

**How do riparian songbirds (Passerines) coexist?
Effects of vegetative structural complexity on habitat selection in
willow (*Salix* spp.)**

**Student: Alexander H. Nelson
Mentors: Michelle Gooch and Patrick Magee**

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How do riparian songbirds (Passerines) coexist? Effects of vegetative structural complexity on habitat selection in willow (*Salix* spp.)

Alexander H. Nelson

Abstract

The diversity of avian species and their coexistence in riparian habitat has become increasingly significant in the face of rapidly decreasing vegetation along hydric areas, primarily due to pollution, urbanization, overgrazing, and climate change. The complex and rare riparian habitat system is primarily supported by willow (*Salix* spp.) vegetation in the high-altitude areas along the East River Valley in the Rocky Mountains, which provide a multitude of niche types for many species of songbird (Passerines). The objective of this study was to evaluate songbird community response to differences in vegetative structure of willow, concentrating on the overall avian abundance, richness, and species diversity, as well as a number of individual focal species. We predicted that the warbler species would demonstrate a more specialized habitat selection to more complex willow vegetation, while the sparrow group would likely select for less complex vegetative structure. We sampled bird abundance and vegetative composition in riparian habitat along the East River near Gothic, CO for three weeks, performing both a series of point count observations and a suite of vertical and horizontal vegetation measurements at each site. Overall species richness and diversity was found to increase with higher vegetative complexity, while species abundance was shown to be significantly lower at sites with more complex vegetation. The focal species selected were the Wilson's Warbler (*Cardellina pusilla*), Yellow Warbler (*Setophaga petechia*), MacGillivray's Warbler (*Geothlypis tolmiei*), White-Crowned Sparrow (*Zonotrichia albicollis*), Fox Sparrow (*Passerella iliaca*), Lincoln's Sparrow (*Melospiza lincolnii*), and the Willow Flycatcher (*Empidonax traillii*). The sparrows demonstrated selection of willow with less vertical and horizontal complexity, while the Yellow and MacGillivray's Warbler, as well as the Willow Flycatcher, were present in greater abundance in more complex willow structure. The Wilson's Warbler was found to demonstrate no significant relationship to any vegetative variable, suggesting the possible use of different strata of vegetation in a more complex life history. The results of this study indicate the importance of understanding the structural habitat requirements of the songbird species in riparian areas in order to effectively manage and improve threatened willow habitat.

Introduction

According to the theory of competitive exclusion, two species in the same habitat must differ in their resource use in order to coexist. In his work with songbirds in the conifer forests of New York, Robert MacArthur demonstrated that species are distributed within ecologically determined niches and utilize different foraging and nesting spaces (MacArthur 1958).

MacArthur also determined how different species of songbird respond to vegetative structure for

their resource needs (MacArthur and MacArthur 1961). Further research in a number of other habitat types reveals resource partitioning of many organisms due to competitive exclusion, both spatially and temporally (Olechnowski 2009, Knopf and Samson 1994). Thus, members of faunal communities dynamically adapt to both environmental factors and their competitors. The mechanisms driving resource partitioning that allow for coexistence of bird species have been studied in several habitats (Hutto 1981, Salewski et al. 2002, Finch 1989); however, the particular effects of vegetative structure on community composition and species occurrences of birds inhabiting willow-rich areas along riparian zones is still relatively unknown (Baril et al. 2009).

Willow (*Salix* spp.), the primary vegetation along streams and rivers in the Rocky Mountains, merges aquatic and upland habitat to create an ecologically important and dynamic environments in the temperate United States (Baril et al. 2009). These riparian zones consist of a diverse and interconnected set of biological and environmental systems. Riparian zones usually extend from the lowest water mark to the highest extent of the water table, and host a wide range of resources for the riparian fauna, including food, nesting and breeding sites, refuge from parasites and predators, and rest stops during migration (Naiman and Decamps 1997). Riparian zones support an estimated 82% of the bird diversity in the northern Rocky Mountains, many of which rely entirely on willow ecosystems for nesting and foraging (Knopf and Samson 1994).

These habitats feature markedly less predation than other montane ecosystems and host a variety of insect species that provide a food source for birds (Bolton and Shellberg 2001). The most notable groups of songbirds that breed in the riparian habitats of the Rocky Mountains are the warblers (*Parulidae* spp.) (e.g., Wilson's Warbler (*Cardellina pusilla*), Yellow Warbler (*Setophaga petechia*), and MacGuillivray's Warbler (*Geothlypis tolmiei*)) and the sparrows (*Emberizidae* spp.) (e.g., White-Crowned Sparrow (*Zonotrichia albicollis*), Fox Sparrow (*Passerella iliaca*), and Lincoln's Sparrow (*Melospiza lincolnii*)), in addition to a number of other willow specialists, including Willow Flycatchers (*Empidonax traillii*) (Ruth and Stanley 2002, Olechnowski and Debinski 2008). The vegetation also plays a large role in several ecosystem services, including preventing erosion of stream banks via root stabilization, supporting and shaping the stream channel structure and controlling the movement of water and organic debris, thus aiding in flood control, and reducing water pollution through chemical or biological filtration (Baril et al. 2009).

A key ecosystem service provided by Rocky Mountain willow riparian wetlands is the provision of habitat for a variety of animal species and supports biological diversity. Removal of riparian vegetation has the direct consequence of local extinction and reduces the ability of bird populations to recolonize viable habitats (Naiman and Decamps 1997). In this way, the abundance and characteristics of willow vegetation in riparian environments are inextricably connected to the distribution and abundance of avian populations. Species that utilize willow vary in their level of dependence on willow habitat as well as their use of different parts of the vegetation. Riparian habitats act as natural buffers between ecosystems and continuing human development, a role which is becoming increasingly important due to tension from climate change and urban expansion (Perry 2012). The status of populations supported by riparian habitats is becoming a vital gauge for the overall stability of willow-stream systems; for example, songbird populations serve as “ecological indicators” of riparian system health and marks of environmental change (Rich 2002). Continued study of current patterns of habitat use among avian species and their ecosystem-level interactions will also contribute to both a finer understanding of the habitat needs of each species, as well as a more detailed understanding of resource partitioning among avian species. Increased knowledge of these biotic systems will aid the preservation of species diversity and habitat integrity (Knopf and Sampson 1994).

To determine how ecologically similar songbird species coexist in riparian habitat, I investigated the relationship between structural complexity of willows and the distribution and abundance of the local bird species around Gothic, Colorado. For this study, structural complexity is defined by a suite of variables including foliage height diversity, average height, coefficient of variation in height, willow frequency, patchiness, and cover at both 100 m and 40 m buffer zones. I hypothesized that more structurally complex willow patches would contain higher species richness and abundance of birds, contributing to overall greater avian diversity. Greater structural complexity of willow implies a greater amount and variety of niche spaces, therefore greater availability of bird habitat and resources. By group, sparrows, such as the White-Crowned Sparrow, Lincoln’s Sparrow, and Fox Sparrow, would likely demonstrate less dependence on vegetative complexity (more generalist in complex structural needs) (Baril et al. 2009). Warblers, on the other hand, particularly the Wilson’s Warbler and the MacGillivray’s Warbler, as well as the Willow Flycatcher, are known to be more specialist in nature (Baril et al. 2009, Sedgwick 1992), and therefore should demonstrate closer correlation to increased willow

structural complexity. Other species, such as the Yellow Warbler, may be considered willow associates, as they rely on willows for only part of their life histories (Bailey and Niedrach 1965). To summarize, I expect generalist and associate species to be less sensitive to vegetative complexity, while specialist species should show greater association with vegetation complexity. To test these hypotheses, I used point counts to measure abundance, richness, and diversity of all songbirds across willow patches with varying degrees of structural complexity.

Methods

Site Selection

In order to choose sites for point counts, random points were generated within riparian habitat along the East River near Gothic, CO using digital aerial photographs in ArcGIS ($n = 40$ points separated by a minimum distance of 150 m). The points were located in the field using a handheld Garmin GPS unit. If a point was inaccessible or inappropriate for the study (i.e., in the middle of a stream), it was shifted to the closest accessible position (with the new coordinates recorded and mapped). Each point was visited three times over the summer season (27 June to 20 July), with the order of points altered or reversed during each visit in order to account for differences in time of morning.

Point Count Method

The birds were sampled using the point count method (Ralph et al. 1993), in which bird individuals are recorded by sight and sound within a defined radius at predetermined points. Point counts began at 0630 and were completed by 1030, and were only conducted on days when weather conditions were calm, without heavy winds or precipitation. Each point count lasted 10 minutes, after a 3-minute acclimation period in order to minimize the effect of human presence on bird activity. Species observed before and after the 10-minute point count, as well as outside the 40 m radius, were also noted separately on the datasheet. During the point count, species were recorded along with their direction, distance from the site center-point (max. 40 m), and sex (if determinable). Double-counts were minimized by vigilant observation by sight and sound, as well as well-spaced points (min. 150 m between points) (Ralph et al. 1993). Bird species response variables were calculated including species richness (total number of species found at a

site across the three visits), total bird abundance, and species diversity using the Shannon-Wiener index. Flyovers and birds detected outside the 40 m radius were excluded from analyses because they are not adequately sampled using point counts (Ralph et al. 1993). Abundance was calculated separately for a suite of focal species, including passerine species that were present in at least 10% of points and were known to rely on willow for part of their life history. All abundance measures were calculated by averaging the abundance (the total number of individuals of a species counted within the 10-minute point count) across the three visits. This allowed for minimizing possible bias due to overestimates from counting juveniles from the current season and underestimates due to birds that were present at a site but not detected.

Vegetation Measurements

Vegetation measurements were taken on the willow surrounding the center-point of each site, focusing on the vegetative horizontal and vertical structural complexity. A circular plot 40 m in radius was measured around each central point. Transects were established along the N-S-E-W axes, with sample points spaced 10 m apart (for a total of 4 points along each axis, as well as the center-point). To determine vertical structural characteristics, I used a modified Robel pole (Robel 1970), which consists of a 3x200-cm PVC pipe marked at four 0.5 m height intervals. The pole was placed at each sample point, and the percent of the pole obscured at each of the height classes was recorded (Baril et al. 2011). To determine the horizontal structure of the willow habitat around each point, line intercept measurements were collected along one 40 m transect in a randomly selected cardinal direction. These included the distance over which willow intersected the meter tape and height of willow at every 1 m interval. The predictor variables derived from these measurements included foliage height diversity (calculated using the Shannon-Wiener formula), average height, coefficient of variation in height (a measure of how variable willow height is within the 40 m radius plot), horizontal cover (total distance over which willows intersect the meter tape in the line intercepts), willow frequency (amount of willow present relative to total vegetative cover), patchiness (average length of patches/total # of patches within a plot), and willow cover within both 100 m and 40 m buffers around each point (measured using aerial photographs in GIS) (Cummings and Smith 2000, Baril et al. 2011) (Table 1).

Statistical Analysis

The relationship between vegetation structure and bird response variables was evaluated using generalized linear regression models using R Statistical Software. For focal bird species that were found in < 50% of plots, logistic regression models were used on species presence/absence data, whereas linear regression models were used on species abundance data for all other focal species.

Variables that were strongly correlated ($r > 0.7$) using the Pearson's correlation coefficients were eliminated from the model selection using biologically informed criteria. To select the best model for each response variable, the two sets of models were first evaluated separately, one with combinations of vertical structural predictors and the other with horizontal structural predictors (Table 1). The model within each set with the lowest AIC (Akaike's Information Criterion) was chosen as the best model for that set. The predictor variables in the best model for each set were then combined into a single model that included both vertical and horizontal predictors. This procedure was used to select the best-fit model for each response variable (i.e., abundance, richness, and diversity, as well as abundance for each focal species).

Results

From three visits to each of the 40 sites along the East River, a total of 38 avian species were observed, with a total bird abundance of 1,398 (Table 2). From these species, the sparrows and warblers were most prevalent and abundant. The focal species from these groups were determined to be the White-Crowned Sparrow, Fox Sparrow, Lincoln's Sparrow, Wilson's Warbler, Yellow Warbler, and MacGuillivray's Warbler. In addition to these species, the Willow Flycatcher was sufficiently abundant to include in further analysis.

From these data, a series of models were chosen using AIC model selection to represent the relationship between response and predictor variables (Table 3). Predictor variables eliminated from the analysis included horizontal cover because it was highly correlated with frequency ($r = 0.99$; Appendix 1) and is incorporated in willow cover at 40 and 100 m. Species richness was best predicted by increasing foliage height diversity ($p < 0.0001$), as well as increasing willow cover at 40 m (but this was not significant; $p = 0.08$, Table 3, Fig. 1). However, species abundance was best predicted by decreasing average height of the willow at

each site ($p = 0.008$), as well as increasing willow cover at 100 m ($p = 0.01$, Table 3, Fig. 2). Species diversity showed a significant positive relationship with foliage height diversity ($p < 0.0001$), as well as average height of willow ($p = 0.06$, Table 3, Fig. 3).

Abundance of both Lincoln's Sparrow and White-Crowned Sparrow demonstrated a significant negative relationship with foliage height diversity ($p = 0.0001$ and $p = 0.02$, respectively, Table 3, Fig. 4-5). Fox Sparrow presence also demonstrated a negative trend with foliage height diversity, as well as a significant negative relationship with the coefficient of variation of height ($p = 0.02$, Table 3, Fig. 6). For the warblers, the Wilson's Warbler showed no significant model for abundance. Yellow Warbler abundance, on the other hand, showed a significant positive relationship with foliage height diversity ($p = 0.003$) and willow cover at 40 m ($p = 0.04$, Table 3, Fig. 7). MacGillivray's Warbler presence demonstrated a positive, though non-significant, association with foliage height diversity ($p = 0.12$) and a negative, marginally significant association with the coefficient of variation in height of willow ($p = 0.06$; Table 3, Fig. 8). Lastly, presence of Willow Flycatcher showed a significant positive relationship with foliage height diversity ($p = 0.02$, Table 3, Fig. 9).

Discussion

To determine the response of songbirds to different willow growth patterns in high-elevation riparian zones near Gothic, CO, the bird community composition was compared to the vegetative structure of the willow habitat. Overall, songbird species diversity increased with greater willow complexity (as a function of vertical and horizontal vegetative measurements). Overall abundance decreased with height and increased with cover. This possibly occurred due to sparrows being highly abundant and having a stronger effect on the results than the warblers and other species. The increase of abundance with cover is likely due to willows providing increased food sources, protection from predators, and cover for nesting. Species richness increased with foliage height diversity, likely because willows with high structural complexity (indicated by foliage height diversity) have more spatial niches to be filled by a variety of riparian species. This niche partitioning appears to be very similar to MacArthur's work with warblers in conifers, and demonstrates how the songbirds are able to select slightly different habitats and coexist in the same microhabitat. Songbird diversity increased with foliage height

diversity and willow height, which reflects the same concept of habitat selection. Willow height is related to foliage height diversity: the taller the willow demonstrated a height the more structural complexity and therefore a greater number of niches to be filled by multiple species.

Of the focal species, the sparrow group demonstrated an overall specialization for low foliage diversity in their habitat selection in willow zones, most strongly with the Lincoln's and White-Crowned Sparrow. The warbler group demonstrated a more specialist habitat selection tendency for more complex willow, with the exception of the Wilson's Warbler, which showed no significant association with willow structure. Lastly, the Willow Flycatcher also appeared to favor more complex willow structure and could therefore be considered a specialist in willow vegetation selection similar to the warblers. These results provide intriguing insight into distribution of avian species in an increasingly important and rare habitat system in Colorado high-elevation riparian zones.

The known foraging and breeding behaviors of the focal species can help explain their associations with willow structure. Sparrows are primarily ground nesting and/or ground feeding. Each focal species of sparrow in this study forages primarily for seeds and arthropods (Chilton et al. 1995, Raley and Anderson 1990, Weckstein et al. 2002). Lincoln's Sparrows especially demonstrate a need for abundant seed sources around ground level or at the mostly dense ground vegetation (Chilton et al. 1995). The sparrow family is also known for nesting on the ground in willow habitat or in dwarf shrubby thickets (Anderson 2007, Chilton et al. 1995, Weckstein et al. 2002). Lincoln's Sparrows are noted to select for more open habitat, likely in order to facilitate increased ground foraging and nesting (Chilton et al. 1995). This was in agreement with our findings that Lincoln's Sparrows were associated with low foliage height diversity. White-Crowned Sparrows demonstrated similar results, though have been shown to be a more specialized species to subalpine zones, likely due to a preference for increased visibility for territoriality, smaller shrubs, and/or fewer competing avian species (Finch 1989).

Our results from the Fox Sparrow deviate from those of several other studies, which found that Fox Sparrow abundance is often strongly positively correlated with average willow height and the species often forages and nests in taller dense cover, perching high in willows to feed and stake out territory (Weckstein et al. 2002). They feed more on arthropods than do the other focal sparrow species, as well as occasionally seeds, fruits, and plant matter, therefore the Fox Sparrow would require a more dense willow structure to attain a greater amount of flying

invertebrate food source (Weckstein et al. 2002). In contrast, we found that Fox Sparrows were associated with low foliage height diversity and low coefficient of variation in height, as well as increasing willow cover at 100m (but marginally significant). Interestingly, Fox Sparrows are known to vary geographically in their habitat selection, making their behavioral tendencies for different vegetation structures in different areas due to the selective pressures very likely (Weckstein et al. 2002). In high altitude willows around Gothic, CO, Fox Sparrows appear to prefer homogenous willow with low structural complexity, but this could be a geographic anomaly. It is possible that in this habitat system, the species is being outcompeted from complex willow niches by other more specialized riparian species.

Warblers, on the other hand, appear to specialize on complex willow structure. This has been found in previous studies as well, with warblers demonstrating strong foraging and nesting associations with dense willow cover (Baril et al. 2009, Finch 1989). The MacGillivray's Warbler is noted to be the most specialized to willow habitat, as they are primarily restricted during the breeding season to riparian habitat in the Rocky Mountains and their eastern foothills (Pitocchelli 1995). They often require dense undergrowth and moderate cover in their breeding habitat and nest in wet thickets and on the ground and forage for insects in similar habitat, often less than 1 meter above the ground (though foraging height is known to vary with geography and season) (Pitocchelli 1995). Their preference for lower foraging and nesting may explain their negative association with the coefficient of variation of willow height, indicating that they are found more frequently in sites with a consistent overhead canopy cover. The Yellow Warbler is also known to demonstrate a specialist habitat selection and requires unsuppressed willows of a certain height and greater horizontal cover than other riparian songbird species (Lowther et al. 1999). In other studies, they are known to show a strongly positively correlation to average willow height and select taller vegetation to glean insects from willow vegetation (Baril et al. 2009). This species is known to forage around 6 to 8 meters off the ground and even when nesting in larger, more open shrubs, they never forage directly on the ground (Lowther et al. 1999). This preferential nesting pattern often demonstrates a large amount of horizontal patterning, which likely conceals the nest from predation and brood parasitism (Knopf and Sedgwich 1992). Data on Yellow Warblers may be skewed by the increased visibility of males however, as they forage higher and glean more often than females, which suggests males foraging conspicuously in order to promote territory establishment and maintenance (Finch

1989). Other studies have also indicated that while Yellow Warblers are the numerically dominant species in many Western riparian habitats, they should be considered, at best, willow associates or even generalists, due to their ability to use widespread vegetative resources in a number of elevational gradients (Baril et al. 2009, Bolton and Shellberg 2001, Cain et al. 2003, Finch 1989). Such discrepancy in defining their overall habitat use classification may be due to differences in Yellow Warbler abundance associations in areas of natural habitat where they show strong specialist willow selection, versus areas of disturbed and early successional habitat, where they appear to also be able to adapt in a more generalist manner to recently developed riparian systems.

The finding that Wilson's Warblers showed no association with willow structure conflicted with our hypotheses. Many studies indicate this warbler is at least a willow associate, if not certainly a willow specialist (Ammon and Gilbert 1999, Baril et al. 2009, Finch 1989). Baril et al. 2009 found that they are quite abundant in willow habitat and are associated with tall, dense willow and thick undergrowth structures. However, previous studies have found associations of Wilson's Warblers with willows of intermediate height and nesting located primarily on the ground, foraging from willow twigs on medium sized arthropods only 60 to 120 centimeters off the ground (Ammon and Gilbert 1999). Their use of the higher vegetative strata may be based in territoriality or breeding behaviors, though their primarily understory-based use of willows may help explain their lack of significant correlation with any vegetation variables.

Our results agree with those from other studies done on the Willow Flycatcher, which is universally considered a willow specialist due to its need for unsuppressed tall and dense willows for perching sites for sit-and-wait aerial foraging of flying insects (Sedgwick 2000). This uncommon to rare species of songbird is highly adapted to this type of complex willow habitat and therefore could demonstrate a high degree of vulnerability to changes in vegetation. The Willow Flycatcher and other high-density willow specialists have been the subject of new analyses of their responses to dramatic shifts in vegetative structure based on ungulate browse and human activities that can break down their habitat structure, including changes in hydrology, pollution, and urbanization (Baril et al. 2011, Cain et al. 2003, Sedgwick 2000).

Studies of the effects of rapid environmental change to riparian habitat are beginning to reveal the fragility of these vital ecosystems and continuing studies of the avian communities could be developed serve as indications of the health of these systems. For instance, grazing of

ungulates has been shown in numerous studies to significantly alter riparian habitat, lowering species diversity and abundance, likely due to selection pressures on specialized species, increased detectability of nests to brood parasites, or through vulnerability to foraging predators (Jackson 1992, Knopf et al. 1988, Olechnowski and Debinski 2008). Browse also increases the edge habitat in willow vegetation, thereby increasing susceptibility to predation and diminishing optimal breeding and foraging habitat (Cain et al. 2003). Decreasing populations of beavers have also been shown to negatively affect willow vegetation through changes in stream hydrology and therefore the native avian community stability and species diversity (United States Department of Agriculture 1990). Changes in vegetation are also driven by abiotic factors such as changing climates and stream flow in willow habitats, which often drive harsh selective pressures such as decreased cover and food availability for songbirds. These pressures are likely strongest in these high altitude riparian zones, as the songbird species are more specialized in higher elevational gradients, and therefore less likely to be able to rapidly adapt to habitat changes (Bolton and Shellberg 2001). Reduction of willows from human structural development and pollution will continue to decrease avian populations and an overall decrease in species diversity (Baril et al. 2011, Saab 1999). Human effects have the potential to be countered by human efforts in the areas of conservation and management of willow habitat in riparian areas. Many proposals and recommendations have been presented for supporting riparian habitat, including increasing forested stream buffers of certain widths (Bolton and Shellberg 2001), allowing the release of previously suppressed willow habitat (Baril et al. 2009), and even using natural riparian vegetation in existing golf courses (Merrola-Zwartjes and DeLong 2005). However, this study suggests that the best method of developing plans to maintain and improve the health of willow habitats is that of a systematic assessment of the behavioral patterns of individual riparian species and understanding their relationship to differences in the vegetative structures present in willow habitat, as well as the overlap and balance between the habitat use of the community of avian species. Through these types of studies, data on bird abundance can also indicate the health of the ecosystem and their selective niche needs and allow for “tailor-made” conservation strategies for the increasingly rare and critical riparian areas.

Further directions for research in this area that would increase our understanding of songbird habitat selection in high altitude riparian habitat include behavioral observations at a finer scale. Moving beyond broad-scale measures of distribution and abundance, monitoring

which parts of the vegetation birds are using for foraging and breeding, as well as other behaviors, would increase our understanding of habitat needs. In addition, a more detailed vegetative analysis of riparian areas, including plant species composition, would further elucidate the floral structure of songbird habitat. Finally, a comparison of species habitat use of riparian areas across a larger spatial scale in the United States could reveal patterns that could help inform the most effective land management and conservation of a diverse avian population.

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Figures and Tables

Table 1. Description of the environmental variables used in the model selection, including observed range, mean, and 1 standard deviation (n=40).

Category	Variable	Description	Range	Mean	SD
Vertical	Foliage Height Diversity	Measurement of vegetative diversity/density using data from the Robel Pole, calculated using the Shannon-Weiner Diversity Index	0.37 - 1.38	0.95	0.30
	Average Height	Average height in cm of vegetation along line transects at 1m intervals	6.83 - 294.28	99.48	61.73
	CV Height	Coefficient of variation in cm (SD/mean) in height of vegetation along line transects in 1m intervals	0.14 - 2.19	0.73	0.44
Horizontal	Frequency	Number of willow “hits” along the line transects at 1m intervals relative to total cover	0.13 - 1.00	0.65	0.27
	Patchiness	Average willow patch size (in cm)/number of patches along line transects	8.58 - 4000.00	708.52	1307.56
	Willow Cover 100m	Amount of willow (sq. meters) within a 100m buffer around the central point	7585.77 - 27388.50	16935.61	5222.98
	Willow Cover 40m	Amount of willow (sq. meters) within a 40m buffer around the central point	1670.05 - 5010.23	3593.13	982.91

Table 2. Species recorded from all sites (focal species in bold) (n=40). Abundance was averaged across three visits to each plot and summed across all plots.

Species	Plots Present	Frequency (% plots present)	Total Abundance
Lincoln's Sparrow	40	100.0	129.0
Wilson's Warbler	40	100.0	64.8
White-Crowned Sparrow	38	95.0	93.5
Yellow Warbler	35	87.5	31.2
Spotted Sandpiper	32	80.0	26.2
Fox Sparrow	30	75.0	23.0
American Robin	27	67.5	24.3
Green-tailed Towhee	15	37.5	8.0
Broad-Tailed Hummingbird	12	30.0	5.0
Red-Napped Sapsucker	12	30.0	4.7
Willow Flycatcher	12	30.0	10.3
MacGillivray's Warbler	11	27.5	6.2
Song Sparrow	11	27.5	4.3
Northern Flicker	9	22.5	3.67
Olive-Sided Flycatcher	9	22.5	4.33
Warbling Vireo	8	20	3.33
Swainson's Thrush	6	15	2.17
Common Snipe	5	12.5	2.00
Red-Winged Blackbird	5	12.5	3.33
Brown-Headed Cowbird	4	10	2.00
Ruby-Crowned Kinglet	4	10	1.67
Yellow-Rumped Warbler	4	10	1.33

Species	Plots Present	Frequency (% plots present)	Total Abundance
Cordilleran Flycatcher	3	7.5	1.33
Mountain Chickadee	3	7.5	1.67
Western Wood-Pewee	3	7.5	1.00
Brewer's Blackbird	2	5	1.33
Dusky Flycatcher	2	5	0.67
Pine Siskin	2	5	0.67
American Dipper	1	2.5	0.33
Brewer's Sparrow	1	2.5	0.33
Hairy Woodpecker	1	2.5	0.67
Mallard	1	2.5	0.33
Mountain Bluebird	1	2.5	0.33
Orange-Crowned Warbler	1	2.5	0.33
Red-Tailed Hawk	1	2.5	0.33
Unknown Sparrow	1	2.5	0.33
Unknown Warbler	1	2.5	0.33

Table 3. Summary of best models (lowest AIC) for each response variable (species richness, total bird abundance, Shannon-Weiner Diversity, and focal species abundance or presence)
Significant predictor variables are bold. YEWA= Yellow Warbler, WIWA = Wilson's Warbler, LISP = Lincoln's Sparrow, WCSP = White-Crowned Sparrow, FOSP = Fox Sparrow, WIFL = Willow Flycatcher, MAWA = MacGillivray's Warbler

Model Set	Estimate	St. Error	p-value	Model Adjusted R ²	Model p-value
<i>Total Bird Abundance</i>				0.25	0.0036
Intercept	8.13	1.52	<0.0001		
AvgHeight	-0.0019	0.0067	0.008		
WillowCover100	0.00076	6.84E-05	0.014		
Frequency	1.02	1.62	0.530		
<i>Species Richness (log-transformed)</i>				0.41	1.89E-05
Intercept	1.29	0.20	<0.0001		
FoliageDiversity	0.72	0.41	<0.0001		
WillowCover40	0.000076	4.23E-05	0.0817		
<i>Shannon-Weiner Diversity</i>				0.53	1.13E-06
Intercept	0.81	0.18	<0.0001		
FoliageDiversity	0.81	0.16	<0.0001		
AvgHeight	0.002	0.00089	0.064		
CVHeight	0.21	0.11	0.070		
<i>YEWA (log-transformed)</i>				0.25	0.0018
Intercept	-0.29	0.22	0.199		
FoliageDiversity	0.48	0.15	0.003		
WillowCover40	9.91E-05	4.57E-05	0.037		
<i>WIWA</i>					
Null Model	1.62	0.10	<0.0001		

<i>LISP</i>				0.34	0.00018
Intercept	6.2	0.69	<0.0001		
FoliageDiversity	-2.99	0.70	0.0001		
Patchiness	-0.00021	0.00016	0.199		
<i>WCSP (log-transformed)</i>				0.11	0.020
Intercept	1.69	0.26	<0.0001		
FoliageDiversity	-0.64	0.26	0.020		
<i>FOSP (Pres/Abs)</i>				-	-
Intercept	3.95	2.98	0.185		
FoliageDiversity	-3.87	2.24	0.084		
CVHeight	-2.6	1.14	0.022		
WillowCover100	0.00021	0.00011	0.070		
<i>WIFL (Pres/Abs)</i>				-	-
Intercept	-6.65	2.56	0.009		
FoliageDiversity	4.57	1.95	0.019		
CVHeight	1.52	0.93	0.102		
<i>MAWA (Pres/Abs)</i>				-	-
Intercept	-0.63	3.06	0.838		
FoliageDiversity	2.88	1.78	0.106		
CVHeight	-5.00	2.62	0.057		
Frequency	-0.45	2.4465	0.856		

Figure 1.

A.

B.

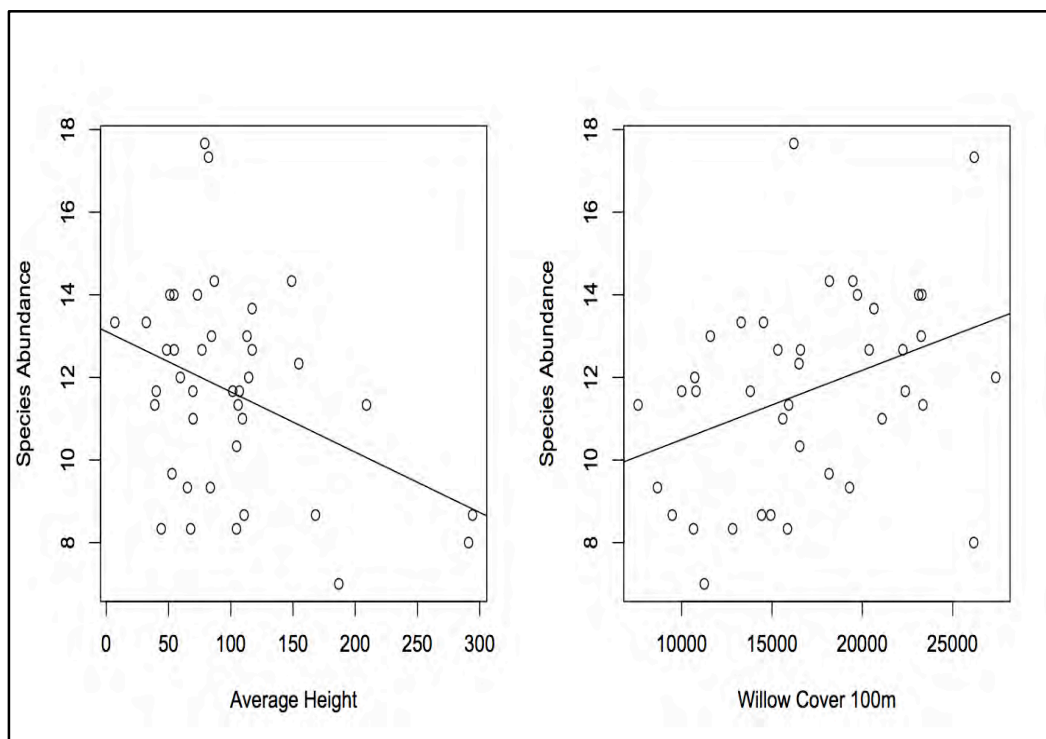


Figure 1. Species Abundance as a function of Average Height and Willow Cover at 100m. 1A: $p = 0.008$, $n = 40$ sites. 1B: $p = 0.01$, $n = 40$ sites.

Figure 2.

A.

B.

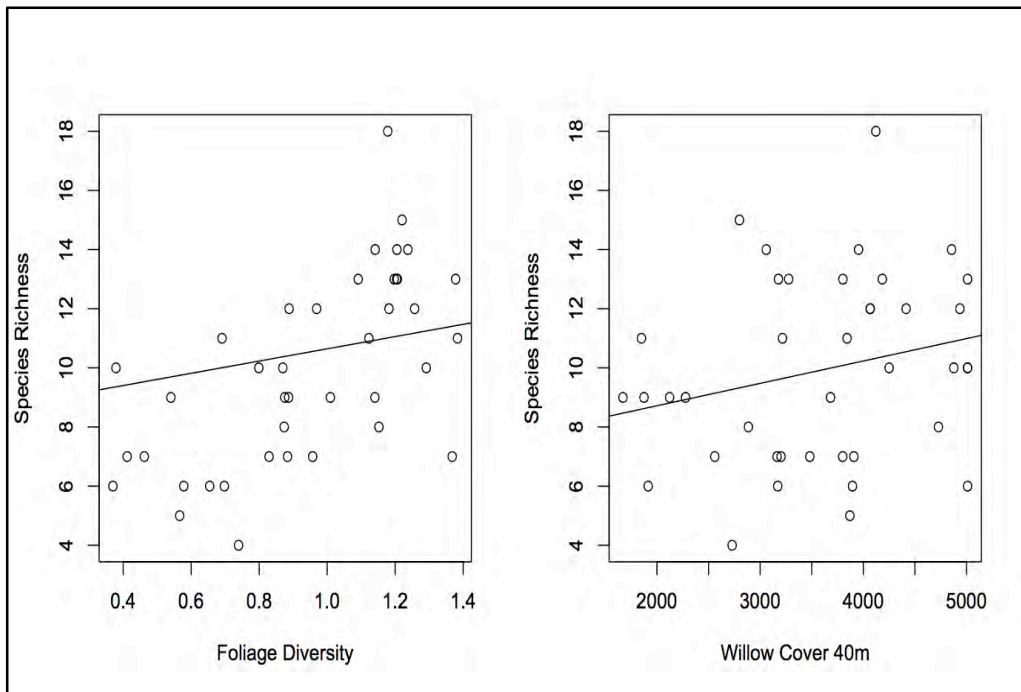


Figure 2. Species Richness as a function of Foliage Diversity and Willow Cover at 40m. 2A: $p < 0.0001$, $n = 40$ sites. 2B: $p = 0.08$, $n = 40$ sites.

Figure 3.

A.

B.

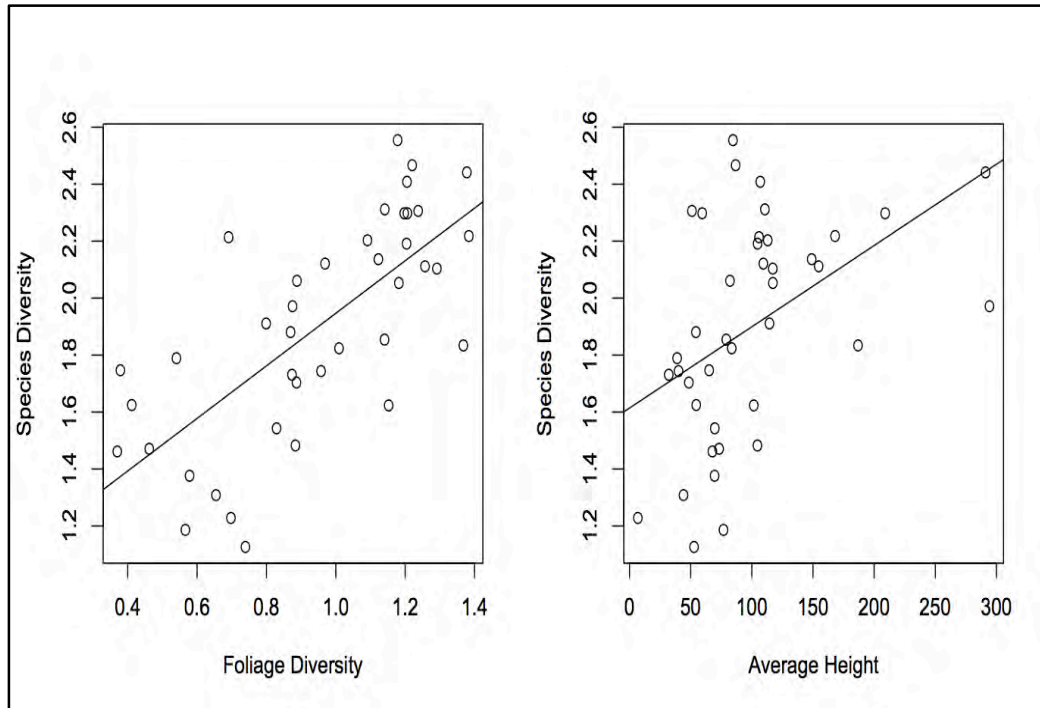


Figure 3. Species Diversity as a function of Foliage Diversity and Average Height. 3A: $p < 0.0001$, $n = 40$ sites. 3B: $p = 0.01$, $n = 40$ sites.

Figure 4.

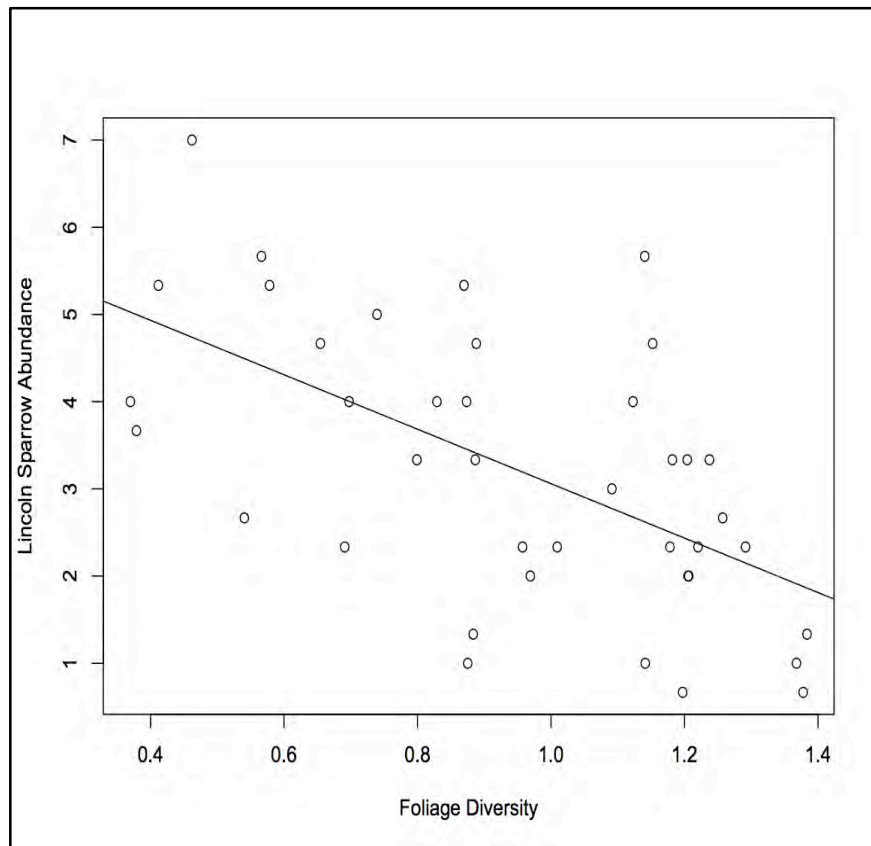


Figure 4. Lincoln's Sparrow Abundance as a function of Foliage Diversity: $p = 0.0001$, $n = 40$ sites.

Figure 5.

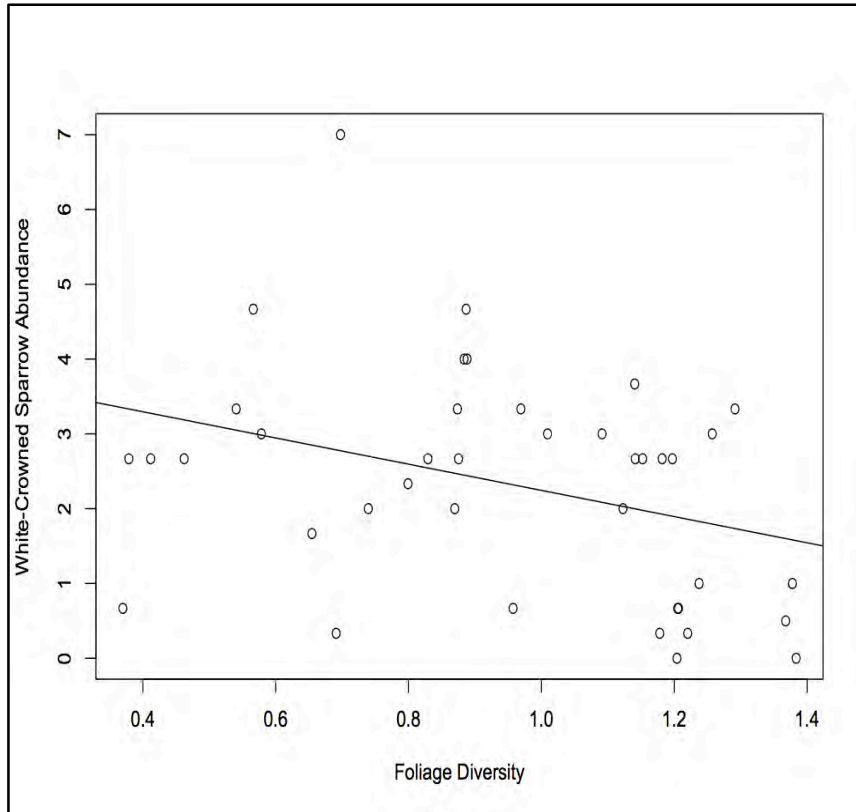


Figure 5. White-Crowned Sparrow Abundance as a function of Foliage Diversity: $p = 0.02$, $n = 40$ sites.

Figure 6.

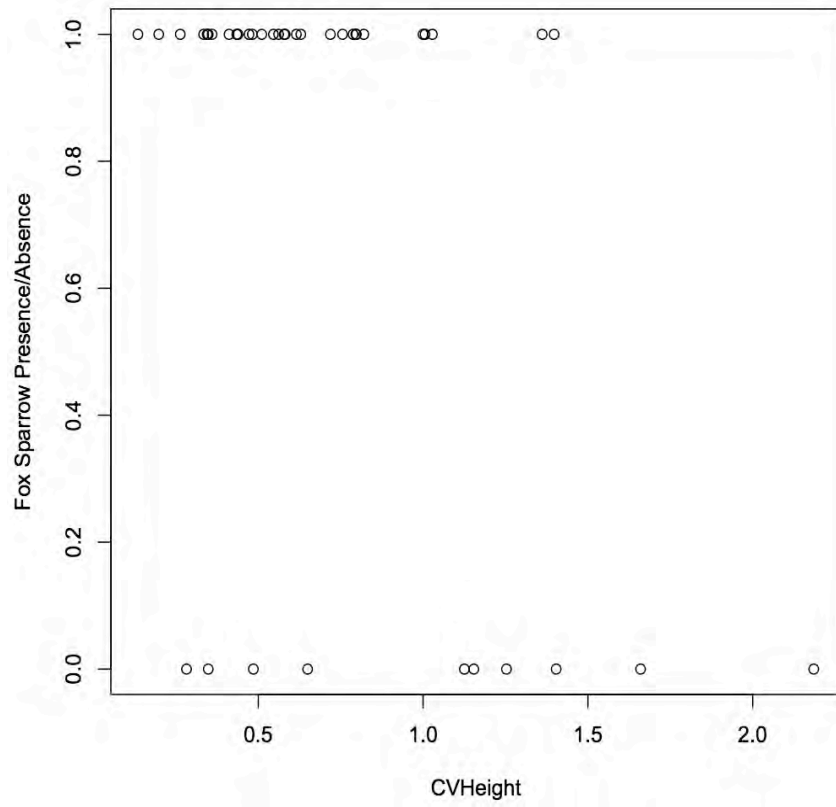


Figure 6. Fox Sparrow presence/absence as a function of Foliage Diversity and CV of Height of Willow: $p = 0.02$, $n = 40$ sites.

Figure 7.

A.

B.

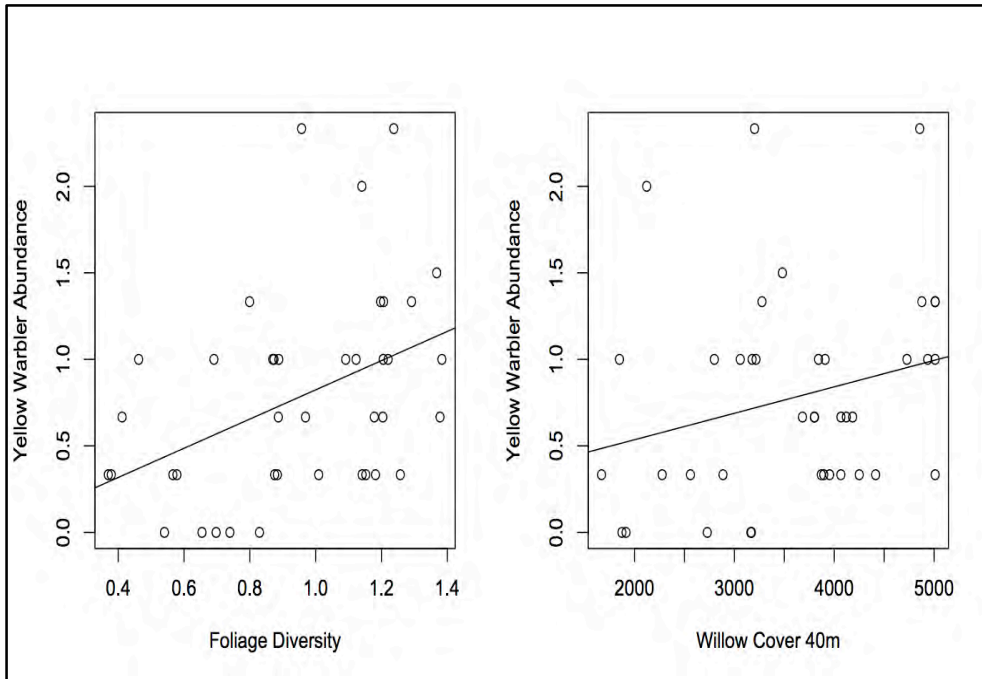


Figure 7. Yellow Warbler Abundance as a function of Foliage Diversity and Willow Cover at 40m. 7A: $p = 0.003$, $n = 40$ sites. 7B: $p = 0.04$, $n = 40$ sites.

Figure 8.

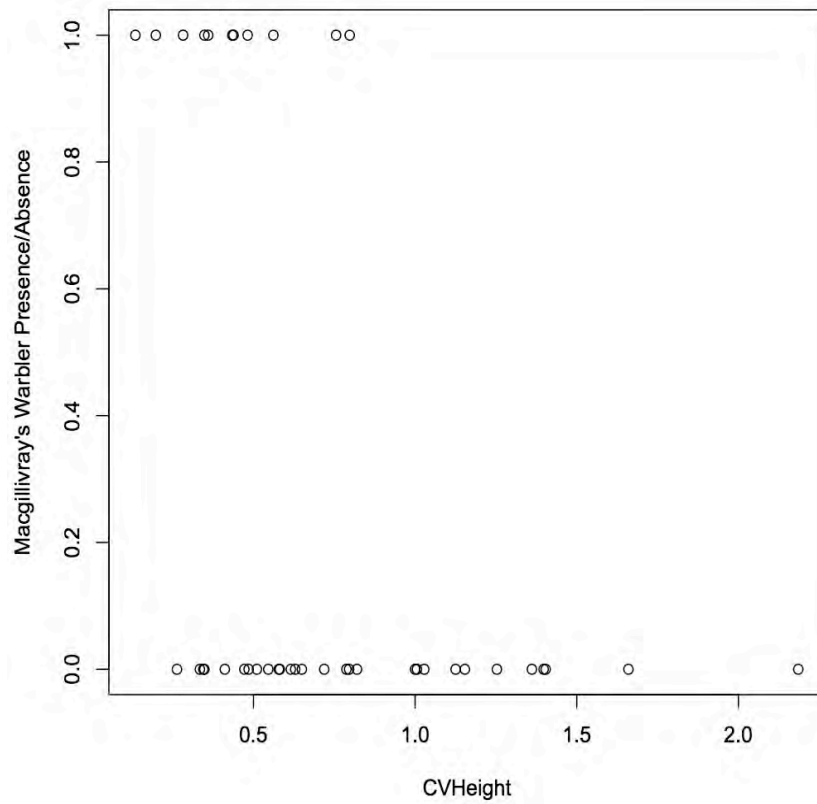


Figure 8. MacGillivray's Warbler presence/absence as a function of Foliage Diversity and CV of Height of Willow: $p = 0.06$, $n = 40$

Figure 9.

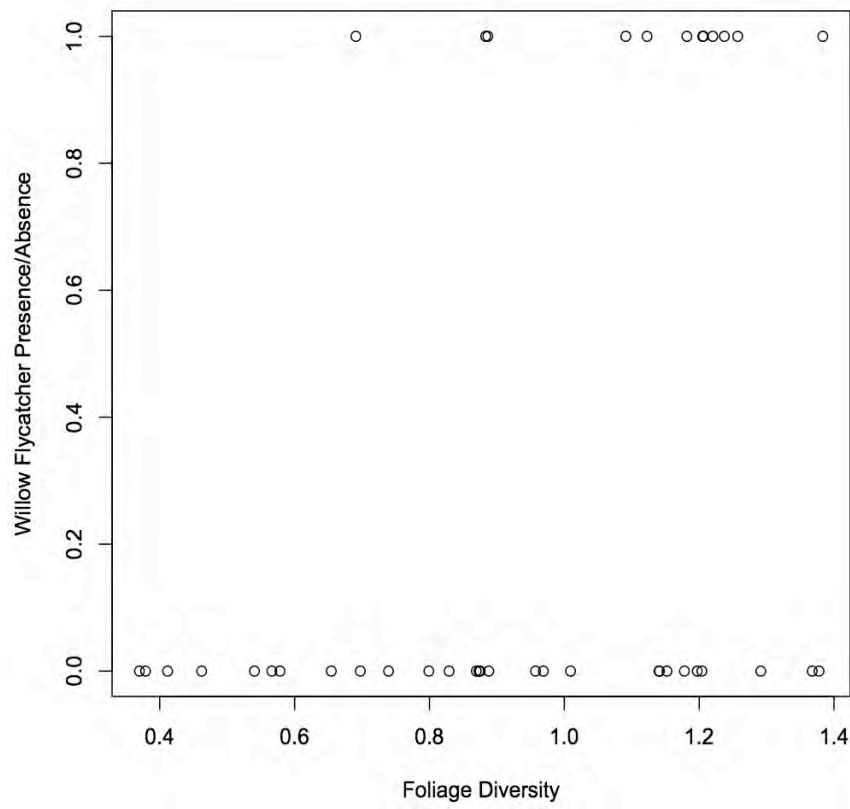


Figure 9. Willow Flycatcher presence/absence as a function of Foliage Diversity: $p = 0.02$, $n = 40$ sites.

Appendix 1. Pearson's correlation coefficients (r) for all vegetation predictor variables. $r > 0.5$ are in bold.

Willow Cover40	Willow Cover100	Patchiness	Number Patches	Avg Patch Size	Frequency	Horiz Cover	CV Height	Avg Height	Foliage Diversity	
0.02	0.02	0.15	-0.08	0.18	0.32	0.31	-0.19	0.49	1.00	Foliage- Diversity
-0.04	0.11	0.68	-0.41	0.71	0.57	0.58	-0.51	1.00	0.49	Avg-Height
-0.14	-0.33	-0.42	0.13	-0.50	-0.75	-0.73	1.00	-0.51	-0.19	CV-Height
0.22	0.33	0.54	-0.10	0.63	0.99	1.00	-0.71	0.58	0.31	HorizCover
0.24	0.33	0.51	-0.06	0.60	1.00	0.99	-0.75	0.57	0.32	Frequency
0.13	0.27	0.98	-0.62	1.00	0.60	0.63	-0.50	0.71	0.18	AvgPatchSize
0.14	-0.06	-0.55	1.00	-0.62	-0.06	-0.10	0.13	-0.41	-0.08	NumberPatches
0.13	0.26	1.00	-0.55	0.98	0.51	0.54	-0.42	0.68	0.15	Patchiness
0.75	1.00	0.26	-0.06	0.27	0.33	0.33	-0.33	0.11	0.02	WillowCover 100
1.00	0.75	0.13	0.14	0.13	0.24	0.22	-0.14	-0.04	0.02	WillowCover 40