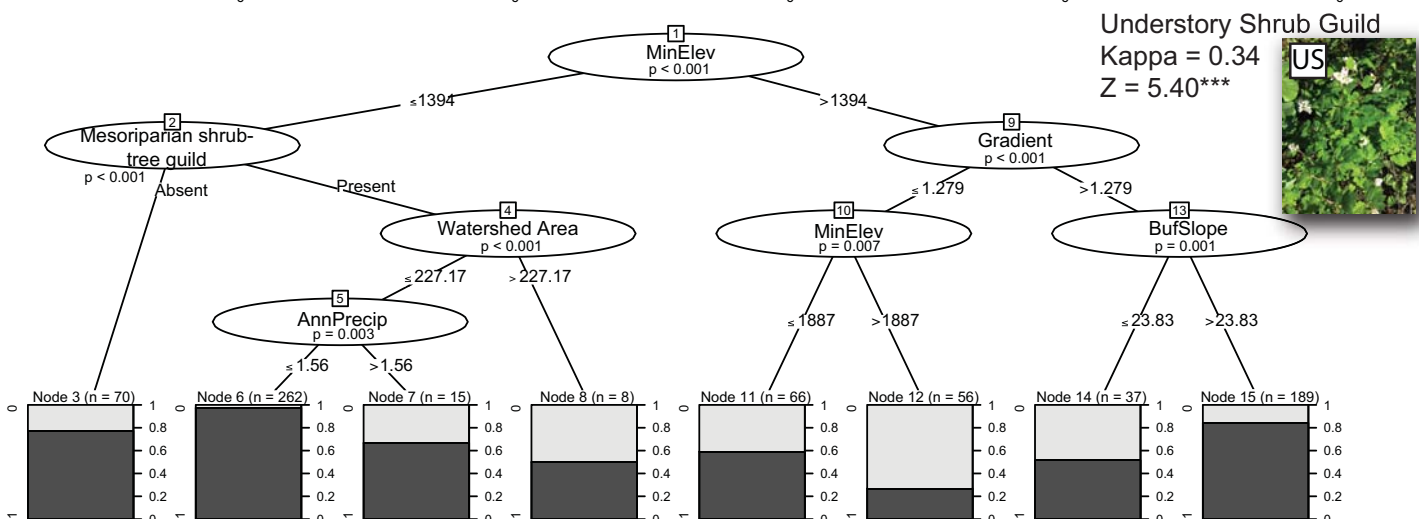
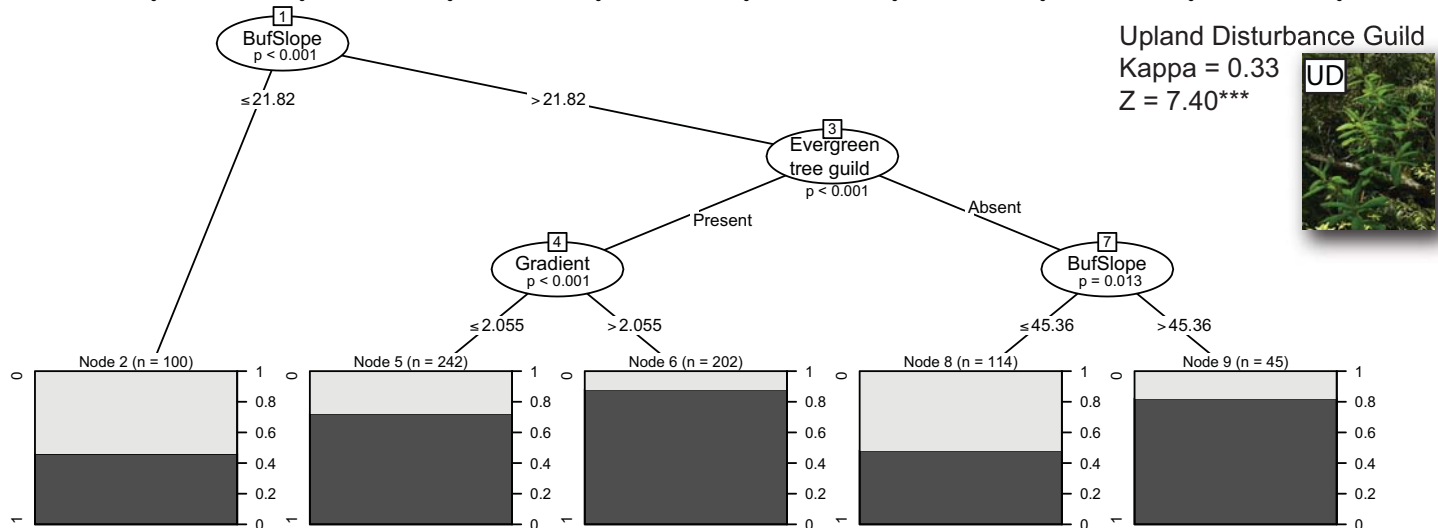
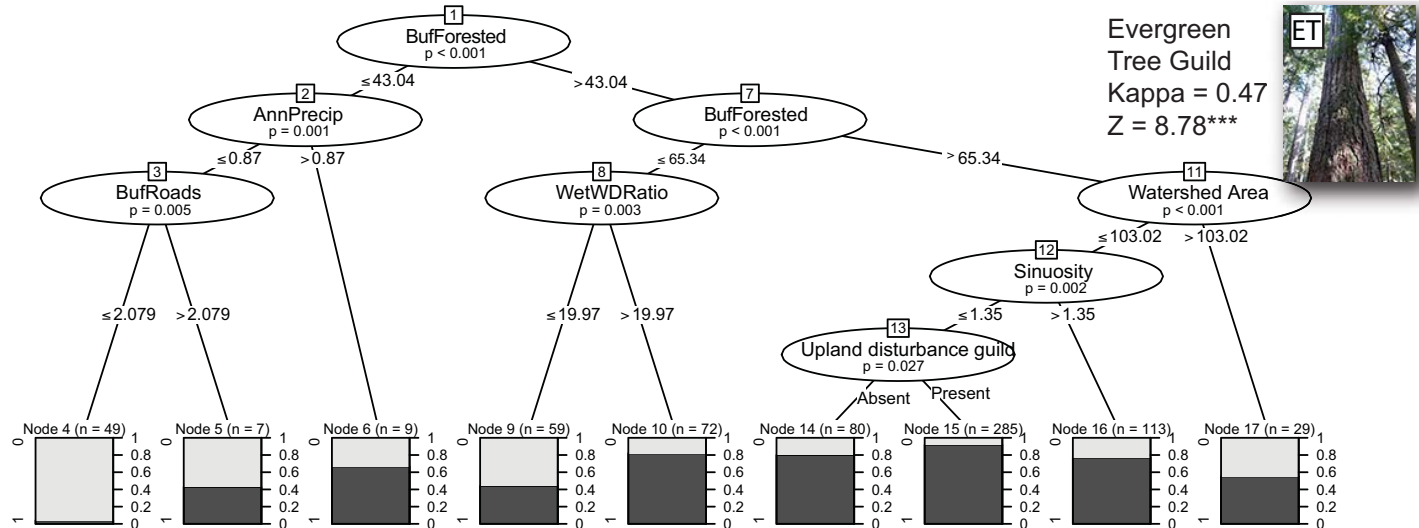
Figure 6. Significant conditional inference trees (CITs) for four of the five riparian guilds showed that guild presence and absence are predicted by both environmental filters and the presence and absence of complementary functional guilds. The mesic shrub guild's final CIT was not a better predictor of guild presence or absence than random chance and is not presented here.

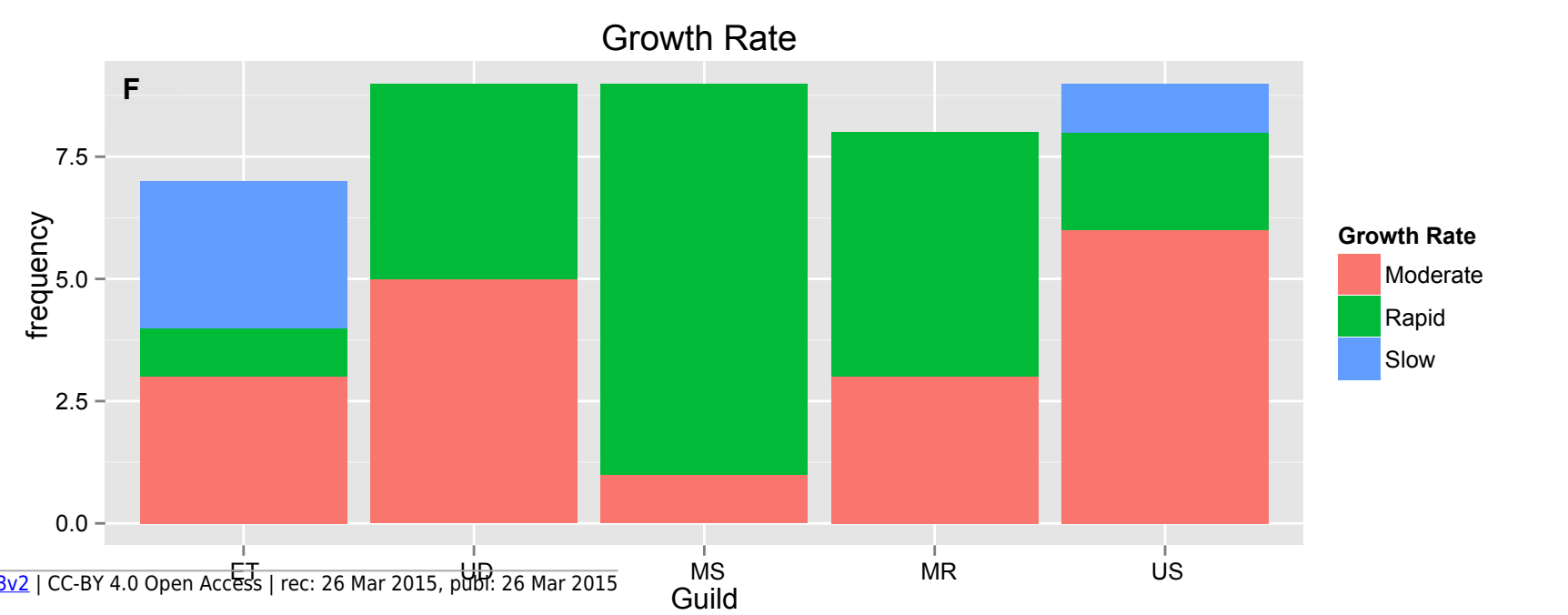
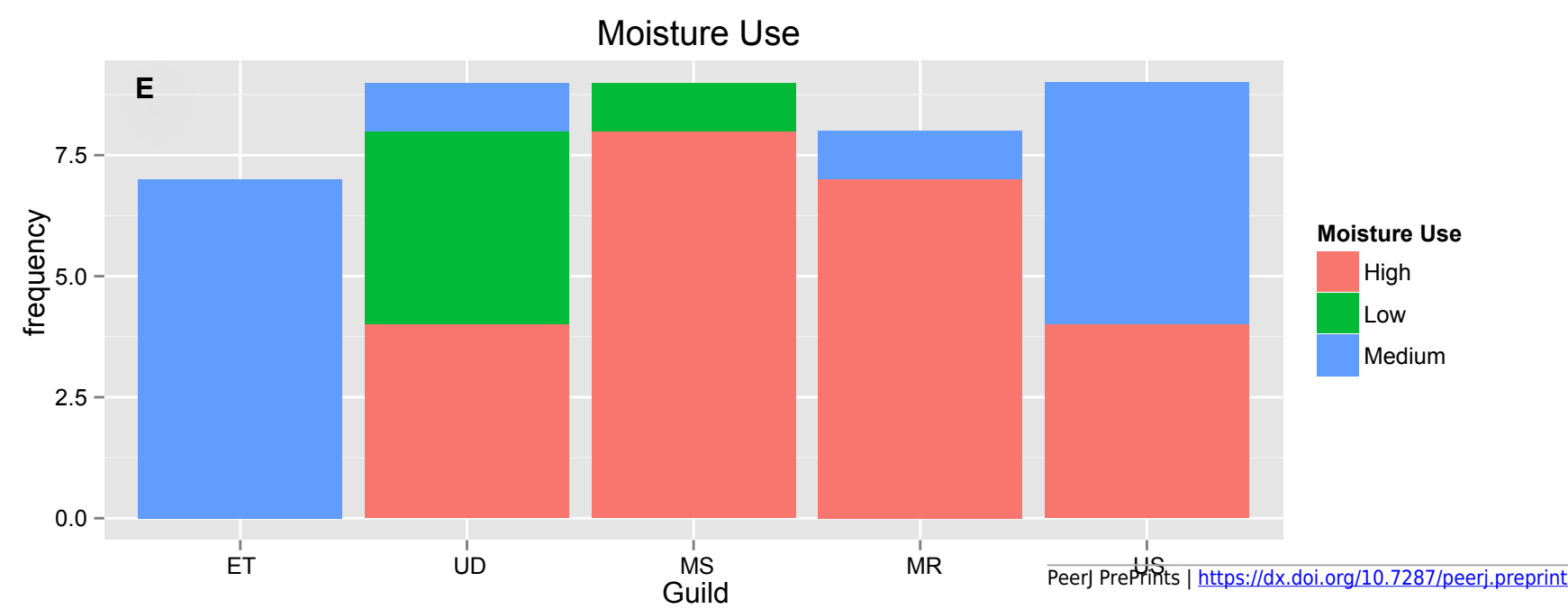
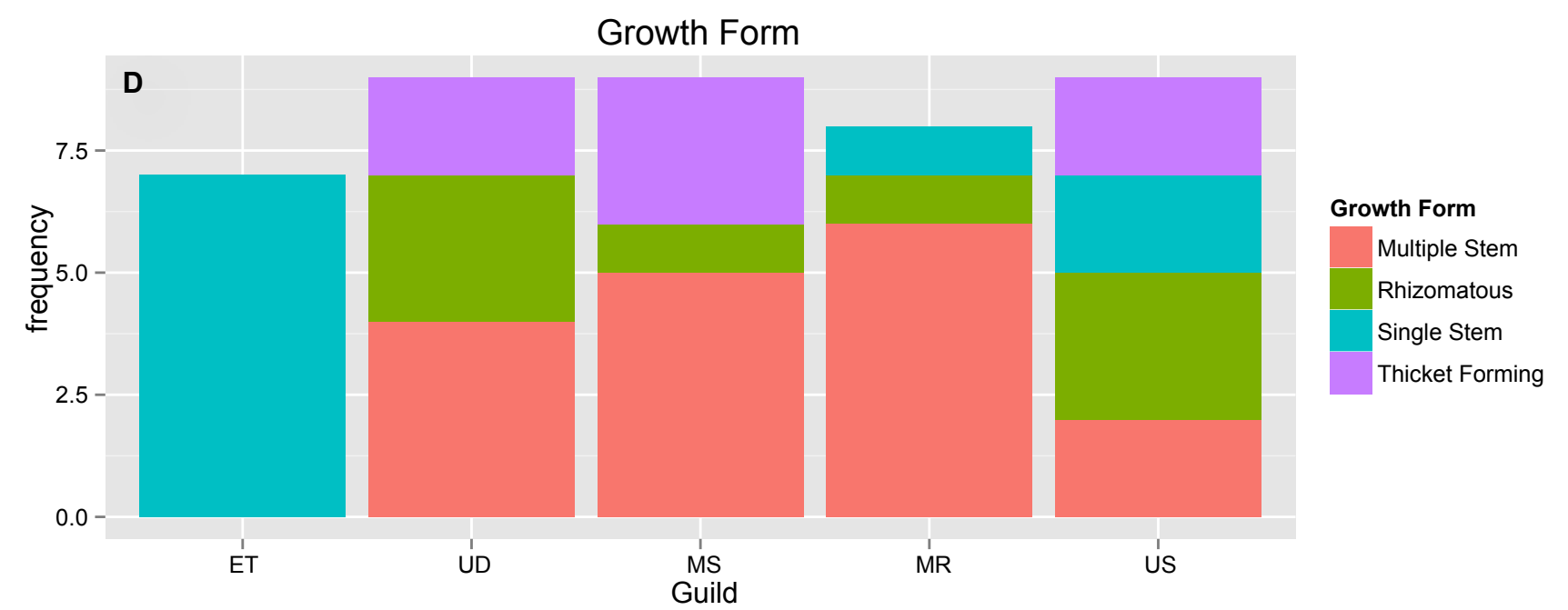
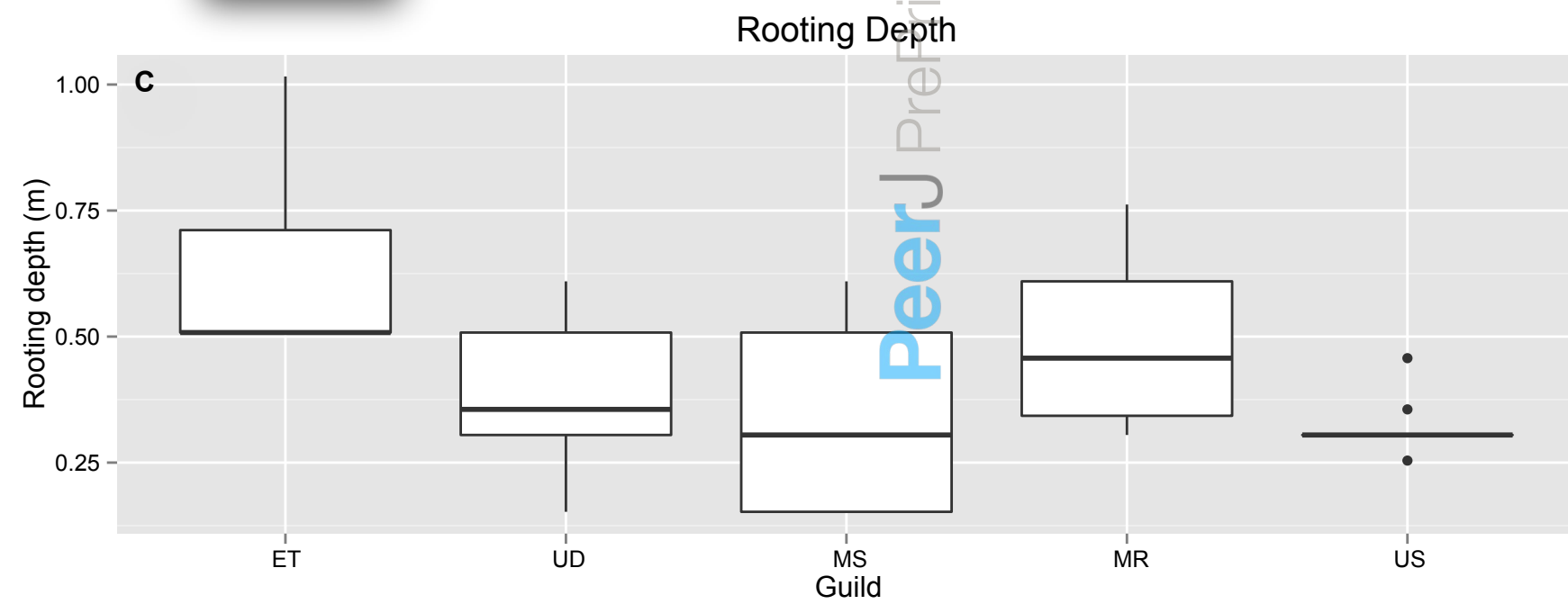
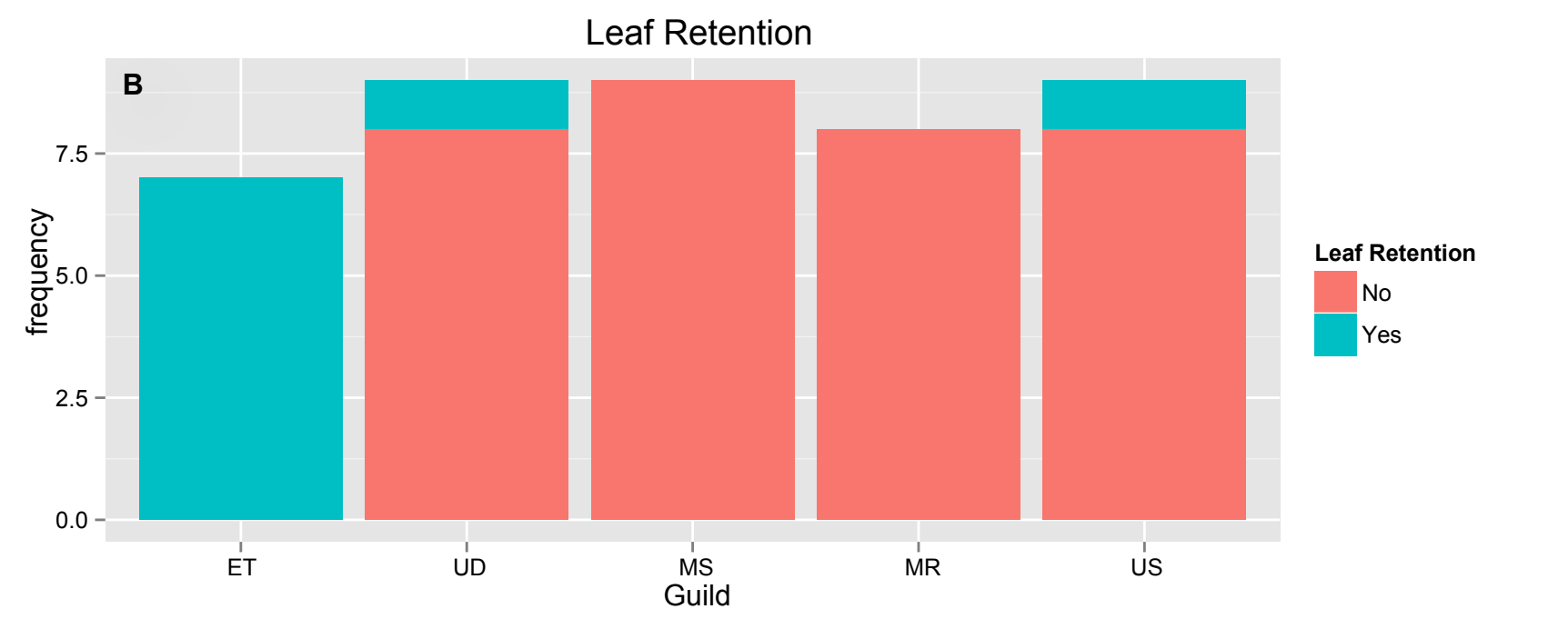
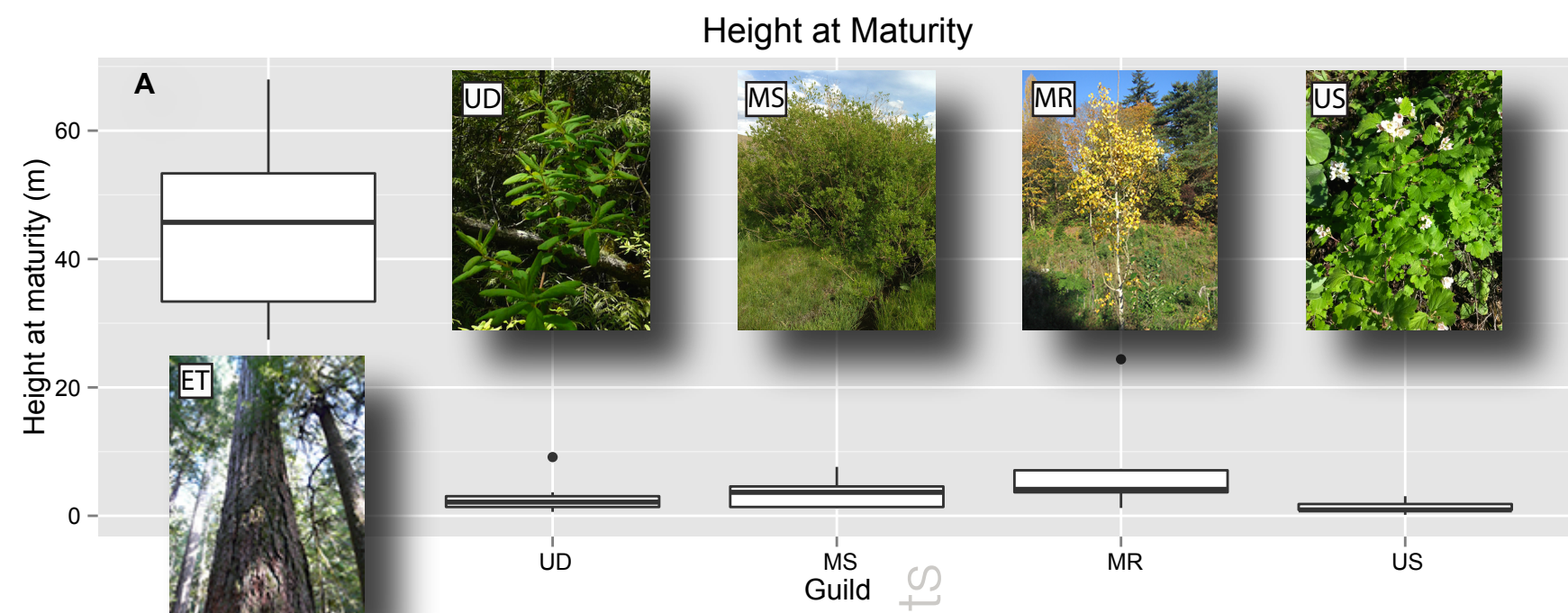












1 **Appendices**

2 Appendix A. Summary of the categorical, morphological and physical attributes by guild. Counts

3 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

Filtering, niche partitioning, and riparian guilds

	Tolerant	4	2	3	1	7
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

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- 6 Appendix B. Correlations between species' life history traits and the principal coordinate
7 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

Appendix C. 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 three. 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

18 Appendix D. Alternative plausible generalized linear models as determined by AIC.

Guild (short guild name)	Final model terms (effect)	AIC	Δ AIC	Log- like- lihood	Pseudo R^2	
					Cragg and Uhler	Max. like- lihood
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
Rapidly growing, multi-stemmed, rhizomatous and thicket-forming, drought-plastic, shrub 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)	760.70	0	-367.34	0.23	0.16

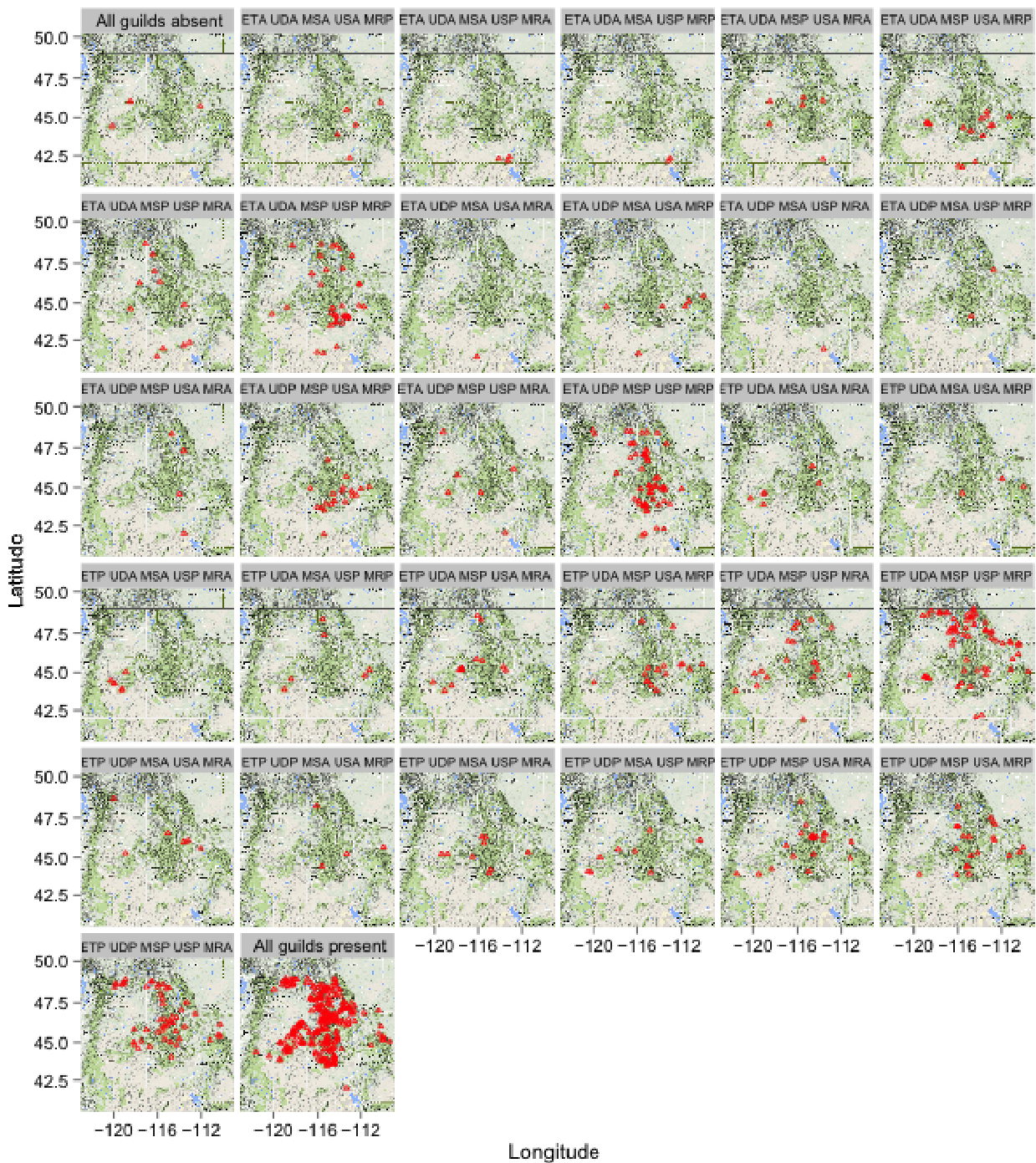
(upland disturbance guild)	BfWidth:WetWDRatio (-0.00) ET (0.57)					
	WatershedArea (-) AvgTemp (+) BufForested (+) BufSlope (-) BankAngle (-) BfWidth (+) WetWDRatio (+) Gradient (+) AvgWaterTable (-) BufSlope:BankAngle (+) BfWidth:WetWDRatio (-) ET (+) MR (+)	760.77	0.07	-366.39	0.24	0.17
Low-stature, hydrophytic, multi-stemmed thicket forming shrubs (mesic shrub guild)	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
	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
Medium-deeply rooted, vegetatively reproducing	AvgTemp (-0.43) AnnPrecip (-0.66) MinElev (-0.00) BufGrazing (0.01) BufRoads (0.12) BufSlope (0.05) BfWidth (0.12) Gradient (0.18)	657.50	0	-315.73	0.26	0.17

shrubs and trees (mesoriparian shrub and tree guild)	AvgSoilThick (1.73) ET (-0.51) MS (0.67) US (0.68)					
	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

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21 **Figures**



23 Appendix E. Map of combinations of guild assemblages across the Columbia and Missouri River
24 basins showed that a majority of reaches contained all possible guilds. Only a few reaches were
25 absent of all woody guilds. Map labels consist of guild initials and “P” for guild presence and
26 “A” for guild absence. For example, UDP corresponds to *upland disturbance present* while ETA
27 corresponds to *evergreen tree absent*, etc.

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