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

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

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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 and favor specific vegetation guilds within riverscapes is a critical step in setting baseline expectations for how riparia may respond to the environmental conditions anticipated under future global change scenarios. In this study, we ask (1) what functional riparian plant guilds exist across two major North American river basins? (2) What environmental filters shape riparian guild distributions? (3) Does resource partitioning between guilds influence guild distributions and co-occurrence? We identified riparian plant guilds, examining relationships between regional climate and watershed hydrogeomorphic characteristics, stream channel form, and co-occurring riparian guilds. Woody species composition was measured at 703 streams and each species' traits were extracted from a database in five functional areas: life form, persistence and growth, reproduction, and resource use. We clustered species into guilds by morphological characteristics and attributes related to environmental tolerances, modeling guild distributions as a product of environmental filters (stressors and resources) 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 one another species' rooting depth, canopy height and potential to resprout and grow following biomass-removing disturbance. 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

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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 riparian guilding provides a useful framework for assessing how disturbance and bioclimatic gradients shape riparian functional plant diversity. Multiple processes should be considered when the riparian response guilds framework is to be used as a land-use decision-support tool framework.

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

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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 and how can these factors be managed to achieve desired conditions for riparian areas?

To answer this question, riparian 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 trait-based approach to riparian community assembly, riparian vegetation guilding, or determination of riparian "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

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78 communities. Environmental filtering, it its most simple form, assumes that as environmental
79 conditions change, specific life history strategies and traits will be selected for at a given
80 location, leading to the assembly of communities with morphological and physiological
81 tolerances suited to a given environment (Keddy 1992, Díaz et al. 1998). When the dominant
82 environmental filters that shape riparian biodiversity are known, then riparian guilds can be
83 probabilistically modeled to predict ecosystem change as environmental filters shift (Merritt et
84 al. 2009).While many environmental filters shape riparian plant communities (Hough-Snee et al.
85 2014b), the most commonly studied environmental drivers of riparian vegetation are fluvial
86 processes in large, alluvial rivers (Naiman et al. 2000, Merritt and Cooper 2000, Stella et al.
87 2013).
88
89 Not coincidentally, riparian plant communities have commonly been characterized based on the
90 relationships between species composition and the depth, duration, and timing of stream flow or
91 surrogate flow measurements like stream order (Ekness and Randhir 2007, Stella and Battles
92 2010, Viers et al. 2012, Perry et al. 2013). Indeed, within large rivers, hydrogeomorphic
93 processes that dictate intra- and interannual shifts in overbank flooding, erosion, deposition, and
94 hydrologic recession play a strong role in shaping vegetation functional diversity, including
95 guilds (Shafroth et al. 2002, Katz et al. 2009). However, many riparian ecosystems, especially
96 those in low-order settings or headwater streams, are tightly linked to more than just reach-level
97 hydrogeomorphic gradients (Hough-Snee et al. 2014b). Additional environmental filters include
98 biotic interactions (Whigham et al. 2012) and landscape to local-scale processes including
99 climate and disturbance (Hough-Snee et al. 2014b).
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Despite the global importance of riparian ecosystems, 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 large landscapes. The environmental filters that control riparian plant functional diversity in low-order streams have rarely been elucidated at broad spatial scales or across multiple process domains (Hough-Snee et al. 2014b). Riparian plant communities assemble in response to 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). These filters select for sets of traits, both within and between species, which allow those species and guilds with shared life history strategies to successfully grow, reproduce, and maintain populations. While riparian environmental filters may occur at multiple spatial and temporal scales within a given environment, filtering can select for comparable sets of traits or guilds with shared life history strategies regardless of the dominant processes at work.

Identifying trait-based plant assemblages provides a reasonable 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). 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 guilding may also provide insights into the larger environmental filters that shape riparian plant functional diversity across landscapes. Riparian guilding 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

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environmental filters, including water availability and the frequency and magnitude of disturbance, 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 where individual species may not be shared.

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:

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147 1. Can riparian woody plant guilds be identified based on species' shared morphological and life
148 history attributes? If so, what are the functional roles of these guilds and the nature of their
149 dominant life history strategies?
150 2. How do environmental filters and the presence and absence of complementary guilds shape
151 the distribution of *individual* riparian guilds across landscapes? How do environmental filters
152 shape *guild assemblages*, the combination of all guilds present at a given site, across landscapes?
153

154 **Methods**

155 *Study Sites*

156 We selected 703 low-order stream reaches within the interior Columbia and upper Missouri
157 River basins (Figure 1) for inclusion in the study. These reaches are part of an existing stream
158 monitoring program and were sampled under a spatially balanced, probabilistic sampling design
159 (Kershner et al. 2004). All reaches were low-gradient (≈ 3%) and occur within subwatersheds
160 (USGS 6th order hydrologic unit code) with > 50% federal ownership upstream of the sampled
161 reach. Study reaches are managed by the U.S. Bureau of Land Management (BLM) or Forest
162 Service (USFS) and occur across the physical and climatic gradients representative of the interior
163 Columbia and upper Missouri River basins.
164

165 *Vegetation field data*

166 Riparian vegetation was sampled during base flow conditions during the growing season
167 (June-September). Greenline vegetation data were collected in 42–50 quadrats (50cm x 20cm)
168 per reach, based on reach length and bankfull width. The greenline is the point at which the first
169 rooted perennial vegetation is present along a stream (Winward 2000, PIBO EM 2012a) and is

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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 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 trait category based on that attribute's predominant role in species survival, growth, or reproduction in the riparian environment (Table 1).

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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).

Environmental metrics

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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; (PIBO EM 2012b). We 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 patchess serve as corridors for propagule dispersal following disturbance and tree canopies shape understory light and humidity, we identified the proportion of each watershed and reach covered by overstory forest vegetation using LANDFIRE (USGS 2012). We also used LANDFIRE data to estimate the proportion of each watershed that had burned between 1997 and 2007. We calculated road density (km/km^2) within each buffer and watershed because roads serve as plant dispersal vectors and alter local hydrology. We 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).

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

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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 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. 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 $p < 0.05$.

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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.

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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, Figure 2). 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, guild functional attribute plots (Appendices A, B, C), and PCoA plot of species and guild by functional attributes (Figure 2). 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 2 and 3, Appendices B, C). 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

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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 4, Appendix F). 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 4, Table 4, Appendix C, 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 4A, 4B, 4C, Appendix D). The guilds assemblages within the NMDS ordination space (Figure 4D) 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 4; 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 (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

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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

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353 slope-bank angle interaction were negatively correlated to guild presence, while buffer slope,
354 bank angle, bankfull width and the mesoriparian shrub and tree and understory guilds' presence
355 positively correlated to this guild. The mesic shrub guild's CIT was solely comprised of the
356 understory shrub and mesoriparian shrub and tree guilds' presence and absence. This model
357 correctly predicted mesic shrub guild presence and absence at 89.9% of reaches, but failed to
358 successfully predict any absences and did not show more predictive power than random chance
359 (Kappa = 0; Z = 0; $P = 0.5$).
360
361 The understory shrub guild was inversely correlated to average temperature, annual precipitation,
362 minimum elevation, buffer forest cover and bank angle, predominantly landscape scale
363 environmental filters, within its final GLM. This guild was positively correlated to the presence
364 of all other guilds, except the upland disturbance guild, which was not included in the final
365 GLM. Gradient and buffer slope were also positively correlated to the presence of this guild
366 indicating a preference toward steeper streams and riparian areas. The presence and absence of
367 the mesoriparian shrub and tree guild was significant in the CIT modeling of the understory
368 shrub guild's distribution (Figure 5). The final understory guild CIT successfully predicted guild
369 presence and absence at 82.7% reaches.
370
371 The mesoriparian shrub and tree guild was positively related to the mesic shrub and understory
372 shrub guilds, but negatively associated with the evergreen tree guild. This guild was also
373 negatively related to temperature and elevation and positively related to bankfull width, buffer
374 slope, and grazing frequency in the buffer. The CIT model for the mesoriparian shrub and tree
375 guild showed that in less steeply sloped reaches the mesic shrub and understory shrub guilds

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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 are tied to 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 from guilds that responded to primarily other stressors 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 fire 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 the occurrence of these guilds can be predicted by multiple environmental gradients that filter life history strategies from individual reaches. Our results build on previous

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399 research that showed riparian forest regeneration strategies are tied to multiple environmental
400 gradients and biotic interactions (Sarr et al. 2011) and that functional guilds that respond to such
401 gradients are informative. The occurrence of each guild was strongly associated with
402 environmental conditions at landscape (e.g., elevation, precipitation and temperature),
403 watershed-buffer (e.g., fire, grazing), and local scale hydrogeomorphic variables (e.g. watershed
404 area, water table depth, sinuosity, gradient). Functional guilds' distributions suggest that life-
405 history strategies are selected for by multiple environmental filters (selective pressures) that are
406 reflective of particular process domains, such as hydrogeomorphic processes, local disturbance
407 effects, and climate patterns that vary across large watersheds. For example, parameters such as
408 stream width, gradient, and sinuosity were predictors of multiple guilds, suggesting that
409 hydrogeomorphic processes exert control on local life history strategy diversity. This finding
410 corresponds to research that showed wetland and riparian communities comprised of co-existing
411 species were similarly correlated to multiple environmental filters (Lemly and Cooper 2011,
412 Hough-Snee et al. 2014b).
413
414 In addition to identifying environmental filters that predict guild distributions, we found
415 evidence for the coexistence of multiple guilds at the same reach. Individual guilds were
416 consistently found either to be complementary to or mutually exclusive with other guilds,
417 suggesting that in some cases guild's species differentially partition their niches within similar
418 environments. For example, the evergreen tree guild was positively associated with both the
419 upland disturbance guild and the canopy understory guild, likely because these guilds acquire
420 resources differently when co-existing in similar environments. The less disturbance adapted
421 evergreen tree guild is unlikely to occupy disturbed forest edges suitable for the upland

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422 disturbance guild, and thus the two were often found together at a site (i.e., the two guilds
423 occupied different unique locations within a site, preventing competitive exclusion). The
424 understory shrub guild is positively associated with the evergreen tree guild because the tall,
425 mature overstory trees provide suitable shaded habitat for the shade-tolerant understory guild.
426 Both the evergreen tree and upland disturbance and understory shrub guilds' rooting depths
427 differ enough to suggest that each guild acquires soil resources independently within the soil
428 profile.
429
430 Previous work identifying and predicting the occurrence of riparian guilds has focused primarily
431 on limited environmental filters, namely flow modification, at the scale of a few reaches within a
432 stream network (Bejarano et al. 2011, 2012). This work may have limited utility when
433 considering riparian functional plant diversity across broad landscapes and large watersheds with
434 diverse climatic and hydrogeomorphic settings and upland and fluvial disturbance regimes. We
435 took advantage of extensive riparian monitoring data to show that the riparian guilds concept can
436 and should be extended to landscapes with diverse physiographic and bioclimatic settings such
437 as the Columbia and Missouri River Basins. For example we showed that riparian guilds were
438 structured directly by flow-related metrics that shape channel form and that many guilds with
439 upland life-history strategies were linked to upland disturbances, like fire and grazing, and
440 bioclimatic factors that influence species' broad range limits and environmental tolerances.
441
442 To extend the concept of riparian guilds as a useful tool for understanding how riparian
443 communities are structured across broad landscapes, species' traits for guilding must be selected
444 for multiple disturbances, life history stages (dispersal, establishment, persistence) and limiting

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445 resources. For example, in low-order streams with high hillslope connectivity, traits that
446 comprise versatile non-riparian life history strategies are likely to be important in identifying
447 distinct guilds. Linking riparian guilds to multiple environmental filters and process domains
448 should improve understanding of how riparian communities are likely to respond to future
449 changes in climate and disturbance.
450
451 By extending the guild concept, our approach provides a basis for quantifying trait-based
452 vegetation groups and community assembly, which can be used to model probable riparian
453 vegetation outcomes in future disturbance and climate scenarios (Kominoski et al. 2013). The
454 multi-scale approach used here shows utility across diverse landscapes where stream physical
455 setting and local management (e.g., grazing and logging pressure) are likely to vary within large
456 catchments, and regional drivers such as climate and climate-induced flow alteration influence
457 plant communities more broadly. The riparian guild framework as applied in this study, provides
458 a powerful, flexible approach to identify and prioritize the responses of functional plant diversity
459 to multiple environmental filters. Because riparian ecosystems will respond to multiple
460 environmental stressors under future global change scenarios, managers should consider building
461 multi-tiered guild models that account not only for flow, but also those disturbances that are
462 likely to change under probable land-use and climatic scenarios.
463
464 The utility of the riparian guild framework is developing rapidly and its utility will improve as
465 increased stream morphology, riparian vegetation, and measured plant trait data become
466 available. The riparian vegetation and environmental data in this study are relatively coarse,
467 using reach-level species presence without linking guild locations to hydraulic models that

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differentiate landforms' hydrogeomorphic settings along a reach. Because riparian plants are likely to respond to micro-site differences in environmental parameters such as groundwater elevations, exceedance probabilities and patchy soil nutrient availability, guilding will likely reach peak utility when fine-scale geomorphic and vegetation data are paired with carefully selected landscape variables that are relevant to specific catchment locations. 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 could be captured by trait plasticity information and measured trait data, building more robust 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 fish habitat quality. In watersheds like the Columbia, where endangered salmonid habitat condition is a national management priority, the

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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 and other plant communities. The guilding approach presented here showed that 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 the dominant filters within the region of interest. Adopting this guilding approach in explanatory and predictive capacities will likely allow the development of generalizable theories on functional plant ecology that can be applied to riparian management at large scales.

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Statement of author contributions

NH-S, DMM, BGL, ALL, LLN, 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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674 **Tables**

675 Table 1. Initial functional and morphological attributes used in the determination of riparian
676 functional guilds. Species trait values were acquired from the USDA PLANTS database (USDA
677 NRCS 2010).

678

679 Table 2. Summaries of environmental variables measured for each reach and used to predict
680 riparian guild presence and absence. Buffer variables were summarized within a 90-m buffer of
681 the stream reach, while watershed and landscape variables were summarized for the upstream
682 area above each field-sampled reach. Stream variables were field-sampled at individual reaches.

683

684 Table 3. Riparian functional guilds identified based on shared species traits.

685

686 Table 4. Final generalized linear models for the presence and absence of each habitat guild. Bold
687 parameters were significant terms in the final model. Models were selected using backward
688 variable selection and iteratively comparing AIC and log-likelihood at each step. Pseudo R^2 are
689 reported using the Cragg and Uhler (1970) and maximum likelihood methods.

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691 Table 1.

Life history and morphological attributes	Variable type	Dominant life history stage	Plant-environment associations in the riparian environment
Growth Form	Categorical	Life Form	Overbank flooding response, light and water acquisition within canopies
Lifespan	Categorical	Life Form	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	Persistence and Growth	Seed dispersal, germination and plant water relations in alluvial substrate
Adapted to Medium Textured Soils	Categorical	Persistence and Growth	Seed dispersal, germination and plant water relations in alluvial substrate
Anaerobic Tolerance	Categorical	Persistence and Growth	Depth, duration and timing of soil saturation from overbank flooding
Drought Tolerance	Categorical	Persistence and Growth	Response to seasonal soil drying and moisture deficit
Fire Tolerance	Categorical	Persistence and Growth	Ability to for stems to resprout, and/or seeds to disperse or germinate following fire
Growth Rate	Categorical	Persistence and Growth	Biomass production from photosynthetic carbon gains minus respiration costs
C:N Ratio	Categorical	Persistence and Growth	Leaf-level photosynthesis, tissue construction and maintenance from soil nutrition and atmospheric light, H_2O and CO_2
Height at Maturity	Continuous	Persistence and Growth	Ability to acquire atmospheric light and CO_2; response to flooding and fluvial shear stress
Leaf Retention	Categorical	Persistence and Growth	Maintenance and construction costs of photosynthetic tissues
Resprout Ability	Categorical	Persistence and Growth	Response to flooding and fluvial shear stress, fire, and herbivory
Shade Tolerance	Categorical	Persistence and Growth	Capability to account for cellular respiration costs and gain carbon in reduced light environments like forest understories
Vegetative Spread Rate	Categorical	Persistence and Growth	Ability to reproduce and grow rapidly following disturbance
Bloom Period	Categorical	Reproduction	Timing of flowering in response to environmental cues (flooding, fire, climate, etc.)
Fruit/Seed Abundance	Categorical	Reproduction	The amount of seed corresponds to the dispersal and reproductive strategy of a species during flood recession
Fruit/Seed Period Begin	Categorical	Reproduction	Timing of seed set relative to freshet and peak floods in snow-melt dominated streams

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Fruit/Seed Persistence	Categorical	Reproduction	How long propagules remain viable and persist following dispersal
Live-Staking	Categorical	Reproduction	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	Resource Use	Potential for an individual to acquire soil resources, including deep moisture, nutrients, etc.
Nitrogen Fixation	Categorical	Resource Use	Symbiotic relationships with atmospheric nitrogen-fixing bacteria in plant roots allows nitrogen acquisition in nutrient-poor alluvial substrates

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693 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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696 Table 3.

Guild name (Short 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*
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*

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698 Table 4.

Riparian guild	Final model terms (effect)	AIC	Log-like-lihood	Pseudo R^2	
				Cragg and Uhler	Max. like-lihood
Long-lived, deeply-rooted, shade tolerant, evergreen tree (Evergreen tree guild)	**WatershedArea** (-) AvgTemp (-) **AnnPrecip (+) BufForested (+) WatershedBurned** (-) BufRoads **(+) BufSlope (-) WetWDRatio (+) Sinuosity (-)** Gradient + **AvgWaterTable (-) UD (+) US (+)** WR (-)	591.59	-280.80	0.42	0.28
Rapidly growing, multi-stemmed, rhizomatous and thicket-forming, drought-plastic shrub guild (Upland disturbance shrub guild)	WatershedArea **(-) AvgTemp (+) BufForested (+)** BufSlope **(-) BankAngle (-) BfWidth (+)** WetWDRatio **(+) Gradient (+) AvgWaterTable (-) BufSlope:BankAngle (+)** BfWidth:WetWDRatio **(-) C (+)**	760.70	-367.34	0.23	0.16
Low-moderate stature, hydrophytic, multi-stemmed thicket forming shrubs (Mesic shrub guild)	WatershedArea (-) **AvgTemp** (-) AnnPrecip (-) **MinElev** (-) **BufSlope (+) BankAngle (+) BfWidth (+)** WetWDRatio (-) Sinuosity **(-)** BfWidth:WetWDRatio (-) **BufSlope:BankAngle (-) US** (+) **WR** (+)	376.25	-174.13	0.31	0.15
Medium-deeply rooted, vegetatively reproducing, alluvial substrate preferring shrubs and trees (Mesoriparian shrub and tree guild)	**AvgTemp** (-) AnnPrecip (-) **MinElev** (-) **BufGrazing** (+) BufRoads (+) **BufSlope** (+) **BfWidth** (+) Gradient (+) **AvgSoilThick** (+) C (-) **MS** (+) **US** (+)	657.50	-315.73	0.26	0.17
Short-statured, shade-tolerant, water stress and flooding intolerant understory shrubs (Understory shrub guild)	WatershedArea (-) **AvgTemp** (-) **AnnPrecip** (-) **MinElev** (-) **BufForested** (-) BufRoads (+) **BufSlope** (+) BankAngle (-) **Gradient** (+) **AnnPrecip:Elev** (+) **C** (+) **MS** (+) **WR** (+)	581.67	-276.83	0.33	0.21

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701 **Figure legends**

702 Figure 1. The 703 study reaches in the Missouri and Columbia River basins where riparian
703 vegetation and stream attributes were sampled.

704

705 Figure 2. Principal coordinate analysis (PCoA) of species based on trait composition showed that
706 guilds occupy distinct niches within the riparian envionment. Figure 2A shows the individual
707 species by their guild membership. Continuous traits (vectors) and categorical traits (text)
708 significant at an alpha of $p < 0.01$ are plotted over the PCoA solution by life form (B),
709 persistence and growth (C and D), reproduction (E), and resource use (F). Traits are shown in the
710 PCoA ordination space over points that correspond to each species, colored by functional guild
711 (A). The full suite of traits and species used in guilding are described further in Tables 1 and 3.

712

713 Figure 3. Summaries of the six morphological and physical attributes most strongly correlated to
714 the principal coordinate analysis of clustered species and guilds showed different life history
715 strategies for each guild. Guilds along the horizontal axis are from left to right, (1) evergreen tree
716 guild, (2) upland disturbance guild, (3) mesic shrub guild, (4) mesoriparian shrub and tree guild,
717 and (5) understory shrub guild.

718

719 Figure 4. Fitting of environmental vectors to the final nonmetric multi-dimensional scaling
720 solution showed that landscape (A), watershed and buffer (B) and stream (C) scale
721 environmental filters were all correlated to the distribution of guild assemblages across the study
722 area. The presence and absence of individual species guilds (D) within a reach showed clear

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723 separation between guild assemblages. Abbreviations for environmental factors and guild vectors
724 correspond to those found in tables two and three.
725
726 Figure 5. Significant conditional inference trees (CITs) for four of the five riparian guilds
727 showed that guild presence and absence are predicted by both environmental filters and the
728 presence and absence of complementary functional guilds. The mesic shrub guild's final CIT did
729 was not a better predictor of guild presence or absence than random chance and is not presented
730 here.

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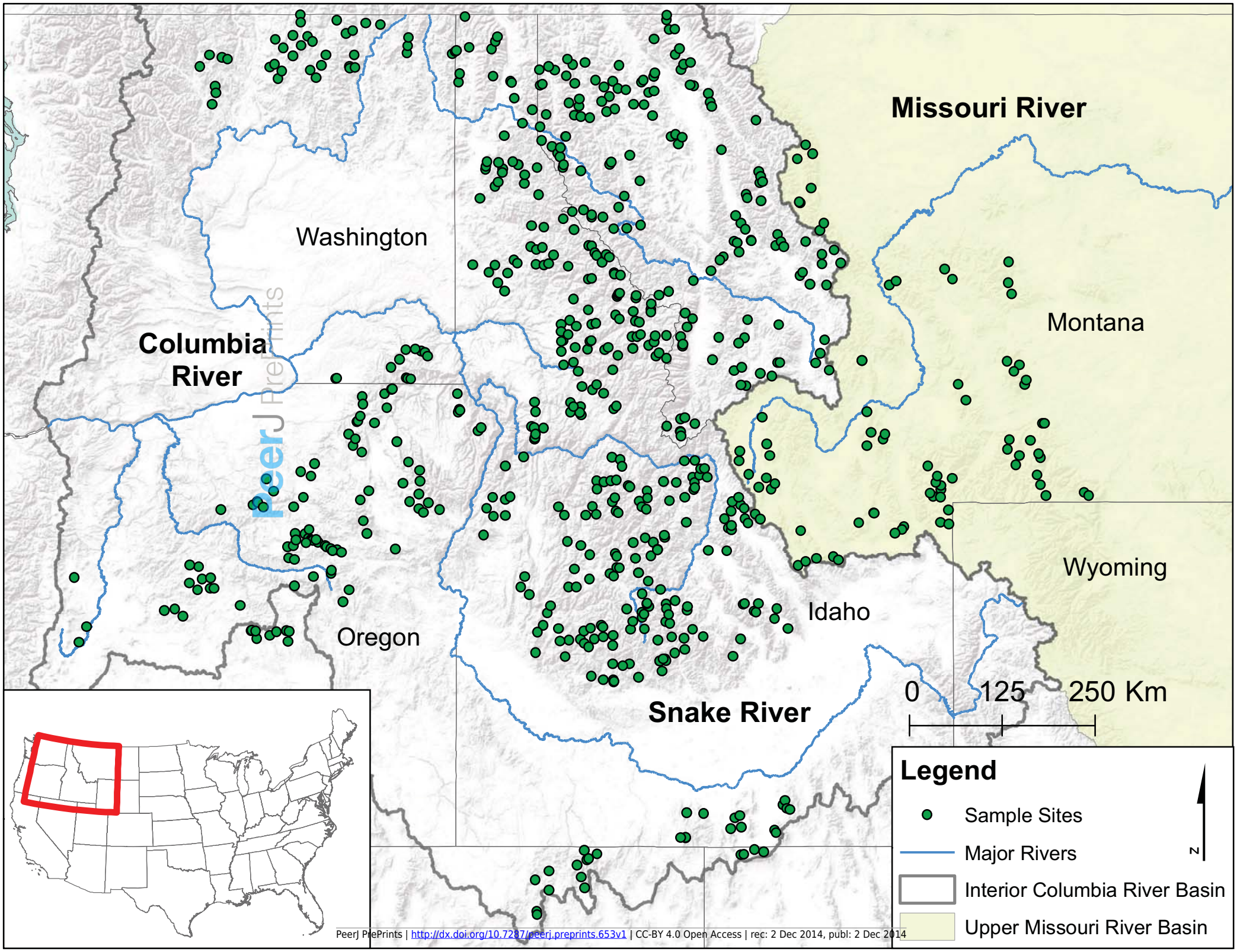

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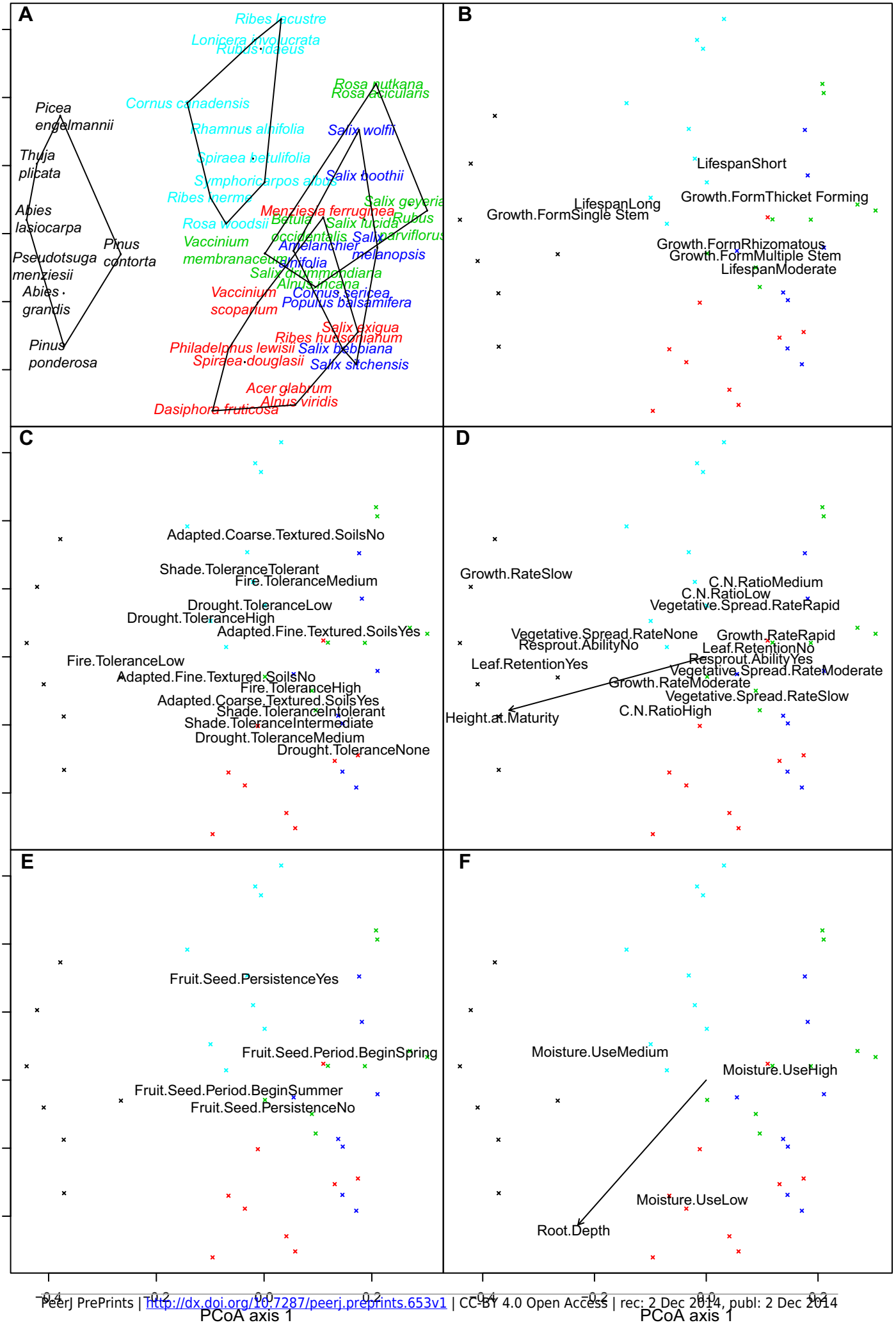

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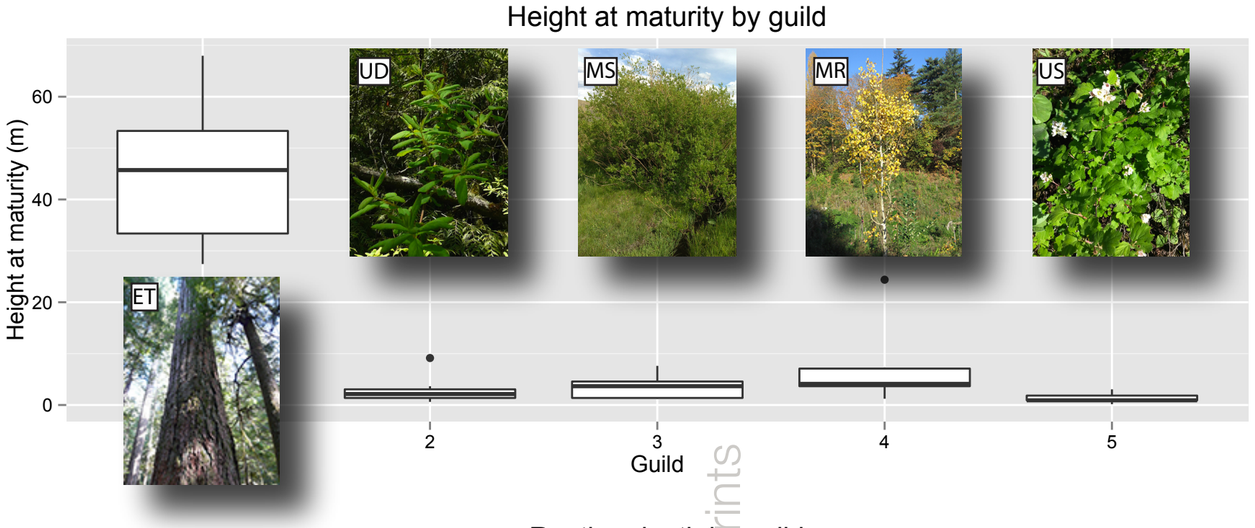

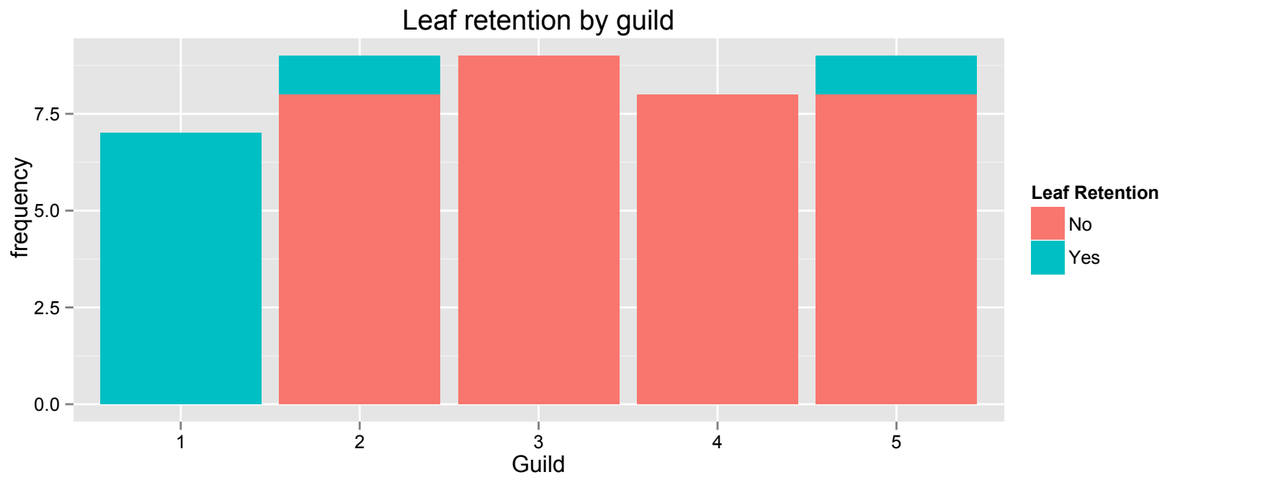

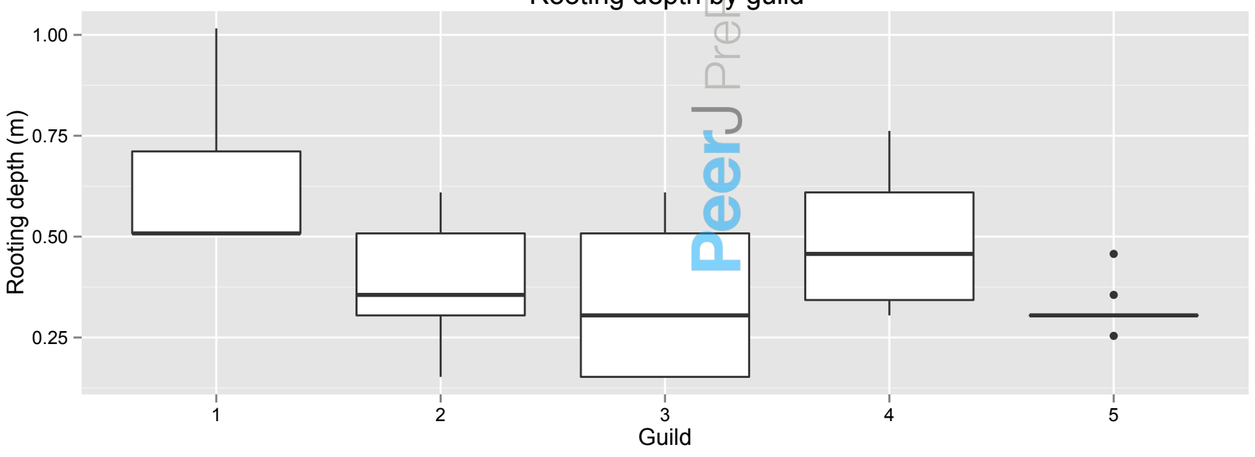

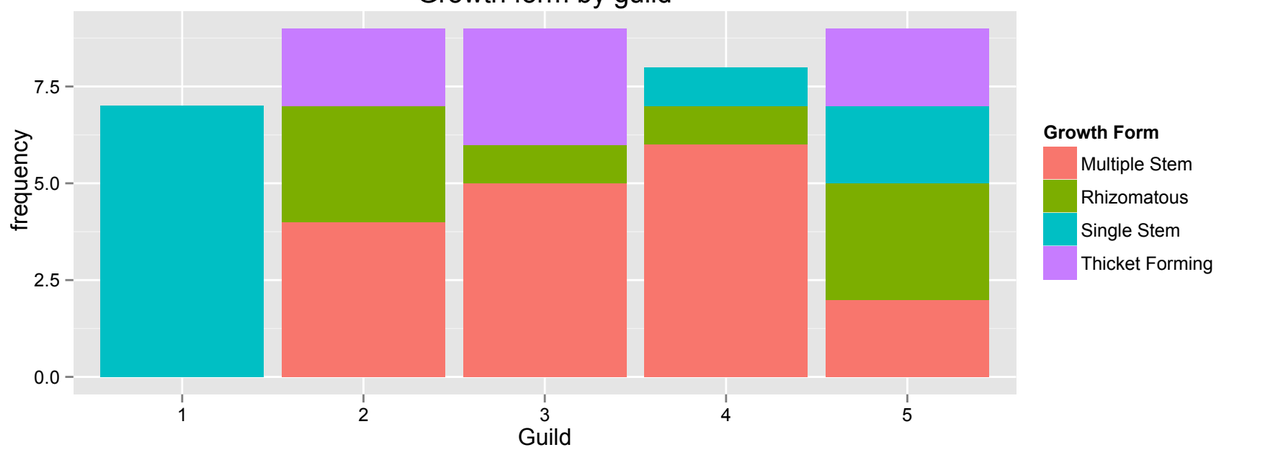

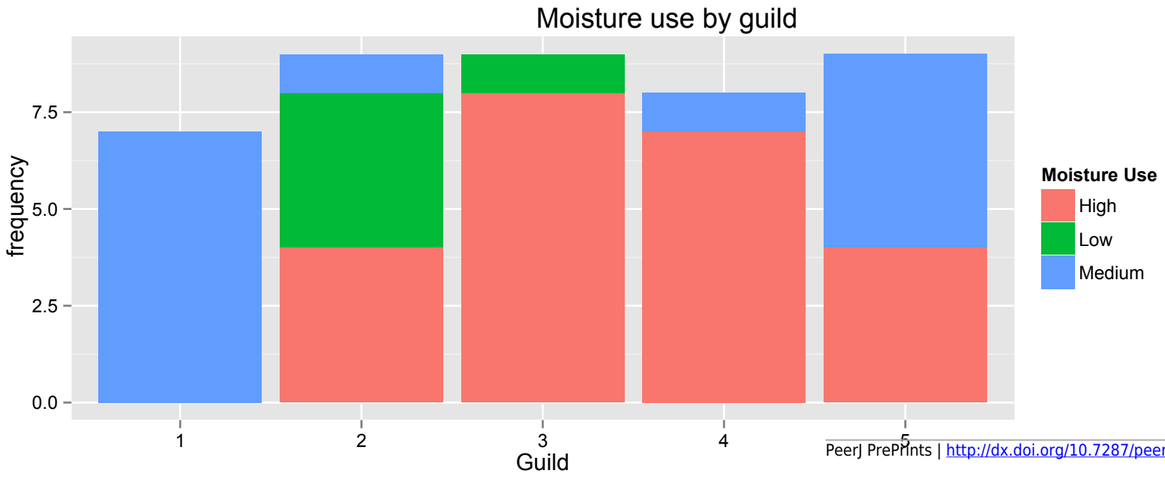

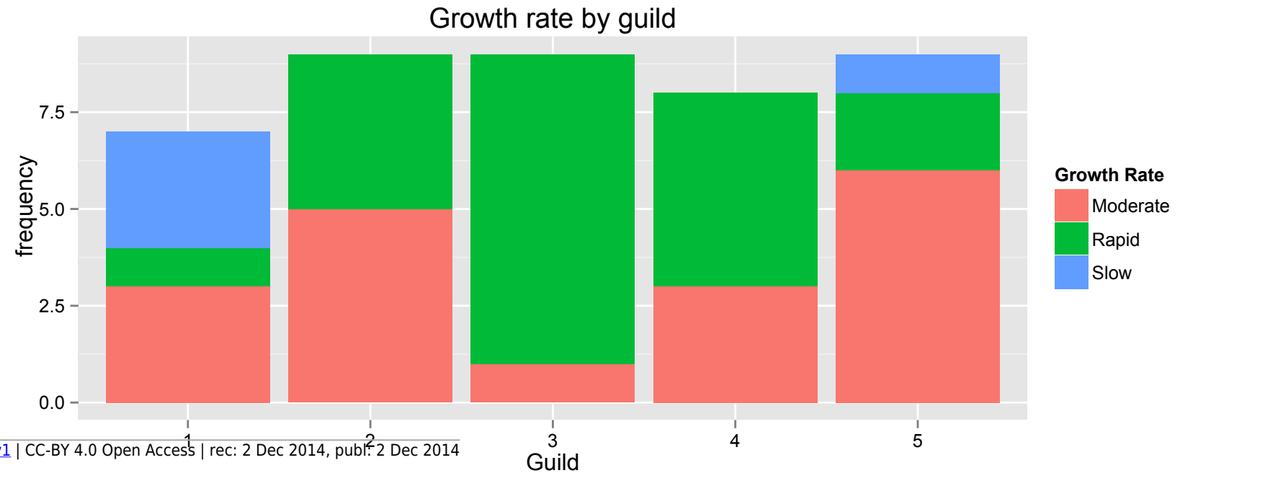

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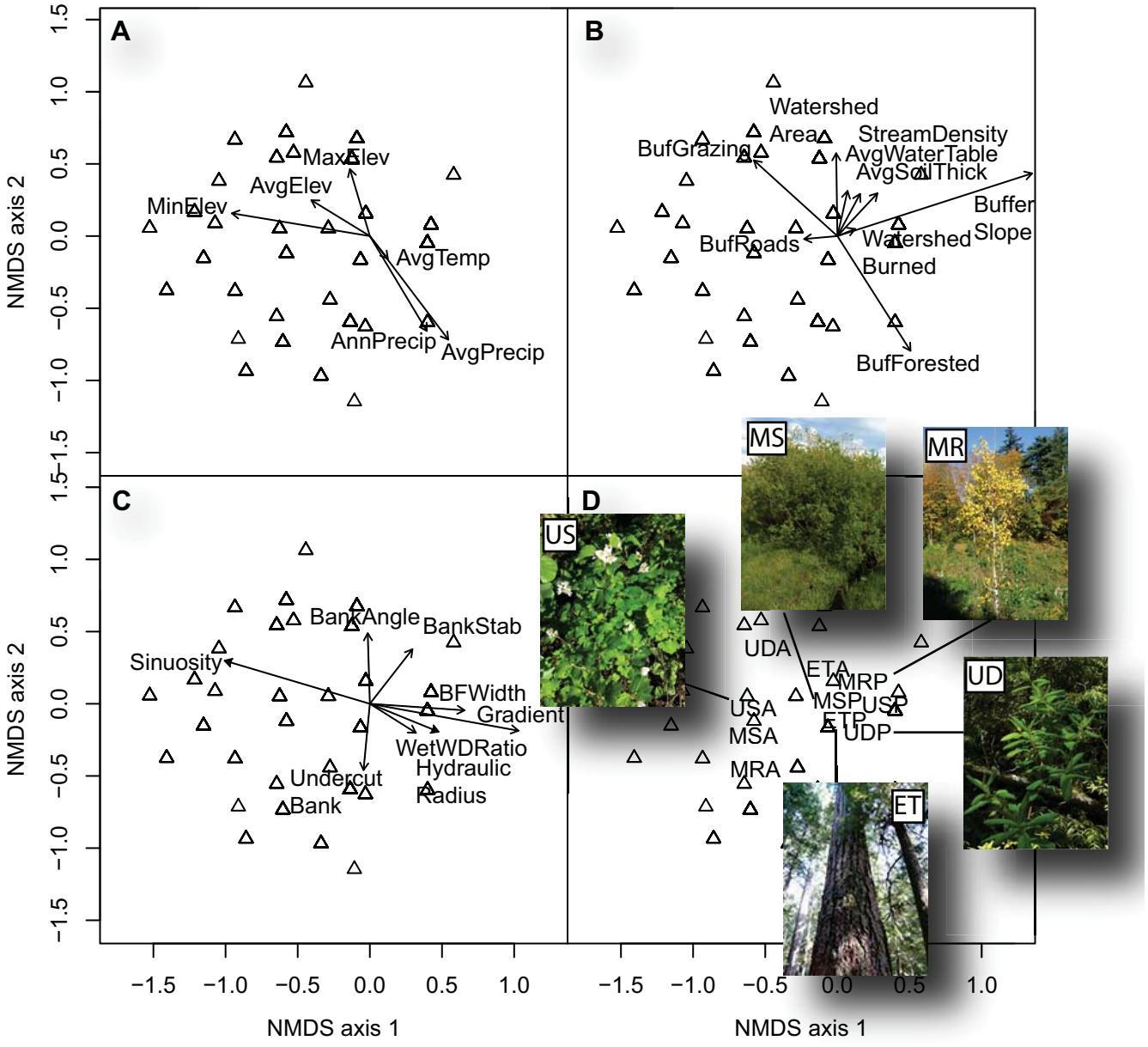

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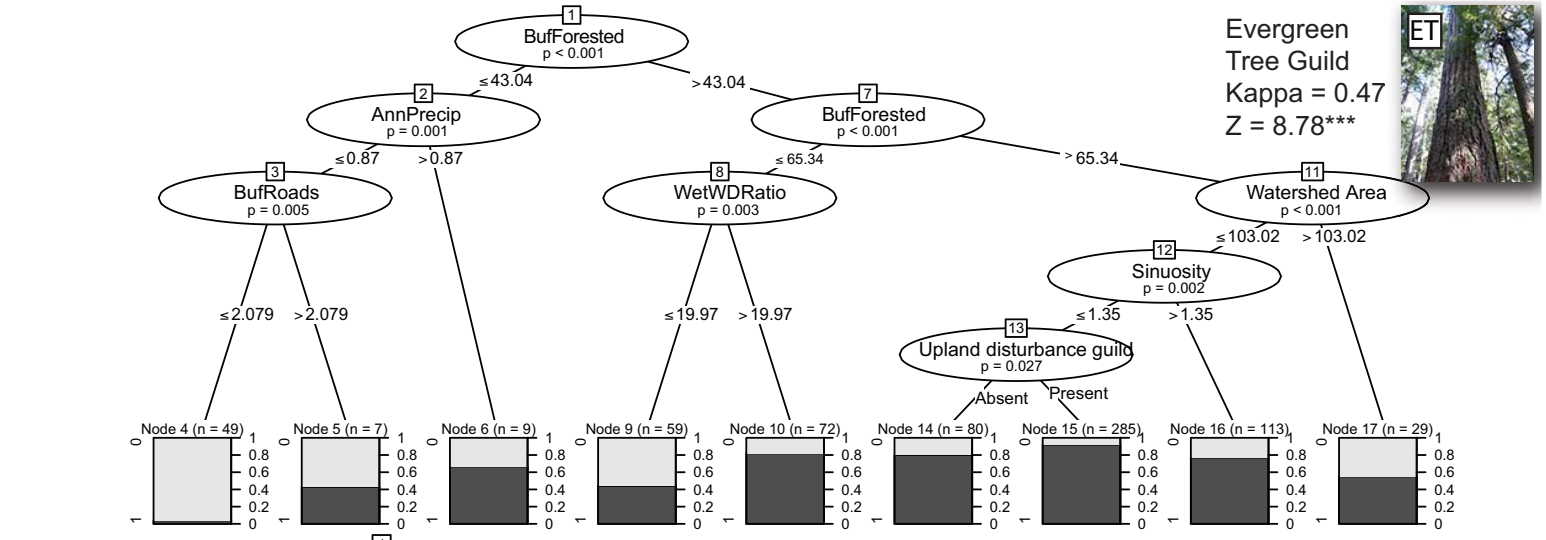

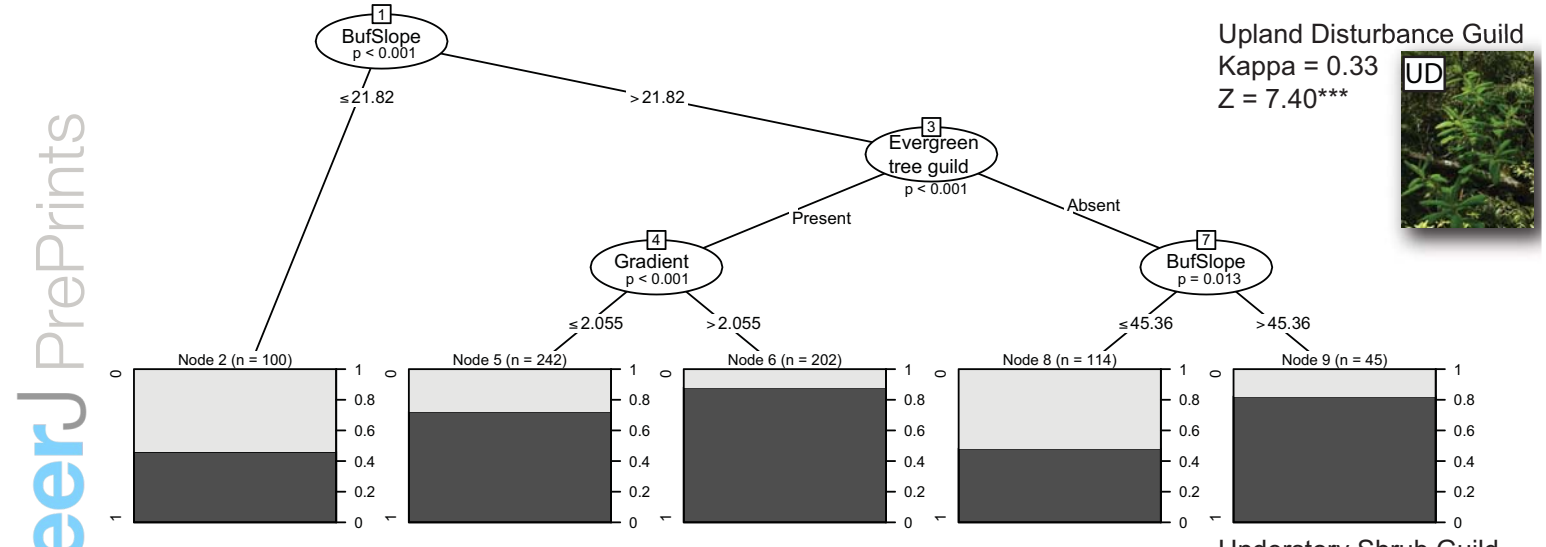

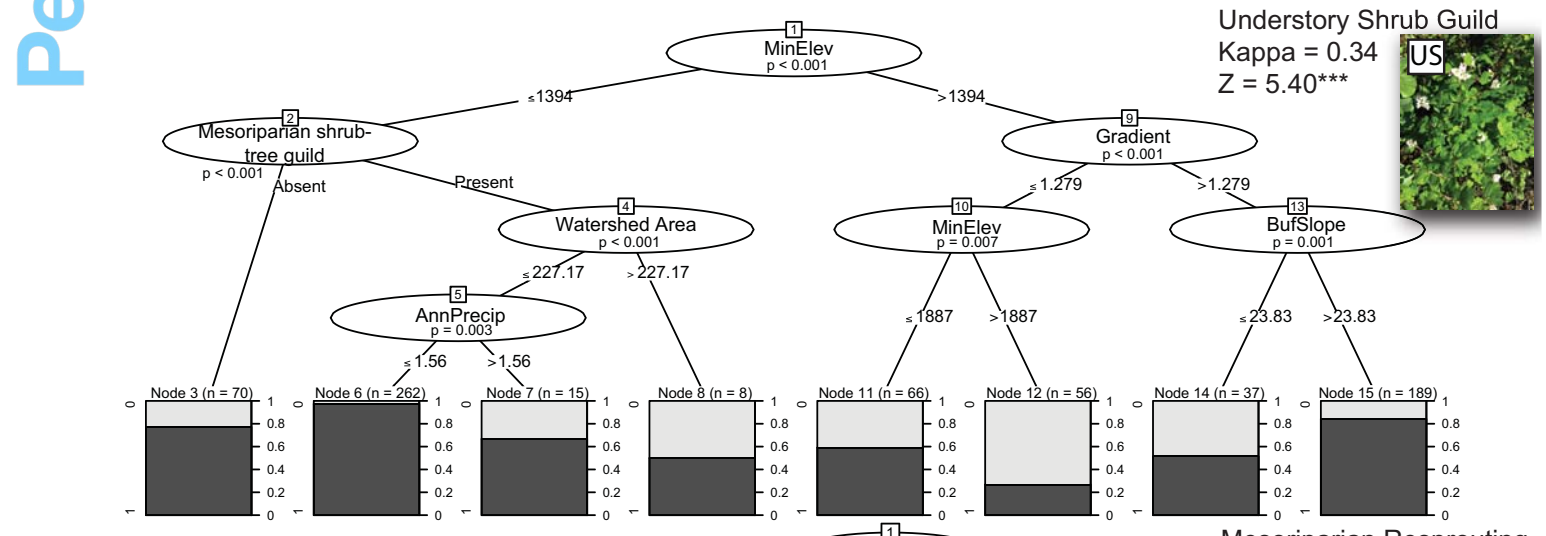

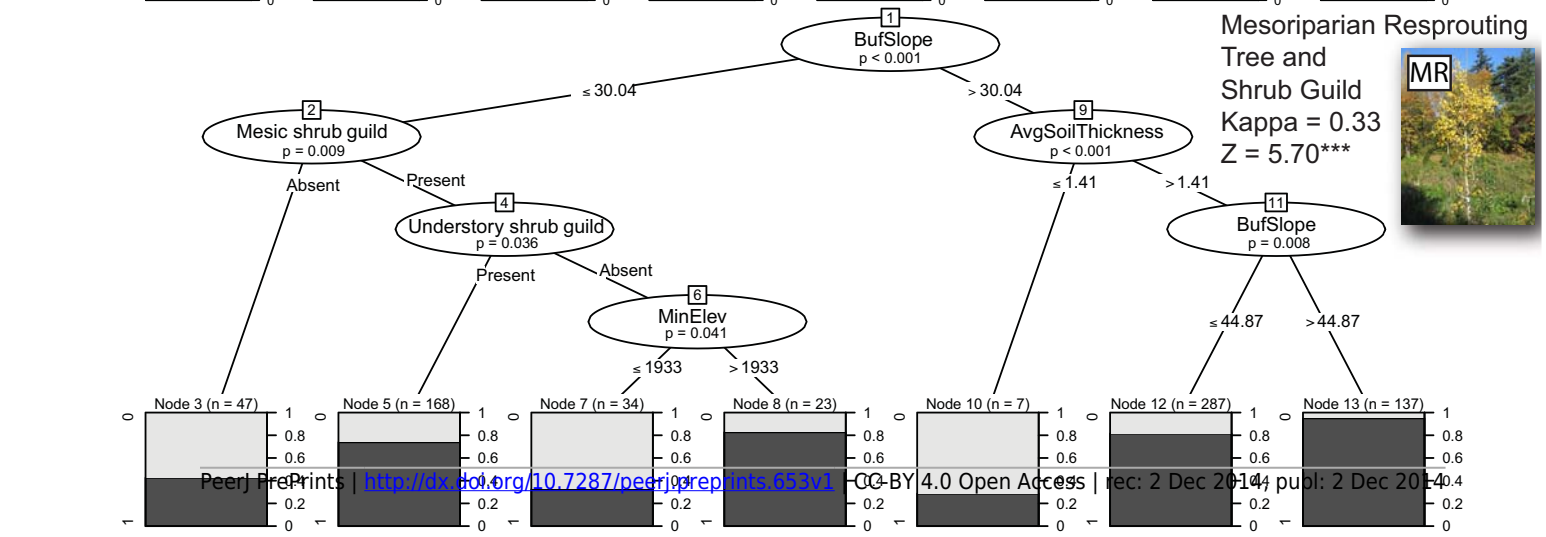

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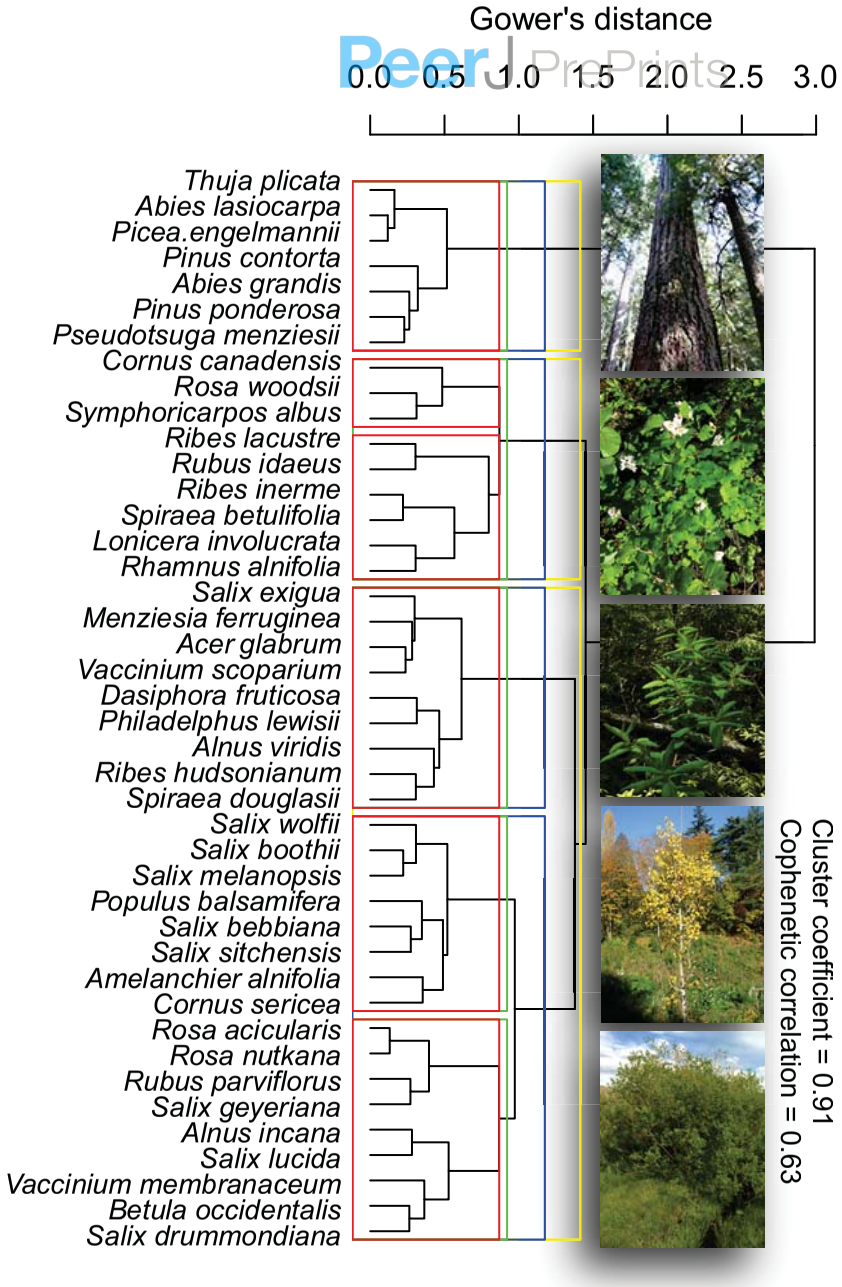

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1 **Appendices**

2 **Figures**

3 Appendix A. The resulting final dendrogram from cluster analysis of species by their traits.
4 Colored bands indicate four (yellow), five (blue), six (green) and seven (red) guilds. Five guilds
5 were selected based on their observed ecological niches within the study region and guild fidelity
6 using PERMANOVA analysis.

7

8 Appendix F. Map of combinations of guild assemblages across the Columbia and Missouri River
9 basins showed that a majority of reaches contained all possible guilds. Only a few reaches were
10 absent of all woody guilds. Map labels consist of guild initials and "P" for guild presence and
11 "A" for guild absence. For example, UDP corresponds to upland disturbance present while CA
12 corresponds to conifer absent, etc.

13

14 **Tables**

15 Appendix B. Summary of morphological and physical attributes by guild. The count of each
16 level for each attribute are presented for each guild.

Life history and morphological attributes	Levels	Attribute count by guilds				
		Ever-green tree	Upland disturb-ance shrub	Mesic hydro-phytic shrub	Meso-riparian tree and shrub	Under-story 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

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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
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	No	6	9	7	8	3

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Persistence	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

Appendix C. 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

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Appendix D. 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	Conifer	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

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30 Appendix E. Alternative models considered as potential final models.

Riparian guild	Final model terms (effect)	AIC	Delta 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** (-) AvgTemp (-) **AnnPrecip (+) BufForested (+) WatershedBurned** (-) BufRoads **(+) BufSlope (-) WetWDRatio (+) Sinuosity (-)** Gradient (+) **AvgWaterTable (-) UD (+) US (+)** WR (-)	591.59	3.83	-280.80	0.42	0.28
	WatershedArea (-) AvgTemp (-) **AnnPrecip (+)** MinElev (-) **BufForested (+) WatershedBurned** (-) BufRoads **(+) BufSlope (-) WetWDRatio (+) Sinuosity (-)** Gradient (+) **AvgWaterTable (-) UD (+) US (+)** WR (-)	593.06	5.3	-280.53	0.42	0.28
	WatershedArea (-) AvgTemp (+) AnnPrecip (+) MinElev (-) **BufForested (+) WatershedBurned** (-) BufRoads **(+) BufSlope (-) WetWDRatio (+) Sinuosity (-)** Gradient (+) AvgWaterTable (-) **UD (+) US (+)** WR (-) 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 (+)** WR (-) **AnnPrecip:MinElev (+)**	587.76	0	-276.88	0.43	0.29
Rapidly growing, multi-stemmed, rhizomatous and thicket-forming, drought-plastic, shrub guild (upland disturbance guild)	WatershedArea **(-) AvgTemp (+) BufForested (+)** BufSlope **(-) BankAngle (-) BfWidth (+)** WetWDRatio **(+) Gradient (+) AvgWaterTable (-) BufSlope:BankAngle (+)** BfWidth:WetWDRatio **(-) C (+)**	760.70	0	-367.34	0.23	0.16
	WatershedArea **(-) AvgTemp (+)**	760.77	0.07	-366.39	0.24	0.17

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	BufForested (+) BufSlope **(-) BankAngle (-) BfWidth** (+) WetWDRatio **(+) Gradient** (+) **AvgWaterTable (-) BufSlope:BankAngle** (+) BfWidth:WetWDRatio **(-) C** (+) **WR** (+)					
	WatershedArea **(-) AvgTemp** (+) **BufForested** (+) BufSlope **(-) BankAngle (-) BfWidth** (+) WetWDRatio **(+) Gradient** (+) **AvgWaterTable (-) BufSlope:BankAngle** (+) BfWidth:WetWDRatio **(-) C** (+) AvgSoilThick (+)	761.43	0.73	-366.72	0.23	0.17
Low-stature, hydrophytic, multi-stemmed thicket forming shrubs (mesic shrub guild)	WatershedArea (-) **AvgTemp** (-) AnnPrecip (-) **MinElev** (-) **BufSlope** (+) **BankAngle** (+) **BfWidth** (+) WetWDRatio (-) Sinuosity **(-)** BfWidth:WetWDRatio (-) **BufSlope:BankAngle (-) US** (+) **WR** (+)	376.25	0	-174.13	0.31	0.15
	WatershedArea (-) **AvgTemp** (-) AnnPrecip (-) **MinElev** (-) **BufSlope** (+) **BankAngle** (+) **BfWidth** (+) WetWDRatio (-) Sinuosity **(-)** BfWidth:WetWDRatio (-) **BufSlope:BankAngle (-) US** (+) **WR** (+)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** (+) **WR** (+) AvgWaterTable: AvgSoilThick (+)	379.12	2.87	-172.56	0.31	0.15
Medium-deeply rooted, vegetatively reproducing shrubs and trees (mesoriparian shrub and tree guild)	**AvgTemp** (-) AnnPrecip (-) **MinElev** (-) **BufGrazing** (+) BufRoads (+) **BufSlope** (+) **BfWidth** (+) Gradient (+) **AvgSoilThick** (+) C (-) **MS** (+) **US** (+)	657.50	0	-315.73	0.26	0.17
	AvgTemp (-) AnnPrecip (-) **MinElev** (-) **BufGrazing** (+) BufRoads (+) **BufSlope** (+) **BfWidth** (+) Gradient	659.31	1.81	-315.65	0.26	0.17

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	(+) **AvgSoilThick** (+) C (-) **MS** (+) **US** (+) AvgWaterTable (+)					
	AvgTemp (-) AnnPrecip (-) **MinElev** (-) **BufGrazing** (+) BufRoads (+) **BufSlope** (+) **BfWidth** (+) Gradient (+) **AvgSoilThick** (+) C (-) **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 (-) **AvgTemp** (-) **AnnPrecip** (-) **MinElev** (-) **BufForested** (-) BufRoads (+) **BufSlope** (+) BankAngle (-) **Gradient** (+) **AnnPrecip:Elev** (+) **C** (+) **MS** (+) **WR** (+)	581.67	0	-276.83	0.33	0.21
	WatershedArea (-) **AvgTemp** (-) **AnnPrecip** (-) **MinElev** (-) **BufForested** (-) BufRoads (+) **BufSlope** (+) BankAngle (-) **Gradient** (+) **AnnPrecip:Elev** (+) **C** (+) **MS** (+) **WR** (+) AvgSoilThick (+)	583.31	1.64	-276.65	0.33	0.22
	WatershedArea (-) **AvgTemp** (-) **AnnPrecip** (-) **MinElev** (-) **BufForested** (-) BufRoads (+) **BufSlope** (+) BankAngle (-) **Gradient** (+) **AnnPrecip:Elev** (+) **C** (+) **MS** (+) **WR** (+) AvgWaterTable (-)	583.63	1.96	-276.81	0.33	0.21

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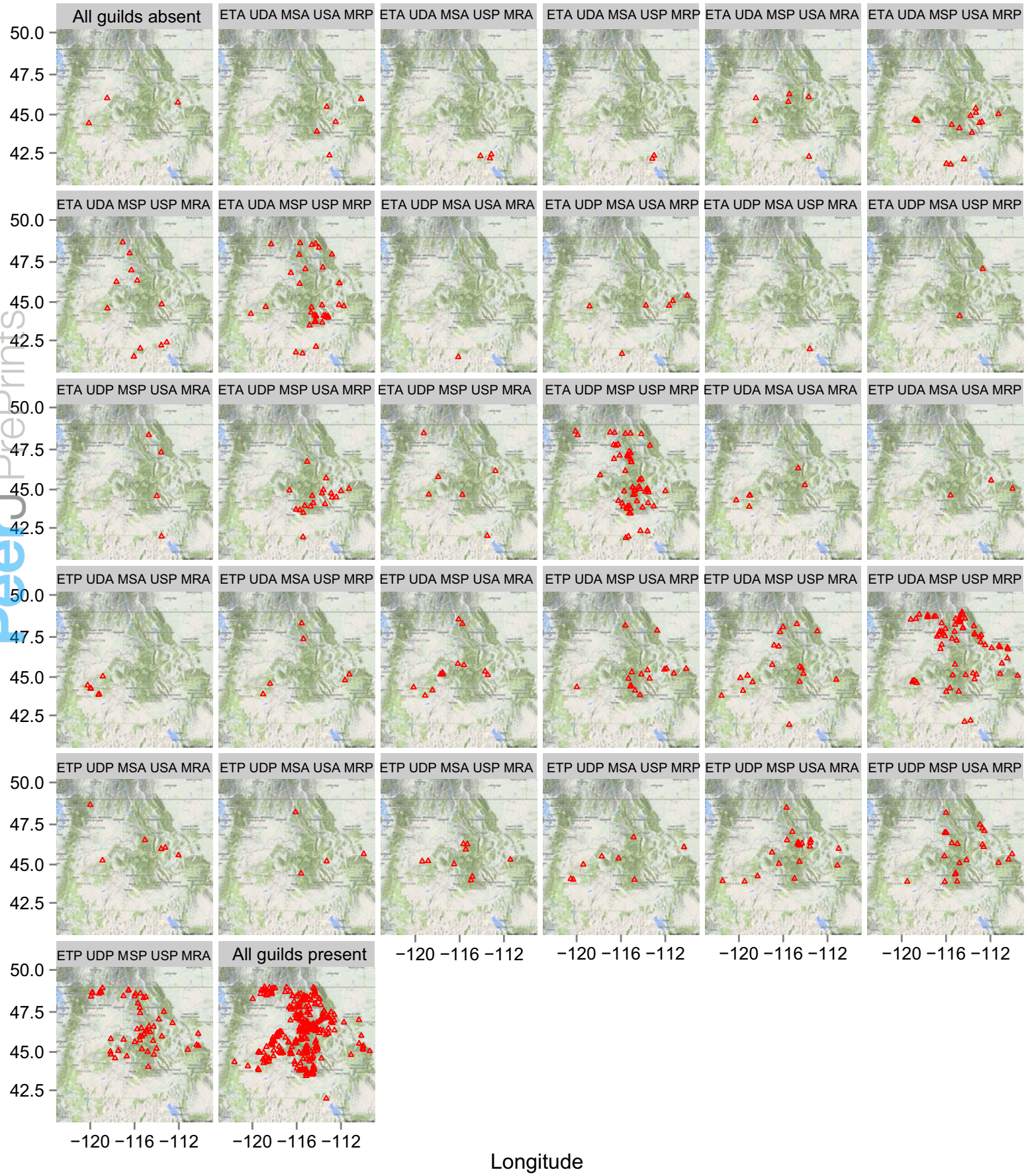

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