Simplified structure or fewer arthropods to eat? Disentangling the impacts of an invasive plant on breeding bird diversity in agricultural hedgerows

by
Madeline Grace Edmonds

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Name:	**Madeline Edmonds**
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Examining Committee:	**Ruth Joy** Supervisor and Chair Faculty, SFU
	Susan Owen Examiner Faculty, SFU
	Shawn Chartrand Examiner Faculty, SFU
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Abstract

In agricultural landscapes, hedgerows provide critical habitat for songbirds. Himalayan Blackberry (*Rubus armeniacus; HBB*) is a widespread invasive species in the Pacific Northwest that has been linked to lower breeding songbird diversity. My study explored two possible explanatory mechanisms: reduced structural complexity and lower arthropod abundance as a food source. I conducted avian point counts in 51 hedgerow segments at two locations in the Lower Mainland of British Columbia. In these segments, I quantified vegetation structure using a Foliage Height Diversity (FHD) metric derived from LiDAR data. I sampled arthropod abundance on the foliage of woody understory vegetation. I used multiple regression to identify best fit generalized linear models. Songbird diversity decreased with HBB % cover and increased with FHD. However, arthropod abundance was unrelated to bird metrics, and similar between HBB and other native shrubs. This suggests that hedgerows should be managed to control HBB and maximize vegetation structure.

Keywords: songbird diversity; Himalayan Blackberry; agricultural landscapes; hedgerows; arthropods; LiDAR

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List of Acronyms

AIC	Akaike Information Criterion
BCIT	British Columbia Institute of Technology
FHD	Foliage Height Diversity
HBB	Himalayan Blackberry
NWA	National Wildlife Area
SFU	Simon Fraser University
WMA	Wildlife Management Area

Chapter 1.   Introduction

1.1. Background and rationale

Across North America, bird populations are experiencing major declines, with a 29% loss of 2.9 billion individuals since 1970 (Rosenberg et al. 2019). Population declines are not limited to rare and threatened species, but includes common and generalist species over a wide range of taxa (Rosenberg et al. 2019). Reductions in abundance may have negative impacts on ecosystem function and integrity, as well as ecosystem services provided (Hooper et al. 2012; Whelan et al. 2015). While certain groups such as wetland birds and raptors are recovering, others such as aerial insectivores, shorebirds, and grassland birds are declining rapidly (NACBI 2019). Collectively, there has been little change in forest bird populations, although this is due to a mixture of trends, with resident species increasing and long-distance migrants to South America under threat (NACBI 2019). Specifically in agricultural settings, 74% of species that rely on farmland are decreasing, with especially pronounced losses for aerial insectivores (-39%), grassland (-20.8%), and shrubland (-16.5%) associated species (Stanton et al. 2018).

In agricultural landscapes, intensification has resulted in the simplification of landscape structure on multiple scales, drastically decreasing the ability of these areas to support biodiversity and negatively impacting the ecosystem services they may provide (Landis 2017). Within such landscapes, hedgerows are linear strips of woody vegetation along the margins of fields, which exist as part of a network of semi-natural habitats such as verges with non-woody vegetation, ditches, wetlands, woodlots (Graham et al. 2018). They may be purposefully planted, remnant strips from forest clearance, or spontaneously growing (Dover 2019). Hedgerows provide a wide range of ecological services (Dover 2019). Examples include reducing soil erosion, absorbing water, and acting as wind barriers (Dover 2019). Furthermore, hedgerows can provide critical structure for wildlife allowing these areas to support a greater diversity and abundance of species (Dover 2019). They also serve as corridors for mobile wildlife species, improving landscape connectivity (Hinsley & Bellamy 2000). Improving biodiversity in hedgerows can benefit adjacent crops by providing habitat for pollinators, as well as predatory arthropods and birds that control agricultural pests and act as seed

dispersers (Dover 2019). However, drawbacks to the landowner can include the loss of arable area, and concerns that they may harbour agricultural pests, shade crops, or steal water and nutrients (Dover 2019). Furthermore, they are costly to install and maintain (Dover 2019).

In the Pacific Northwest region Himalayan Blackberry (*Rubus armeniacus*; HBB) is a widespread and well established invasive species (Murphy 2006). HBB is often predominant in agricultural hedgerows, since it thrives in areas with high light levels and a history of disturbance (Sandiford et al. 2001). It reproduces vigorously both vegetatively and by seed, forming dense monocultures that choke out native vegetation (Murphy 2006). As a consequence, restoration efforts often focus on HBB removal (Gaire et al. 2015). Objections to these efforts have been raised due to the widely held assumption that HBB is beneficial to songbirds, providing them with food and shelter (Bell & Grass 2008). However, this assertion has recently been called into question by several studies suggesting that a lower diversity and abundance of breeding songbirds occupy HBB monocultures compared to native vegetation (Astley 2010; Newberry 2016; Hartley 2018). In 1999, Canadian Wildlife Services (CWS) surveyed hedgerows at four sites in the Fraser River delta (Sandiford et al. 2001). Their goal was to assess what habitat and landscape features were associated with higher diversity and abundance of breeding and wintering birds in agricultural hedgerows (Sandiford et al. 2001). They ranked models to assess four hypotheses related to hedgerow composition, landscape composition, biogeography, and distance to water bodies across breeding and nonbreeding seasons (Sandiford et al. 2001). They found that the composition of hedgerows was more important during the breeding season (Sandiford et al. 2001). Their results suggested that the negative impacts of high HBB cover could be mitigated by the presence of a tree canopy, but they did not hypothesize any specific mechanism (Sandiford et al. 2001). In order to address the mechanisms by which HBB may reduce breeding songbird diversity, my study investigates two hypotheses: reduced vegetation structural complexity and reduced availability of arthropods.

Invasive plants including HBB have a tendency to form dense monocultures (Gaire et al. 2015). This may reduce the structural complexity of vegetation, leaving fewer niches available for birds to build nests (Gaire et al. 2015; Munro et al. 2011). However, the dense structure of HBB could still provide important cover from predators, raising the possibility of direct positive impacts on birds (Gleditsch 2017). If

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HBB forms the understory of a mature forest, bird species may be able to use the canopy, even if there is lower structural diversity below. While past studies of HBB noted that sites with high levels of vegetation structure were preferred and suggested that this was the reason why HBB was linked to lower bird diversity, none of them measured structure quantitatively (Astley 2010; Hartley 2018; Sandiford et al. 2001; Newberry 2016). Vegetation structure can be measured in multiple ways (e.g. volume, leaf area and density, branching architecture), but one key aspect is structural complexity (Graham et al. 2018). This can be defined as 'the number or magnitude of structural components present and their variability' (Graham et al. 2018). In the case of the vertical profile of a hedgerow it can be thought of as the number of layers occupied by vegetation, which corresponds to the area available to be occupied by birds and arthropods (Clawges et al. 2008).

Accurate assessments of vegetation structure can be extremely challenging to make in habitat types with dense vegetation and access challenges (Clawges et al. 2008). One solution is remote measurement using LiDAR (Light Detection and Ranging), a rapidly developing technology that is becoming increasingly affordable and available (Graham et al. 2019). Airborne LiDAR data are gathered by a drone that sends out series of near-infrared light pulses, and measures "returns" reflected back off the ground and various surfaces (Graham et al. 2019). This yields an xyz point cloud with resolutions finer than 1 m, which can be used in raw form or used to interpolate surface models (Graham et al. 2019). Drawbacks include limits to point density and restricted perspective, as well as massive datasets that require proprietary technology to process (Graham et al. 2019). However resolutions are steadily increasing and costs are coming down, leading to increasing applications including use on a landscape level to classify hedgerows and measure habitat complexity (Zimble et al. 2003; Graham et al. 2019). LiDAR has also been used to quantify vertical vegetation structure in the context of bird habitat in woodland settings (Melin et al. 2018; Clawges et al. 2008). These studies computed a metric of Foliage Height Diversity (FHD) to represent the proportionate distribution of vegetation within the vertical height profile, which was positively correlated to avian diversity (Clawges et al. 2008; Melin et al. 2018). These metrics are similar to standard methods used to quantify vegetation structural complexity (Bibby et al. 2000). They have been verified to correspond well with field measurements, allowing dense and difficult to access habitat types to be measured (Clawges et al. 2008). I used LiDAR

measurements of FHD to measure vertical vegetation structure in hedgerows with a range of HBB % cover, allowing me to link structure to measures of avian diversity.

In addition to influencing hedgerow structure, invasion by HBB may also decrease the abundance of the herbivorous arthropods, which are a critical food source for many songbird species (Tallamy 2004). During the breeding season, food resources often limit reproductive success in passerine birds (Martin 1987). Many species of songbirds rely on a diet of arthropods, especially caterpillars to meet the developmental requirements of their nestlings (Burghardt et al. 2008). Arthropod abundance is often lower on non-native plants, because native arthropods have not adapted to tolerate novel plant defensive compounds (Litt et al. 2014). Declines in arthropod abundance have been documented across the globe, although the extent and spatial scale of these losses remain unknown (Sánchez-bayo & Wyckhuys 2019; Wagner 2020). While not often the focus of conservation efforts, the presence of these organisms is critical to their food webs (Lister & Garcia 2018). Arthropod losses may be attributed to various factors, but one contributor to declines is an increasing predominance of non-native plants in ecosystems (Litt et al. 2014; Gerber et al. 2008). This may lower food availability for insectivorous birds, which can be especially detrimental during life stages with high energy requirements, such as the breeding season (Narango et al. 2018). However, studies have produced inconsistent results and this pattern may not always hold true (Litt et al. 2014).

1.2. Objectives and hypotheses

Given the biodiversity-supporting functions of hedgerows in agricultural landscapes, understanding the structural and compositional features that maximize their usage is important (Graham et al. 2018). This is especially relevant in the context of human-caused declines in bird and insect populations (Rosenberg et al. 2019; Sánchez-bayo & Wyckhuys 2019). The presence of invasive species such as HBB may have impacts on hedgerow habitat function, but the reasons for this are unclear (Sandiford et al. 2001). I hypothesize that a negative association between HBB and bird diversity may result from HBB monoculture reducing vegetation structural complexity. Thus, areas with higher HBB % cover would have a simplified vegetation structure, and lower FHD as measured with LiDAR data. Alternatively, as an introduced species, HBB is less palatable to native arthropods, and I predict that sites with higher HBB % cover will host

a lower abundance of arthropods. I predict that both vegetation structural complexity and arthropod abundance will be positively correlated with passerine diversity. Understanding how hedgerow structure and composition affect songbird communities can inform management and restoration practices.

Chapter 2.   Methods and experimental design

2.1. Site selection and vegetation classification

Surveys were conducted at Alaksen National Wildlife Area (NWA), and Serpentine Fen Wildlife Management Area (WMA), which are both wildlife areas that support active agriculture adjacent to managed hedgerows in the Lower Mainland of British Columbia (Figure 1; ECCC 2020). Alaksen NWA totals 349 ha of protected land located on the northern end of Westham Island in the Fraser River delta, and is managed by the Canadian Wildlife Service of Environment and Climate Change Canada (ECCC 2020). Serpentine Fen WMA is 150 ha of land just south of the Serpentine River in Surrey, and is managed by Ducks Unlimited (City of Surrey 2019).
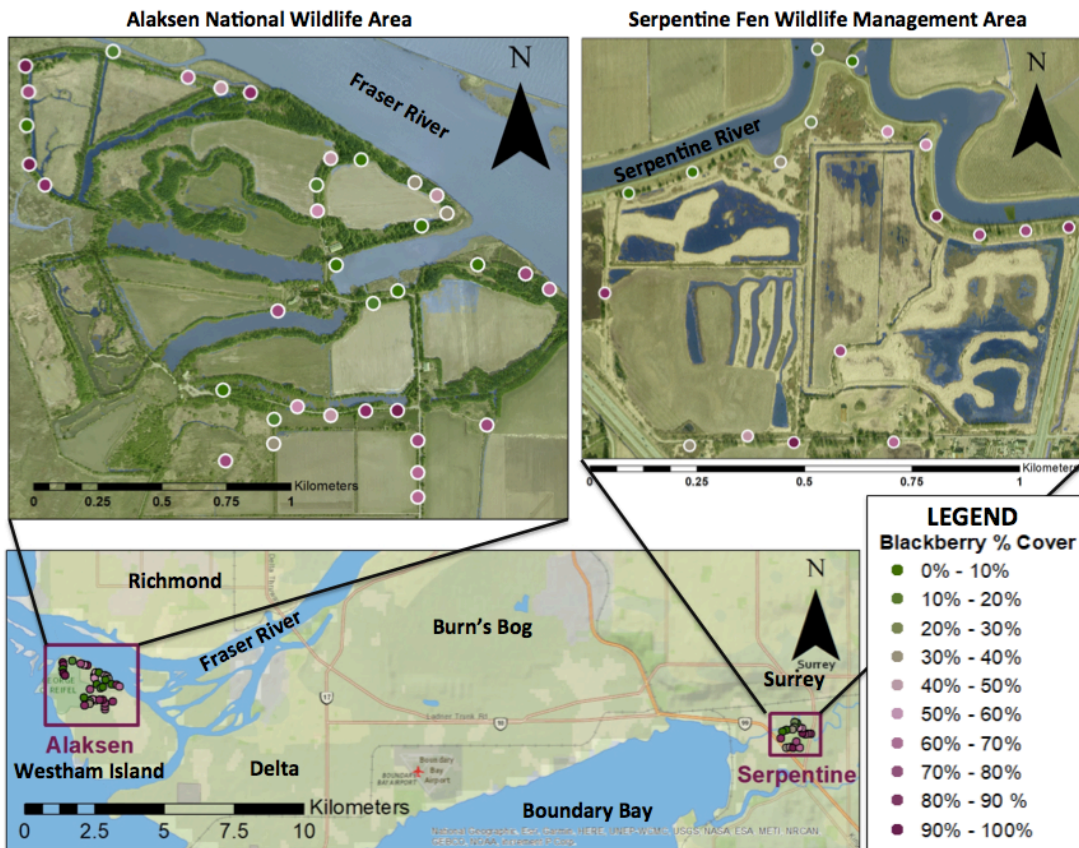
Figure 1. Maps of hedgerow study site locations at Alaksen National Wildlife Area and Serpentine Fen Wildlife Management Area, located within agricultural landscapes in the Lower Mainland of British Columbia. Study sites were 30 m sections of hedgerow chosen with a range of HBB % cover and canopy presence/absence.

Like many lowland areas in the Pacific Northwest, the Fraser River delta has been intensively developed with limited remnant forested patches remaining. The landscape consists a mosaic of agricultural areas and urbanized zones, as well as estuarine habitat, remnant wetland, and riparian forest (ECCC 2020). Active efforts are being made locally to plant and maintain hedgerows, with organizations such as Delta Farmland and Wildlife Trust partnering with private landowners (Thiel et al. 2015).

Farm fields in these wildlife areas are managed to support migrating and overwintering waterfowl, with additional habitat such as woodlots, hedgerows, and saltmarshes providing additional benefits for a range of other wildlife species, especially those of conservation concern including breeding and migrating songbirds (ECCC 2020; City of Surrey 2019). Alaksen is designated as a globally significant Important Bird Area, is part of a Ramsar site, and is a key stopover location along the Pacific Migratory Flyway, annually attracting 1.4 million birds from Siberia to South America (ECCC 2020). HBB is a common invasive species on both properties, but varies in predominance, with some areas remaining mostly native shrubs, and others taken over by HBB monocultures.

For my study sites, I selected 30 m hedgerow segments representing a range of HBB % cover. These included both with a tree canopy and shrub-dominated sites. Sites were spaced a minimum of 100 m apart to avoid double counting (Bibby et al. 2000). This layout was consistent with the methodology of Sandiford et al. (2001), but the exact locations of the historical study could not be resurveyed for direct comparison due to inaccuracy of the GPS technology used at the time. To select segments with a range of vegetation characteristics, sites were initially categorized with 3 HBB levels (high > 75%, mixed 25 - 75%, and low < 25%), and 2 tree canopy classes (canopy with 2+ single-stem trees >10 m tall, or shrub-dominated without; Sandiford et al. 2001; Table 1). HBB % cover and habitat structure were later measured as continuous variables based on field surveys and LiDAR data. A total of 33 sites were selected at Alaksen NWA, and a total of 18 sites were selected at Serpentine Fen WMA, and their locations recorded with a Trimble GNSS unit using TerraSync mapping software. Adjacent habitat types included open areas with low vegetation, such as actively cultivated agricultural fields, old fields, sloughs, saltmarsh, and walking trails. The hedgerow segments selected were at least 5 m wide. Areas with bands of trees greater than 30 m wide were excluded from the study, as these were considered to be borderline woodlots, even though they were

contiguous with hedgerow habitat at Alaksen NWA. Alaksen initially had 36 sites, but three sites were excluded from further analysis, two due to inaccurate field measurements of width resulting in segments greater than 30 m wide, and the other because it had extremely low vegetation density in the LiDAR data available from 2018, and may have been mowed.

Table 1. Counts of hedgerow segments selected in different vegetation categories to achieve a distribution of these characteristics. Prior to the continuous measurement of HBB % cover and LiDAR foliage structure, sites at Alaksen NWA and Serpentine Fen WMA were preliminarily classified as high, mixed, and low HBB and with a tree canopy vs. shrub-dominated.

Alaksen	Tree canopy	Shrub-dominated	Total
Low HBB	4	6	13
Medium HBB	9	4	12
High HBB	6	4	11
Serpentine Fen	**Tree canopy**	**Shrub-dominated**	**Total**
Low HBB	2	2	7
Medium HBB	4	4	7
High HBB	2	4	4

2.2. Vegetation field survey methods

For each study site, vegetation composition was measured by visually estimating percent cover of each shrub species in the understory layer, and counting the number of each tree species within the 30 m section following the same methods laid out by Sandiford et al. (2001). In order to obtain more accurate visual estimates of percent cover, each site was divided into four 7.5 m sections and cover estimates were made for each of four subsections then averaged for the 30 m hedgerow section. Vegetation surveys occurred between August 20 and September 17, 2019.

2.3. Bird survey methods

To estimate the diversity of breeding passerines, I conducted point count surveys at these 51 sites over nine weeks during the main avian breeding season from May 16 – July 8, 2019, within four hours of sunrise (~ 5:30 a.m. – 9:30 a.m.). Stations were visited three times over the course of the season, on days with fair weather (no precipitation and wind speed < 16 km/hr (Beaufort scale 2)). Temperature ranged from 10 to 26 °C.

After an initial rest period of one minute to allow birds to acclimatize to human presence, point counts were conducted for 10 minutes, counting all bird species within the 30 m hedgerow section, with the exception of waterbirds and raptors (MWLAP 1999; Sandiford et al. 2001). Only individuals that landed within the count area were included, so that flyovers of species crossing between adjacent habitat types did not confound results. Two observers collected data, with both present for several initial site visits to calibrate their species identification, and subsequent counts conducted individually.

2.4. LiDAR analyses

Vegetation structure was characterized using LiDAR data. LiDAR data for Alaksen NWA were obtained from the City of Delta through agreement with BCIT. It was collected on June 16 and 17, 2018. Average point cloud density was 10 points per square meter. LiDAR data for Serpentine Fen WMA were obtained through the City of Surrey Open Data Catalogue. It was collected on November 11 and 12, 2018. Average point density for all returns was 30+ points per square meter, 23+ points per square meter for first returns (one laser pulse generates multiple returns, with the first return representing the initial surface the beam reflected off of, and last returns more likely to capture the ground surface). Flights were flown in favourable conditions (light winds and clear skies). LiDAR data were provided as geometrically corrected and calibrated LAS files.

In order to define the boundaries of each of the 51 hedgerow segments, the GPS coordinates for the station centre were buffered with a 30 m diameter circle. The edge of hedgerow vegetation was visually assessed with the LAS Tools 2D profile viewer, and points within the 30 m segments were reclassified as within the study site. A bounding rectangle was then drawn around the reclassified points, and the width of each hedgerow segment was computed. These rectangles were used to define and clip segments in subsequent analyses.

The LiDAR point cloud was filtered to exclude outlier points over 40 m and under -5 m using the LAStools toolbox in ArcGIS. Vertical measurements were scaled so that z values represented height of the ground instead of elevation, as the variables of interest related to vegetation structure with respect to ground level, not absolute elevation. This was accomplished by subtracting the z value of a TIN surface (triangulated irregular

network) constructed from ground-classified points using the lasheight tool. The number of returns above a 0.5 m cut-off were then divided into 17 ~2m height bins for each site (the first bin was 0.5 – 2 m, and subsequent intervals were 2 m; Melin et al. 2018). Density values for each layer were also obtained by dividing the number of returns in each bin by the total number of points and scaled to a percentage. These numbers ensured that LiDAR data was standardized for resolution or number of returns, and resulted in the same FHD values as calculations using the raw counts. FHD was then calculated according to the Shannon Weiner formula ($H = - \Sigma\ p_i \ln p_i$; Clawges et al. 2008). Additionally the mean vegetation height was calculated for all returns above the cut-off. Vegetation density was computed by dividing the number of points above the cut-off by the total number of all returns, and separate density values for the first 2 height bins were also calculated (0.5 – 2 m and 2 – 4 m). Visualizations of LiDAR height returns in each bin can be found in Appendix A.

2.5. Arthropod survey methods

Foliar arthropods were sampled from the branches of woody vegetation using a beat sheet survey method (Hurlbert et al. 2019). Branches of woody shrub and tree species were chosen at 0.5 - 2 m height. Within each 30 m hedgerow section, nine branches were chosen and sampled over the course of three site visits. The first branch was selected randomly, and subsequent branches were spaced 3 m apart. Stations were visited between 06:00 and 13:30 within several days of the bird surveys. To dislodge foliar arthropods, a 71 x 71 cm white canvas sheet was held underneath the branch and the branch was beaten vigorously 10 times in rapid succession with a stick. Shrubs and trees were identified to species; planted hedgerows included a combination of native and introduced species (Table B2). The % cover of foliage over the beat sheet was visually estimated to the nearest 5% to correct for differences in area sampled. All arthropods over 2 mm in length were identified, typically to order (but sometimes to suborder or family; Table B3), and their length was recorded to the nearest millimetre. Arthropods under 2 mm were excluded because they are difficult to identify accurately in the field, and not likely to be important as an avian food source (Hurlbert et al. 2019). Beat sheet sampling was chosen over a visual search and survey method, since it yields a more consistent estimate of phenological patterns (Hurlbert et al. 2019). Both survey types give similar relative and absolute density estimates, although beat sheets capture

relatively more beetles and visual surveys more flies (Hurlbert et al. 2019). Caterpillars (including larval Lepidoptera and Sawflies, Hymenoptera: Symphyta) are detected with similar frequency between the two methods (Hurlbert et al. 2019). Furthermore, caterpillar phenology documented by shrub layer foliage surveys correlated strongly with the results of canopy phenology based on surveys of frass (i.e. caterpillar droppings; Hurlbert et al. 2019).

2.6. Computation of metrics and indices

For the avian point count data, the maximum number of individuals observed at once was recorded as species abundance on a given visit to avoid double counting. Total abundance was then computed as the maximum number observed at once over the course of 3 site visits. From this, species richness was calculated as the total number of species observed at the site. This approach assumes that birds seen on any of the breeding season visits were occupying the site. Two invasive species, European Starling and House Sparrow were excluded from the analyses. The diversity of native songbird species was calculated using the Shannon Weiner diversity index ($H = -\Sigma\, p_i \ln p_i$; Magurran 1988). Birds were classified as either foliar arthropod consumers or non-consumers. This was based on whether their breeding season foraging strategies made it likely that they would be affected by foliar arthropod abundance (De Graaf et al. 1985). Likely foliar arthropod consumers included foliage-foraging omnivores, insectivores, foliar hover-gleaners, but not bark gleaners or granivores (Table B1, Appendix B).

After excluding species that were unlikely to consume foliar arthropods, I recalculated the Shannon diversity index. I calculated arthropod metrics per branch and overall for each site by adding the numbers sampled on each of 9 branches. Arthropod abundance per unit leaf area was calculated by weighting absolute abundance by the % leaf cover over the beat sheet to account for differences in leaf area sampled. Biomass was initially estimated using length-weight regressions, but had a highly skewed distribution and so abundance was selected as an index for food availability (Table C1, Figure C1, Appendix C). The diversity of understory shrub species at each site was computed using the Shannon Weiner diversity index (Magurran 1988).

2.7. Statistical modeling

I investigated hypotheses about hedgerow factors affecting bird diversity by fitting generalized linear models (GLMs). Continuous variables were modeled using Gaussian distributions and identity link functions. Due to differences in measurement units, z-scores were calculated for all variables. We verified that assumptions of model linearity, as well as normality and homoscedasticity of model residuals were met (Daniel and Wood 1980). Statistical significance was set at $\alpha = 0.05$. Summary statistics are reported as mean ± standard error. All analyses were conducted using R version 3.6.1.

I compared insect abundance between plant species on 8 plant species for which I sampled >10 branches. I used a Kruskal-Wallis test, since a Shapiro-Wilk test showed that the insect abundance distributions differed significantly from normality (W=0.77, p>0.001), and a Bartlett's test showed that variances differed significantly between groups (K-squared = 59.67, df = 7, p-value > 0.001). I then used a pairwise Wilcox test for comparisons between groups. I used a t test to compare arthropod biomass between sites with a tree canopy and those without.

Since I expected several of the vegetation structure metrics would be correlated, I constructed a correlation matrix to identify variables that should not be included together in the final model (Figure C2; Appendix C). As predicted, many of these metrics had high and significant R^2 values (Figure C2; Appendix C). To identify the best model predicting Shannon bird diversity and songbird abundance, I used multiple regression. I performed stepwise model selection using the step() function to search for the best-fit model based on Akaike Information Criterion (AIC) values (starting from a null model and both adding and removing terms; Burnham & Anderson 2002). The full model was a GLM relating the response variable (bird diversity or abundance) to HBB % cover, arthropod abundance, width, shrub species richness, FHD, mean height, and vegetation density in the 0.5 – 2 m and 2 – 4 m height classes. Additionally, I fitted GLMs for the subset of birds classified as arthropod consumers as a function of arthropod abundance.

Chapter 3.   Results

3.1. Site characteristics

During avian point counts, 461 individuals of 31 bird species were observed using the 51 hedgerow sections, excluding 2 introduced species (House Sparrow and European Starling; Figure 2, Table B1; Appendix B). On average, 5.8 ± 0.3 species were observed per station, with a range of 2 - 11 species. Total abundance ranged from 2 - 19 individuals, with an average of 9 ± 0.5 individuals occupying each site. Different species were more commonly observed depending on level of HBB % cover (Figure 2).
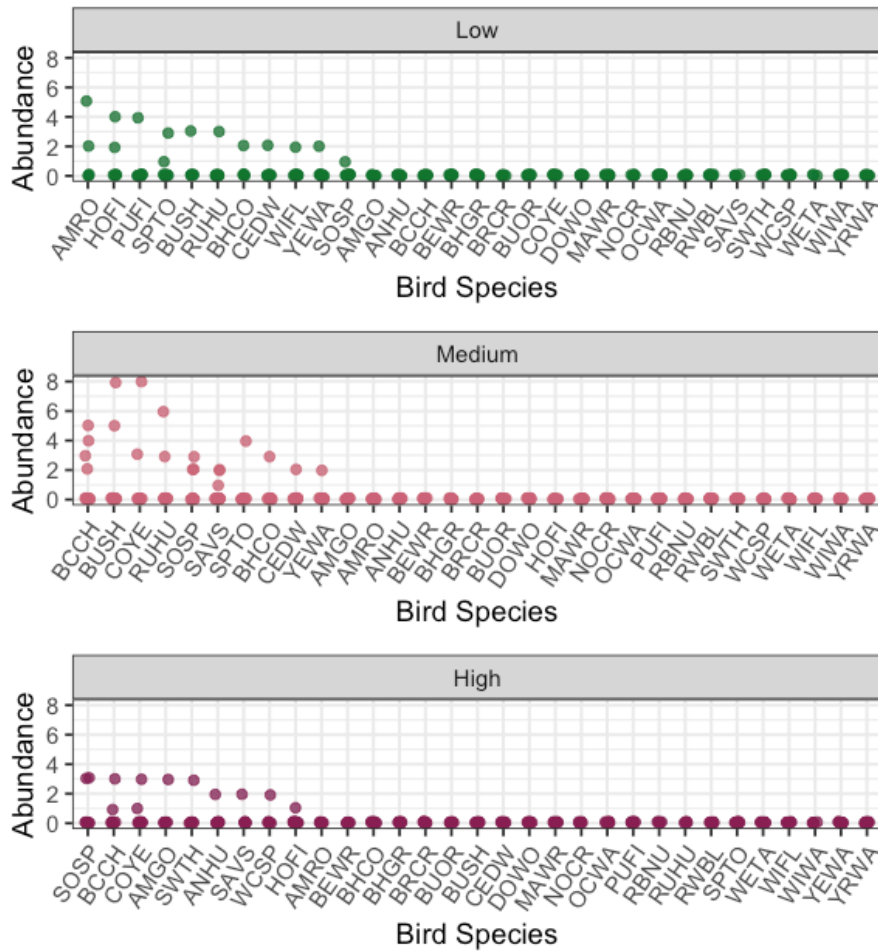
Figure 2. A comparison of bird species between high HBB (>75% cover), medium HBB (25-75% cover) and low HBB (<25% cover). The figure shows the number of individuals observed at each station for bird species seen during breeding-season surveys of agricultural hedgerows in Alaksen NWA and Serpentine Fen WMA (see Appendix B for species codes).
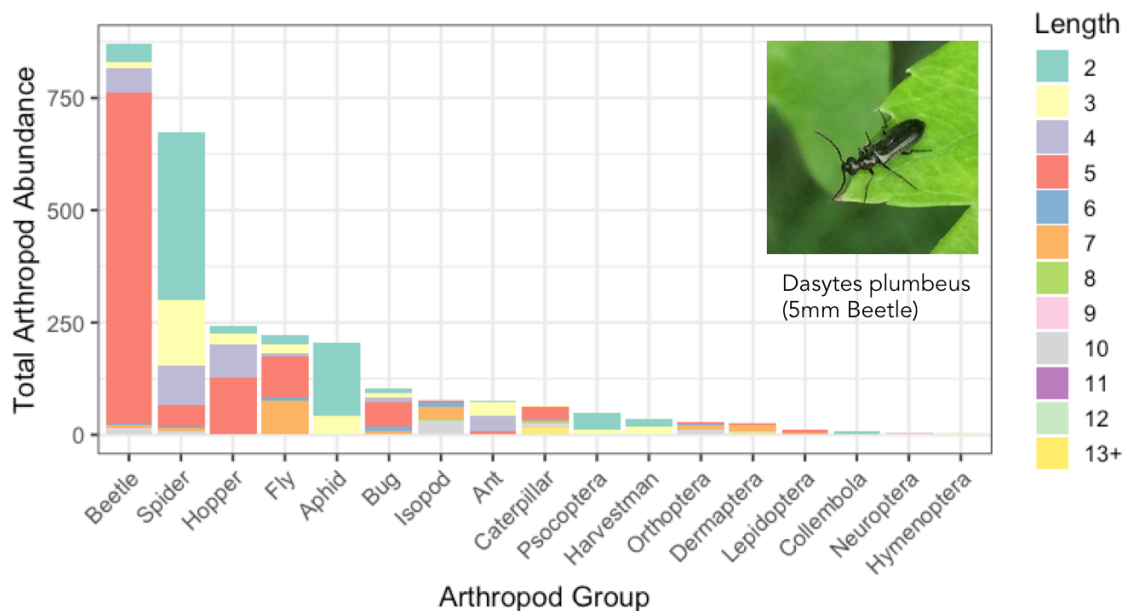
Figure 3. Total abundance of arthropods categories of different lengths sampled on the branches of woody understory vegetation in agricultural hedgerows at Alaksen NWA and Serpentine Fen WMA. Inset is the highly abundant introduced beetle species Dasytes plumbeus.

Foliar sampling of woody vegetation yielded 2558 arthropods in 18 groups representing 13 orders (Figure 3; Table B3, Appendix B). The largest numbers were sampled from Beetles, followed by Spiders and leafhoppers (order Homoptera; Figure 3). I found very high numbers (713 individuals) of an introduced 5mm-long Soft-winged Flower Beetle, *Dasytes plumbeus* (Figure 3; Table B3, Appendix B). Only 65 caterpillars were sampled, mainly on Himalayan Blackberry (17 branches) and Nootka Rose (*Rosa nutkana*; 17 branches), with some on Salmonberry (*Rubus spectabilis*; 8 branches) and Twinberry (*Lonicera involucrata*; 7 branches) as well as lower numbers on 7 other woody shrub species.
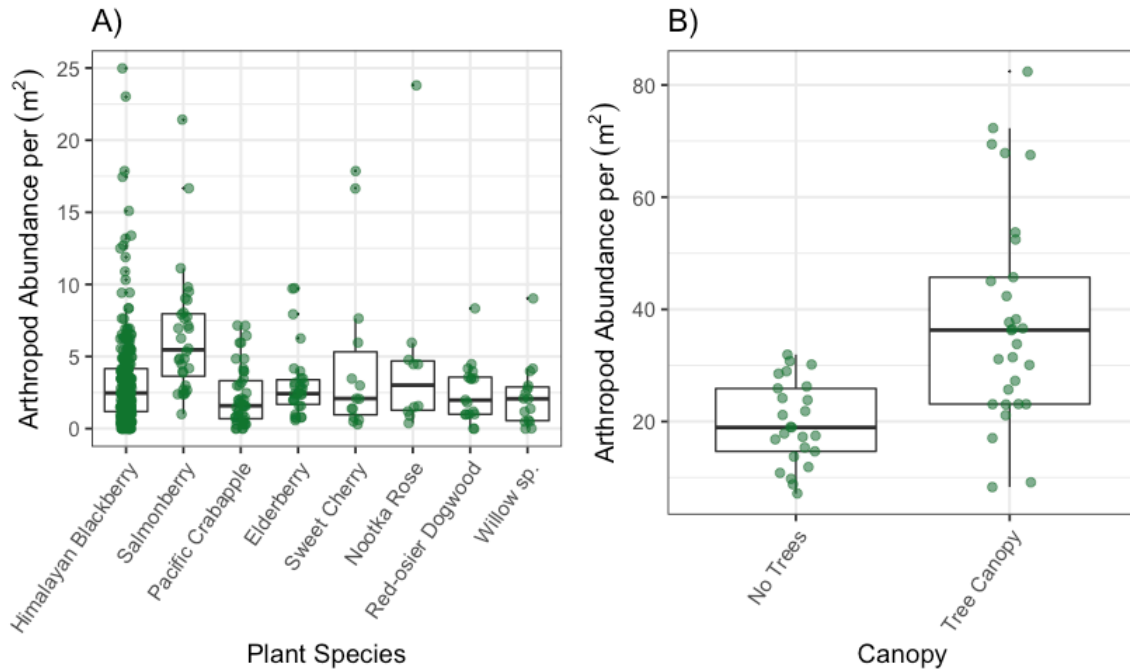
Figure 4. A) Arthropod abundance on the 8 most commonly sampled plant species (n>10 branches) in agricultural hedgerows. B) Arthropod biomass in hedgerow sites without a tree canopy compared to with a tree canopy.

There was no relationship between arthropod abundance and overall HBB % cover at each site ($\beta = 3.15 \pm 2.5$, t = 1.26, p = 0.21). Arthropod abundance did vary between plant species for which >10 branches were sampled ($\chi2 = 30.76$, df = 7, p > 0.001; Figure 4A). Salmonberry had a higher arthropod abundance (6.82 ± 0.8) than Himalayan Blackberry (p>0.001), Pacific Crabapple (*Malus fusca*; p > 0.001), Red Elderberry (*Sambucus racemosa*; p > 0.001), Red-osier Dogwood (*Cornus sericea*; p > 0.001), and Willow sp. (*Salix* sp.; p > 0.001). Additionally, arthropods were more abundant on the foliage of understory shrubs in sites with a tree canopy (40 per site) than with those without trees (20 per site; t = -3.5, df = 46.74, p-value = 0.001; Figure 4B).
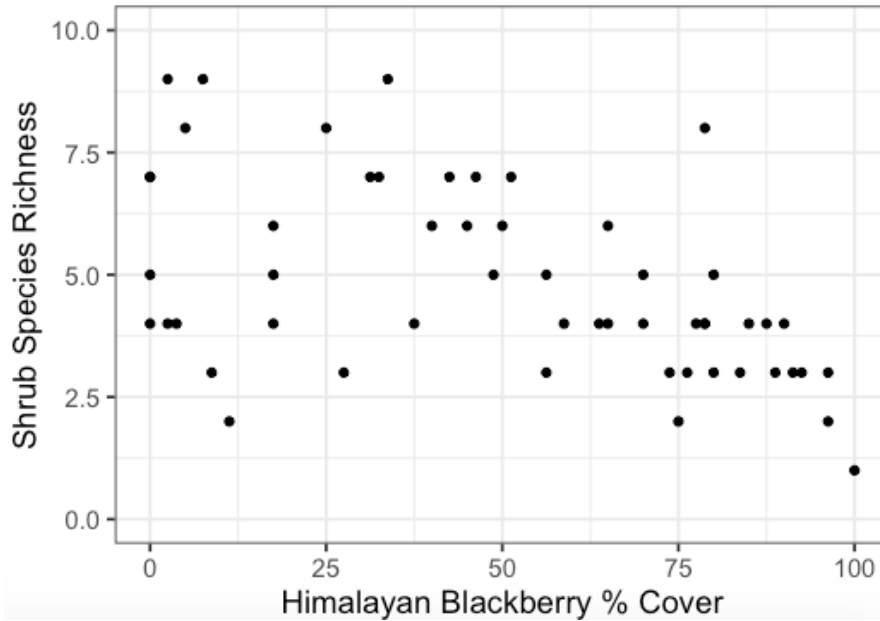
Figure 5. The response of understory shrub species richness to HBB % cover in agricultural hedgerows at Alaksen National Wildlife Area and Serpentine Fen Wildlife Management Area.

Sites had a species richness of 1 – 9 understory shrub species, with an average of 4.7 ± 0.3 species. Mean HBB % cover ranged from 0% – 100%, with a mean value of 50.9 ± 4.5%. At low levels of HBB % cover, shrub species richness varied considerably (Figure 5). As HBB % cover increased, there appear to be fewer co-existing understory shrub species and a stronger negative relationship (Figure 5). When shrub species richness was modelled as a function of HBB % cover, the overall relationship was significant despite the variable species richness at low HBB levels (β = -0.92 ± 0.24, t = -3.8, p < 0.001). According to LiDAR measurements, hedgerow width ranged from 4.8 - 29.7 m and sites were on average 17.5 ± 0.9 m. Mean vegetation height was 6.82 ± 0.69 m, with a range from 1.0 – 19.0 m.

3.2. Effects of hedgerow features on bird metrics
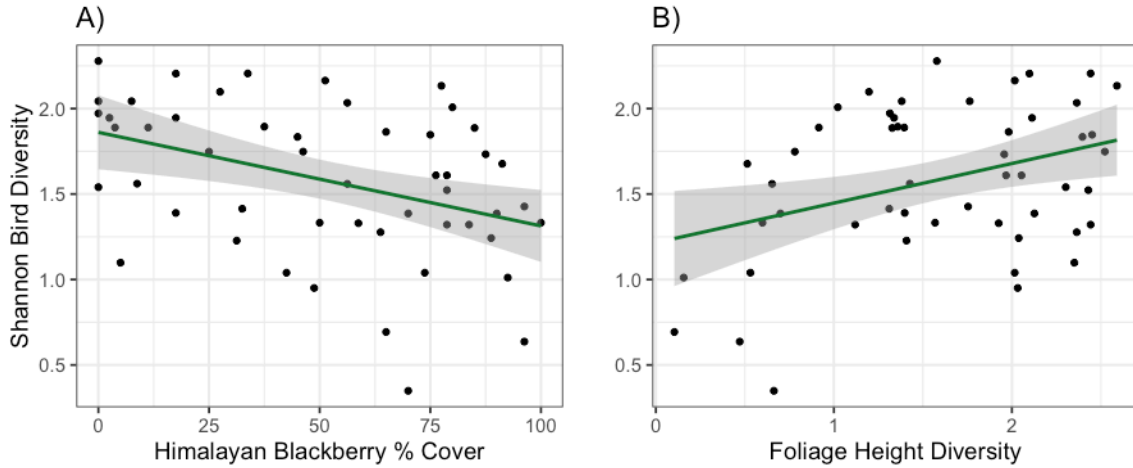
Figure 6. The best fit model for songbird diversity in agricultural hedgerows at Alaksen NWA and Serpentine Fen WMA included a) HBB % cover (visually estimated in the field), and b) FHD (derived from LiDAR data).

The best fit model using AIC selection criteria explaining Shannon songbird diversity included HBB % cover and Foliage Height Diversity, with HBB % cover exhibiting a negative relationship with bird diversity and FHD a positively association (Figure 6; Table 2A; Burnham & Anderson 2002). In contrast, songbird abundance showed a positive relationship with hedgerow width, but HBB % cover was only marginally significant in the best fit model (Figure 7, Table 2B). Shannon diversity and bird abundance were correlated ($\beta = 0.30 \pm 0.05$, t = 6.7, p < 0.001). Significant relationships with individual variables related to Shannon diversity and songbird abundance can be found in the correlation charts in Appendix C, Figure C2.
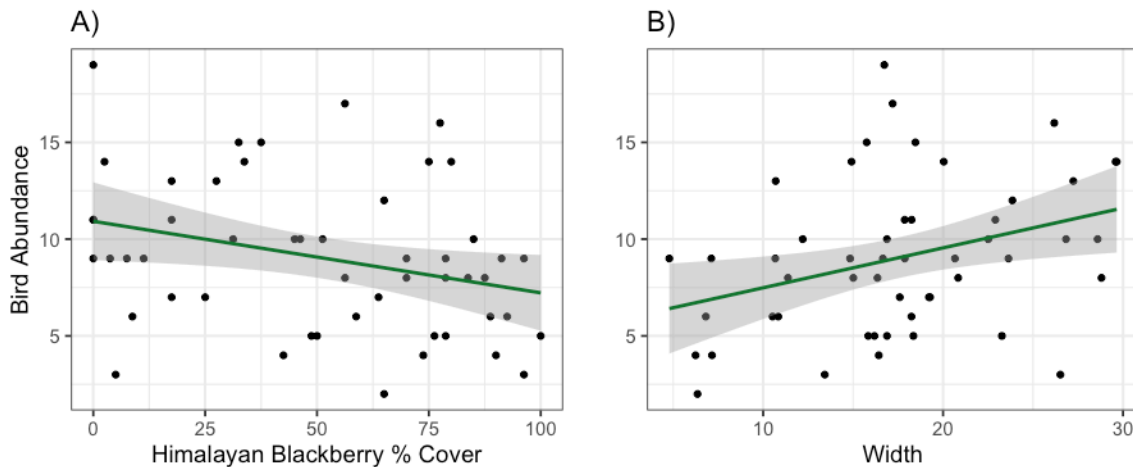
Figure 7. The best fit model for the songbird abundance in agricultural hedgerows at Alaksen NWA and Serpentine Fen WMA included a) HBB % cover (visually estimated in the field), and b) hedgerow width (derived from LiDAR data).

Table 2. Comparison of model results for null, full, and best fit generalized linear models predicting A) Shannon songbird diversity and B) songbird abundance in agricultural hedgerows at Alaksen NWA and Serpentine Fen WMA.

A) Shannon Bird Diversity

	Null Model (~1)			Final Model			Full Model		
Predictors	*Est*	*CI*	*p*	*Est*	*CI*	*p*	*Est*	*CI*	*p*
(Intercept)	1.58	1.46–1.71	**<0.001**	1.58	1.48–1.69	**<0.001**	1.58	1.47–1.69	**<0.001**
HBB % cover				-0.16	-0.26– -0.05	**0.007**	-0.14	-0.29–0.01	0.083
FHD				0.14	0.03–0.25	**0.017**	0.03	-0.28–0.34	0.847
Arthropod Abundance							-0.05	-0.21–0.10	0.496
Width							0.07	-0.09–0.23	0.410
Shrub Species Richness							-0.02	-0.16–0.11	0.740
Mean height							0.06	-0.23–0.35	0.695
Density (0.5 – 2 m)							-0.06	-0.32–0.20	0.657
Density (2 – 4 m)							0.01	-0.16–.18	0.927
Observations	51			51			51		
R^2 Nagelkerke	0.000			0.273			0.305		
AIC	**63.880**			**52.875**			**62.744**		

B) Bird Abundance

	Null Model (~1)			Final Model			Full Model		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	9.04	7.93–10.14	**<0.001**	9.04	8.04–10.04	**<0.001**	9.04	8.03–10.05	**<0.001**
HBB % cover				-0.96	-1.99–0.07	0.073	-0.91	-2.28–0.47	0.203
Width				1.16	0.13–2.19	**0.033**	0.94	-0.53–2.40	0.216
Arthropod Abundance							-0.46	-1.85–0.92	0.514
Shrub Species Richness							-0.57	-1.80–0.66	0.371
FHD							-0.25	-3.03–2.53	0.860
Mean height							1.83	-0.82–4.48	0.184
Density (0.5 – 2 m)							0.07	-2.30–2.44	0.954
Density (2 – 4 m)							1.14	-0.39–2.67	0.150
Observations	51			51			51		
R^2 Nagelkerke	0.000			0.929			0.981		
AIC	**287.302**			**281.508**			**287.706**		
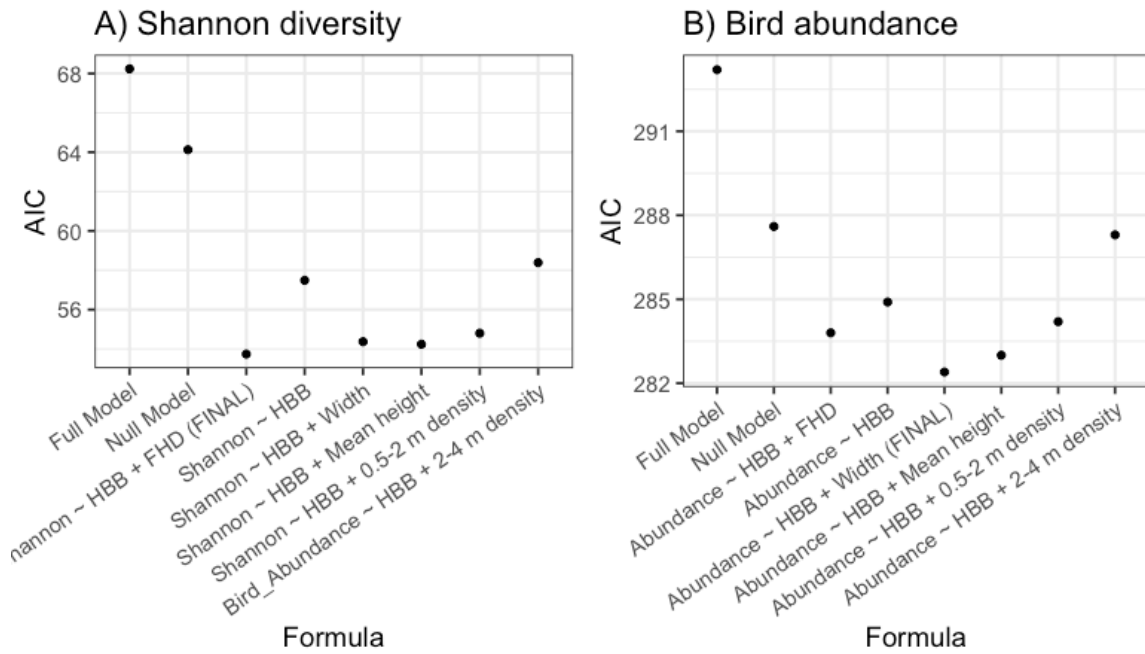
Figure 8 Comparison of AIC values for the full model, null model, final model, and other structural LiDAR variables for a) Shannon bird diversity and b) bird abundance in agricultural hedgerows at Alaksen NWA and Serpentine Fen WMA.

For both bird diversity and abundance, similar AIC values were calculated for models that included both HBB % cover and various correlated LiDAR structural metrics (FHD, width, mean height, 0.5 – 2 m foliage density; Figure 8).
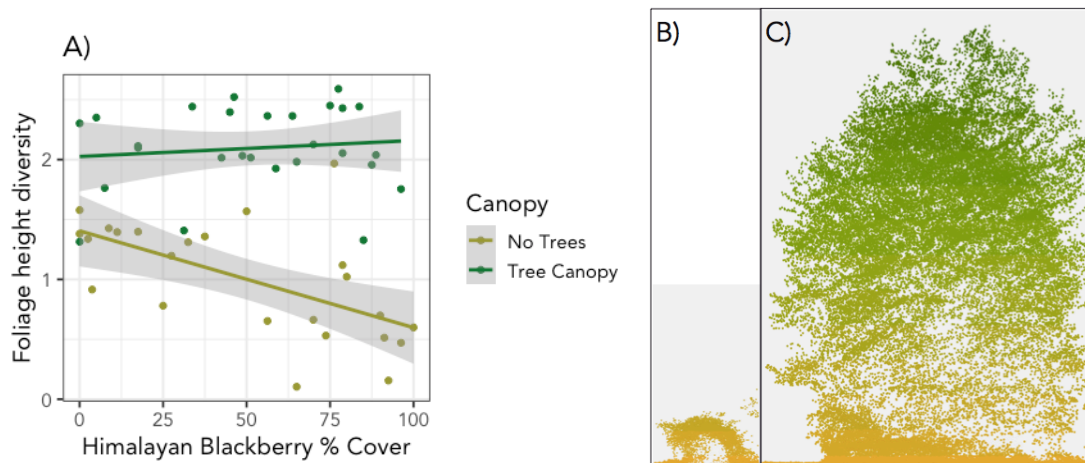
Figure 9. A) FHD decreases with HBB % cover in sites with no trees. Comparison of LiDAR 2D cross sectional profiles for a high HBB % cover site that was shrub-dominated (B) and a high HBB % cover site with a tree canopy (C).

While overall FHD did not have a significant relationship to changes in HBB % cover, adding tree canopy presence as a factor in the model showed that HBB % cover was significantly related to FHD in shrub-dominated sites (β = -0.13 ± 0.05, t = -2.4, p = 0.02; Figure 9A). FHD had significant positive relationships with understory shrub species richness and shrub Shannon diversity, mean vegetation height, and hedgerow width (Figure C2, Appendix C). It exhibited negative relationships with vegetation density in the 0.5 - 2m layer, and the 2 - 4 m layer (Figure C2, Appendix C). HBB % cover had a positive association with vegetation density in the 0.5 - 2m layer (Figure C2, Appendix C). It was negatively correlated with understory shrub species richness and Shannon diversity, and vegetation density in the 2 - 4 m layer (Figure C2, Appendix C).
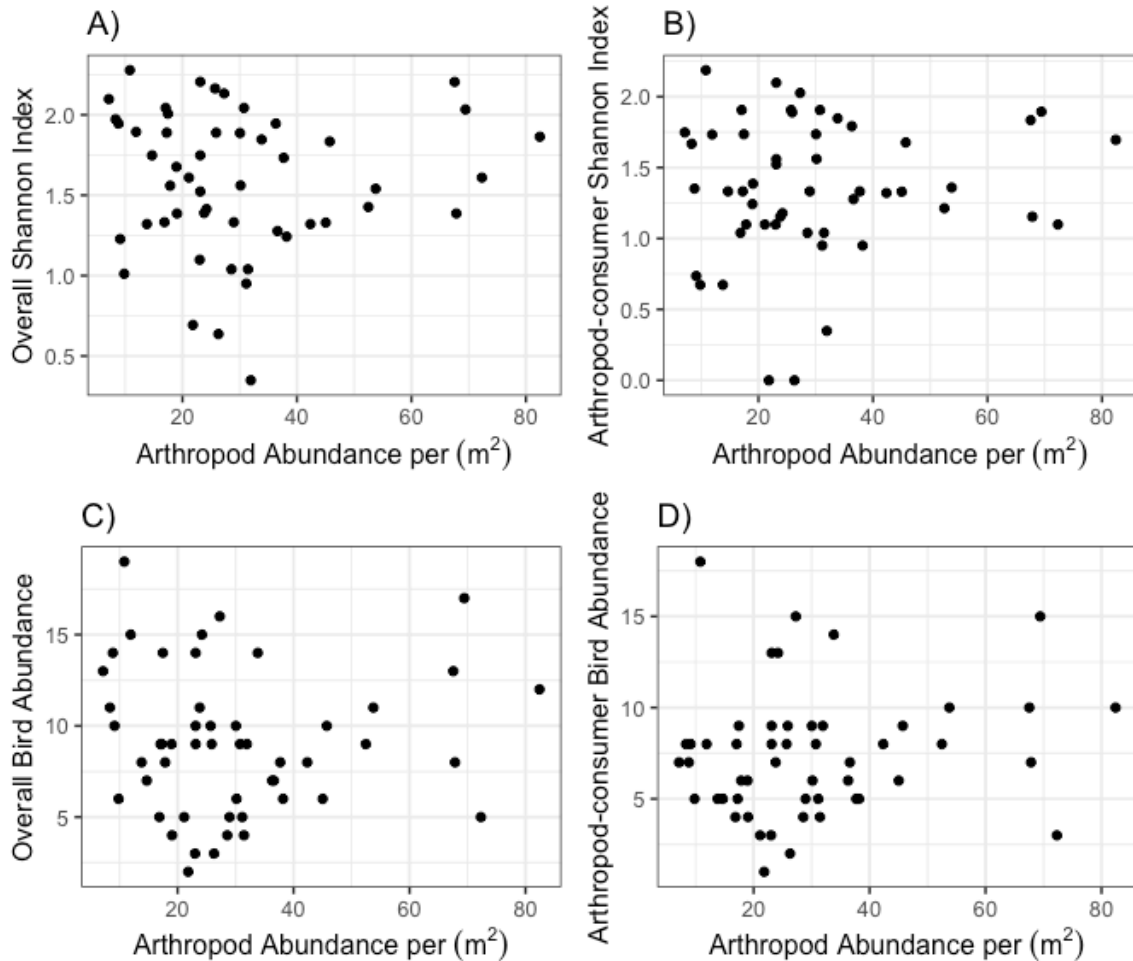
Figure 10. Response of bird metrics to arthropod availability in agricultural hedgerows at Alaksen NWA and Serpentine Fen WMA. Overall bird diversity (a), diversity of foliar arthropod-consumers (b), overall bird abundance (c), and abundance of foliar arthropod-consumers (d) showed no response to arthropod abundance.

When arthropod abundance in hedgerow segments was measured with beat sheet surveys of woody understory vegetation, it was unrelated to both overall Shannon songbird diversity (β = -0.02 ± 0.14, t = 0.15, p = 0.88) and the diversity of songbirds classified as likely consumers of foliar arthropods (β = 0.05 ± 0.7, t = 0.70, p = 0.49; Figure 10 A-B). Similarly, neither overall songbird abundance (β = 0.01 ± 0.14, t = 0.06, p = 0.95) nor abundance of arthropod-consumers varied with foliar arthropod abundance (β = 0.5 ± 0.49, t = 1.0, p = 0.31; Figure 10 C-D).

Chapter 4.   Discussion

The diversity of songbirds occupying agricultural hedgerows was best explained by lower % cover of an invasive species (Himalayan Blackberry; HBB) and higher measures of vertical structural complexity (Foliage Height Diversity; FHD). Additionally, bird abundance was significantly related to hedgerow width, with HBB % cover marginally significant. Invasions by introduced plant species can have a complex range of effects on avian communities – these are frequently negative, but can also be neutral, mixed, or beneficial (Gleditsch 2017; Stinson & Pejchar 2018). The mechanisms driving these interactions are often poorly understood and may differ between plant species and bird community (Nelson et al. 2017). My results add to an accumulating body of evidence that HBB has a negative impact on breeding songbird communities in the Pacific Northwest (Whyte 2018; Hartley 2018; Astley 2010; Sandiford et al. 2001). My study sought to address the reason behind this negative relationship: I hypothesized that songbird diversity decreases with HBB % cover either because HBB decreases foliage vertical structural complexity or because it reduces the number of foliar arthropods available as a food source. Neither mechanism was fully supported by my findings. While FHD showed the expected relationship with songbird diversity, it did not have a simple relationship with HBB % cover (Sandiford et al. 2001; Clawges et al. 2008). Furthermore, contrary to my predictions, similar numbers of arthropods were sampled on HBB and native shrubs, and arthropod abundance had no relationship with native songbird diversity. This suggests that the negative impacts of HBB invasion are not likely explained by the reduction of herbivorous arthropods as a food source. Taken together, these findings illustrate the complexity of avian responses to hedgerow structure and composition in agricultural settings. They highlight the importance of providing sufficient vegetation structure to maximize the capacity of farmed landscapes to support bird life.

4.1. Impacts of Himalayan Blackberry on songbirds

A pattern of decreasing bird diversity with increasing HBB % cover is in line with a number of previous studies, including one conducted 20 years previously by Canadian Wildlife Services examining hedgerow segments in the same wildlife areas (Sandiford et

al. 2001). This study found that HBB monocultures had lower songbird diversity, but that this impact was mitigated by the presence of a tree canopy (Sandiford et al. 2001). There was also considerable variability in the responses of individual species and feeding guilds, and seasonal differences in the effect of hedgerow composition, with summer exhibiting stronger relationships than the winter season (Sandiford et al. 2001). Anecdotally, another study of hedgerows managed by the Delta Farmland and Wildlife Trust in Delta BC compared a single HBB hedgerow to both planted and reference hedgerows, and found notably lower bird abundance and diversity in the HBB monoculture row (Whyte 2018). In woodlot or forested habitats, a number of other studies in the Lower Mainland observed similar patterns of lower bird diversity associated with HBB monoculture (Astley 2010; Hartley 2018; Newberry 2016). However, this relationship was only sometimes evident, highlighting the complexities of these systems. For example, Astley (2010) found that HBB monocultures had a lower Simpson's diversity of breeding birds compared to native vegetation in two of three study sites. However, the final site with no difference had low overall diversity, no tree canopy, and higher levels of human disturbance. Similarly, Newberry (2016) used both mist netting and an observational study to compare areas dominated by HBB and those with native shrubs. A distinction between the habitat types was evident only with the observational study (Newberry 2016). In this case, native and HBB net locations were quite close together, the overall level of HBB predominance was high, and birds were observed using the mist-net lanes as travel corridors (Newberry 2016). Finally, Hartley (2018) found that areas where HBB or English ivy (*Hedera helix*) was the predominant understory species had lower bird presence. Birds preferred edge habitat and areas with higher vegetation diversity (Hartley 2018). While these studies used categorical measures of HBB % cover (either monoculture/native or monoculture/mixed/native), I found a similar trend when I measured HBB % cover as a continuous variable. Despite the complexities of such systems, there is support for a negative impact of this invasive species on songbird diversity.

Published literature on the overall effects of HBB on songbird communities is sparse, although a few species-specific studies have shown neutral or positive effects on certain bird species. For example, Song Sparrows (*Melospiza melodia*) were not affected by HBB colonization in a long-term demographic study of reproductive success and nest site preference (Crombie et al. 2016). In another case, Yellow Warblers

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(*Setophaga petechia*) actually selected territories with higher levels of HBB cover, and Yellow-breasted Chats (*Icteria virens*) selected nest sites with higher HBB cover in reference but not restored study sites (Rockwell & Stephens 2017). In California, endangered Tricolored Blackbirds (*Agelaius tricolor*) had higher reproductive success in HBB dominated upland habitat compared to native wetland plants such as bulrushes and cattails where they had nested historically (Cook & Rine 2005). This illustrates the variable impacts of invasive plant species, which may benefit some wildlife species or have no effect on others, even if as with HBB it seems to be avoided by all but a few bird species (Nelson et al. 2017).

I have focused on songbird diversity as a response variable, which appears to be more strongly linked to HBB % cover than songbird abundance. Abundance was best predicted simply by hedgerow width or area. Shannon diversity incorporates abundance, but also captures species richness and evenness (Magurran 1988). In my study, Shannon diversity was strongly correlated with bird abundance. Other studies have found that width has a positive influence on woodland species richness (Hall et al. 2018). From a functional perspective, diverse communities may be more resilient to disturbances and long-term stressors (Landis 2017). While the abundance of birds may be key in determining their effectiveness in providing ecological services such as pest control, a diverse suite of species may perform better if they have a range of food preferences and occupy various feeding niches (Barbaro et al. 2017). It should also be noted that while I attempted to account for confounding factors, my study is correlational. It is possible that HBB % cover may not directly affect bird diversity, but be associated with some other factor in the landscape that explains the lower diversity. Although HBB % cover was unrelated to hedgerow width, HBB monoculture could be more common in areas with greater distance to other habitat types, more intense adjacent cultivation, and lower structural complexity.

4.2. Vegetation structure and LiDAR analysis

Structural complexity is well established as a predictor of greater songbird diversity in hedgerows (Graham et al. 2018; Hinsley & Bellamy 2000). My best-fit model for songbird diversity included both HBB % cover and FHD. In contrast to diversity abundance was best modeled by HBB % cover and hedgerow width, although HBB % cover was not significant. Notably, the LiDAR structural metrics including FHD, mean

height, density in the 0.5 – 2 m and 2 – 4 m layers, and width were all strongly correlated with each other. The AIC values of the best fit model were quite close to other structural measures (Figure 8). Therefore my findings support the importance of structural complexity for birds.

Notably, these measurements of hedgerow structure such as FHD did not have a straightforward link to HBB % cover. I did find a relationship between FHD and HBB % cover in shrub-dominated segments, though this relationship was not evident overall or in segments with a tree canopy. Where a tree canopy was present, it is possible that HBB is partially shaded out, causing it to grow up through other vegetation and occupy more vertical layers. In some sites with intermediate HBB levels, HBB was observed growing entwined through other vegetation, entering into higher vegetation layers. However, I did have treed sites with a monoculture HBB understory mainly in the 0.5 – 2 m layer. Unsurprisingly, the density of vegetation in the 0.5 – 2 m layer increased with HBB % cover, while the opposite relationship was exhibited in the 2 – 4 m layer. HBB growing at high density low to the ground could reduce vegetation cover in the high shrub layer. Since the FHD metric measures how vegetation is distributed throughout the vertical structural profile from 0.5 – 30 m, sites with a tree canopy may inherently have high FHD values, regardless of whether their understory layers are HBB dominated or not. Alternatively, it is possible that LiDAR returns may be blocked in sites with a dense canopy and fail to completely capture the understory if the canopy blocks LiDAR returns from understory vegetation (Figure 5B-C).

Furthermore, particular aspects of HBB's vegetation architecture may not be captured by the FHD metric. Sandiford et al. (2001) noted that HBB has a horizontal, sprawling growth form, with dead canes topped by extremely dense foliage. Hedgerow density can have a positive impact on bird use (e.g. by providing nest concealment and providing cover while foraging), especially when hedgerows are trimmed and manage to encourage side vegetation growth (Dunn et al. 2016). However, there may be trade-offs as dense foliage can also conceal predators (Whittingham & Evans 2004). Therefore, while it offers a powerful way to measure vegetation height and density remotely across agricultural landscapes, LiDAR may not be suitable to address this particular question of HBB growth patterns in the forest understory. Interestingly, FHD was positively correlated with shrub species richness and diversity, suggesting that the presence of a range of different plant species could contribute to diverse vegetation structure, as well

as management practices (Graham et al. 2018). Further work could clarify the specific aspects of vegetation architecture that are most important to songbird communities, both in terms of their diversity and abundance, and how these relate to HBB % cover. As this study has shown, it is clearly important to provide sufficient vegetation volume and vertical structure.

4.3.   Arthropod abundance analyses

I found no relationship between arthropod abundance per unit leaf area and bird metrics using the beat sheet sampling method with an intensity of 9 branches per site. This was true both of overall bird diversity and abundance, as well as that of foliar arthropod consuming feeding guilds. While there is evidence that food availability may be a limiting factor on avian reproductive success in some systems, it is possible that this is not the case in this particular habitat (Martin 1987). Alternatively, while bird metrics did not have a detectible response to the 'arthropod productivity' per branch area, they did respond positively to greater vegetation volume. More branches could provide more area for herbivorous arthropods to live on and thus more food overall.

Certain arthropod groups were commonly sampled, including large numbers of an introduced 5mm-long Soft-winged Flower Beetle, *Dasytes plumbeus*, as well as high numbers of small (2 – 3 mm) spiders (Figure 2). However it is unclear how important either beetles or spiders would be as a food source for songbirds compared to caterpillars. Further study of songbird dietary composition and preferences could show what prey items are key their reproductive success, and how these relate to hedgerow composition and structure. Although caterpillars were the focus of several past studies, I only sampled 65 in total with the beat sheet sampling method, and my branches were selected randomly from an uneven distribution of plant species. Therefore I could not make conclusions about how caterpillar abundance related to bird diversity or plant host species. Anecdotally, I found that Salmonberry had higher arthropod abundance than other shrub species. A study design with systematic sampling of a variety of invasive and native hedgerow vegetation could address this question, and suggest whether certain species with higher arthropod-hosting capacity could be planted to increase food availability for songbirds and other wildlife.

From my sampling, it also appears that HBB does not host notably lower numbers of arthropods compared to other native shrub species. This contrasts with other work in agricultural hedgerows, showing that those composed primarily of novel plant species had 68% fewer caterpillar species, 91% lower caterpillar abundance, and 96% less biomass than native hedgerows, as well as 57% lower diversity of trophic interactions (Richard et al. 2019). In urban yards with over 70% non-native vegetation, low caterpillar populations were associated with reduced reproductive success and site use in an insectivorous species, the Carolina Chickadee (*Poecile carolinensis*; 2017; 2018). The non-native plant cover in such yards was mainly ornamentals, which are often selected for their lack of palatability to herbivores (Tallamy 2004). Common garden comparisons of caterpillars between native and non-native plant species within a genus have provided evidence that native plants are preferred to closely related introduced species (Burghardt et al. 2010).

In contrast, other studies have shown less pronounced differences between exotic and native plants in the same genus, both in terms of caterpillar abundance and natural enemy communities (Parsons et al. 2020; Frank et al. 2019). The difference between native and introduced species could be variable depending on the degree of evolutionary differentiation between plants in the same genus (Parsons et al. 2020). In the case of HBB, there are several other native species in the *Rubus* genus (including *Rubus spectabilis, Rubus parviflorus,* and *Rubus ursinus*). Furthermore, HBB may use strategies other than toxicity to protect itself from herbivory (e.g. rapid growth, physical defenses; Gaire et al. 2015).

Interestingly, I noted that sites with a tree canopy had more arthropods on their understory vegetation, which could be the result of lower light levels and cooler conditions keeping understory foliage from drying out later in summer. Post hoc comparisons between shrub species in my dataset revealed that Salmonberry seemed to be especially productive, but no other shrubs differed significantly in arthropod abundance. Due to my study design, I sampled unequal numbers of different plant species, with HBB having a much higher sample size than other species. Future studies that sampled more intensively with larger sample sizes for target shrub species might have a better chance at detecting differences in arthropod productivity. Furthermore, studies of songbird dietary preferences and nestling diet could reveal what arthropod groups are most crucial for breeding success.

It should also be noted that a proportion of my hedgerow segments at both wildlife areas were adjacent to active agriculture that involved pesticide application under an Integrated Pest Management protocol (ECCC 2020). Overspray could affect arthropod abundance (Wagner 2020). This makes my findings applicable to typical agricultural landscapes where pesticide use is common, but may have masked variation in arthropod abundance. A controlled experiment with uniform plot conditions would be necessary to determine if this was the case.

While my work showed no trends in bird metrics linked to arthropod abundance, or effect of HBB on arthropod levels, it is worth further investigating how plant species identity may impact the availability of herbivorous arthropods and thus food availability. Choosing productive host plant species may bolster avian breeding success, as well as support other arthropod-consuming wildlife species, allowing agricultural landscapes to support higher levels of biodiversity and provide valuable ecosystem services such as pest control.

4.4. Restoration recommendations

4.4.1. Agricultural landscape design and complexity

In increasingly simplified agricultural landscapes, there is strong evidence that maintaining complex mosaic of habitat types that provide vegetation structure is superior at supporting biodiversity to bare field margins (Heath et al. 2017). Moreover, on a landscape level, hedgerows not only provide habitable area but also function to connect larger patches and other habitat types, such as woodlands, wet ditches, and arable field margins (Dover 2019; Hinsley & Bellamy 2019). For these reasons hedgerows are a key component of sustainable agricultural landscape design, in line with the concepts of 'rewilding' to support biodiversity (Perino et al. 2019; Landis 2017). Biodiversity is desirable both from a conservation perspective and because it can enhance the ecosystem services provided by hedgerows (Landis 2017). The most extensive implementation and study of hedgerows is centred in Western Europe, where they are a key conservation strategy (Graham et al. 2018). Such hedgerows tend to be intensively managed with practices that include not only mowing, but also coppicing and various forms of basal cutting and weaving branches along the edges to increase density and re-sprouting, using a variety of rotation lengths (Staley et al. 2019). This can help to

maintain vegetation density and vigour (Staley et al. 2019). The cost of this management is supported by national policy and funding programs (Dover 2019). In contrast, North American hedgerows may more often fall into the category of 'relict' or unmanaged hedgerows (Graham et al. 2018). This may make European findings less immediately applicable to these habitats, but also raises the possibility of exploring more intensive management schemes.

Hedgerow management practices have the potential to improve their habitat quality for a range of wildlife species, thereby also improving their ability to provide ecosystem services (Dover 2019). My results support the planting of wider hedgerows with more vegetation volume, ideally with a tree canopy and a variety of understory species with diverse vegetation architecture. Larger, denser hedgerows typically have more abundant resources, and greater vegetation structural complexity, allowing them to support both more predatory arthropods and more birds (Graham et al. 2018; Langellotto & Denno 2004). Incorporating snags and decaying plant matter can also benefit both birds and arthropods (Hinsley & Bellamy 2000). However, Graham et al. (2018) note that hedgerow height can have mixed effects on birds depending on their natural habitat associations. Woodland species favour more canopy while farmland or grassland birds prefer lower vegetation (Graham et al. 2018). Since different taxa making use of hedgerows have diverse requirements, management strategies should focus on maintaining hedgerow heterogeneity instead of applying a single practice everywhere (Graham et al. 2018; Hall et al. 2018).

4.4.2. Annual variation in habitat quality

I have focused mainly on explaining the negative impacts of HBB demonstrated in previous studies of breeding songbirds. However, the impacts of HBB may not be uniform throughout the year. Hedgerow use by birds is often associated with different factors depending on season (Hinsley & Bellamy 2019). In the winter, hedgerow importance to bird species is typically dictated by provision of shelter and of a food supply in the form of fruit resources (Hinsley & Bellamy 2019). Fruit resources can also be important for fall migrants, with native species in some cases providing superior nutritional resources (Smith & Desando 2013). HBB sets fruit after the energetically intensive period of the main avian breeding season, but could be more desirable later in the year (Gleditsch 2017; Gaire et al. 2015). However, Sandiford et al. (2001) found that

American Robin (*Turdus migratorius*) and Cedar Waxwing (*Bombycilla cedrorum*) seemed to avoid HBB hedgerows in the winter perhaps because they were searching out English Hawthorn (*Crataegus laevigata*) berries as a preferred food source. Generally, they found that habitat associations were weaker and more varied in the winter (Sandiford et al. 2001). Another possible impact of HBB predominance is if it is outcompeting early-season flowering plant such as Salmonberry, which are an important food source for Rufous Hummingbirds (*Selasphorus rufus*; Calder 1976). Future work could study the multifaceted impacts of HBB across the annual cycle, and reveal whether its use during migratory or overwintering seasons represent a trade-off with breeding season negative impacts.

4.4.3. Control and revegetation strategies

My findings provide additional evidence for the negative impact of HBB on birds, reinforcing the importance of strategic control efforts. HBB is a well-established and widespread invasive species (ISCMV 2019). As it is labour intensive and expensive to control, total eradication from the landscape is not a feasible management goal (ISCMV 2019). In moist temperate environments, HBB is extremely competitive, forming dense impenetrable thickets with dead and live canes (Gaire et al. 2015). These monocultures tend to shade out understory plants and lower native plant diversity (DiTomaso et al. 2013). HBB is biennial, with arcing canes sporting curved thorns, and second year growth yielding abundant shiny, purple berries that are dispersed by birds and other wildlife and build up a sizeable seed bank in the soil (Murphy 2006). Its dual reproductive strategy makes it an especially good invader, propagating itself both sexually and vegetatively by root pieces or 'tip rooting' from the ends of arcing canes (ISCMV 2019). Its success can also be attributed to its ability to tolerate a wide variety of soil conditions with only minor reductions in growth due to limited water and nutrient availability (Caplan & Yeakley 2006).

Due to its vigourous growth and difficult removal, preventing HBB colonization is the optimal method in terms of cost and effectiveness (ISCMV 2019). Sites can be protected by maintaining healthy plant communities and carefully cleaning equipment to prevent dispersal (ISCMV 2019). Establishing native vegetation on disturbed sites prior to HBB colonization or revegetating areas where HBB has been removed is an important strategy to help outcompete this aggressive competitor (Murphy 2006; Gaire et al. 2015).

Mulching is recommended to avoid bare soil that may encourage the seed bank to germinate (ISCMV 2019). While HBB's growth is controlled by shade and could be reduced by establishing a dense canopy, this method may have limited effectiveness in environments like hedgerows where light can penetrate from the edges (Caplan & Yeakley 2006).

Once HBB becomes established, mechanical/manual and chemical removal are the main recommended treatment methods (ISCMV 2019). Manual removal can target small infestations, but mechanical approaches are necessary at larger scales, and are more cost effective when combined with herbicide treatment (King County 2014). With mechanical/manual methods it is extremely important that all roots, root crowns, and canes are removed, or else resprouting will occur (DiTomaso et al. 2013). Mowing or cutting without root removal may stimulate root sprouts and increase density of regrowth (DiTomaso et al. 2013). If roots are not removed, treatments must be repeated 2+ times per year for at least several years in order to exhaust reserves (ISCMV 2019). Mowing can be used to remove biomass, and then root crowns can be removed once vegetation has resprouted to 30 cm (ISCMV 2019). Chemical control can be an effective supplement to mechanical methods, but its use is restricted in riparian margins (10 m from water courses) which may limit its use in hedgerows that border streams (ISCMV 2019). A number of pesticides including glyphosate and triclopyr are appropriate for control (ISCMV 2019). Pesticides can also be used for spot treatment of regrowth (ISCMV 2019). There are no current options for biological control, although an introduced species of rust fungus (*Phragmidium violaceum*) has been discovered in Oregon and is being investigated (DiTomaso et al. 2013). Overall, the best success is achieved through initial intensive treatment, followed by long term maintenance for a minimum of 3 years (ISCMV 2019). Timing of treatment is most effective during flowering, but dense thickets that provide nesting habitat for birds should be treated outside the breeding season during the September-March window (DiTomaso et al. 2013). Finally, since HBB is still used as bird and arthropod habitat, limited areas should be cleared in any given season so that no more than a quarter of available habitat is treated, allowing species to shift to alternative locations and re-establish afterwards (King County 2014).

At many sites, HBB grows intermixed with other native shrubs, instead of in monocultures. Management of mixed vegetation requires more careful treatment to

remove HBB without damaging desirable vegetation, but repeated removal of HBB several times per season may allow native plants to outcompete it (Bennett 2007). Certain native plants such as Willow sp. and Black Cottonwood will sucker when trimmed, and native seeds may germinate when not suppressed by a dense HBB canopy (Bennett 2007). According to Sandiford et al. (2001), mixed hedgerows with high vegetation volume were actually the optimal habitat for many bird species, but he claimed that these mixtures were unstable and would inevitably convert to HBB if left unmanaged. Future studies could investigate whether this is always true, or if a diverse selection of native species could compete when planted where HBB is already present, especially if given an initial head start by HBB spot treatment.

Since structural diversity appears to be an important feature, vegetation with a variety of growth forms should be selected. Although my results did not support arthropod abundance as having an effect on bird diversity, arthropod hosting potential may still be a worthwhile strategy to guide plant selection. Certain genera may host disproportionately large volumes of arthropods, especially caterpillars, and can be emphasized when deciding on hedgerow composition (Narango et al. 2017). In addition to supporting a food web as a food source for arthropods, planting diverse plant species can improve ecosystem services such as pollination and pest control (Staley et al. 2019). Active management practices such as mowing and trimming cycles and landscape factors such as complementary habitat types can also contribute to improved habitat value for wildlife (Staley et al. 2019).

4.5.   Conclusion and significance

Human impacts on the planet continue to intensify, and have been linked with major declines in bird and arthropod populations (Rosenberg et al. 2019; Wagner 2020). The complex effects of invasive species on these ecosystems, and the trade-offs in managing them make this problem even more challenging (Nelson et al. 2017). While HBB may be a permanent feature of these landscapes in the Pacific Northwest, my results highlight the continued importance of preventing its establishment and employing strategies to reduce its dominance. They also reinforce the benefits to birds of planting structurally complex hedgerows with high vegetation volume (Graham et al. 2018). This has ancillary benefits to farmers and land managers by supporting ecosystem services (Landis 2017). In combination with other landscape features that support wildlife

populations, proper hedgerow installation and management can maximize the biodiversity supporting potential of agricultural landscapes (Dover 2019; Landis 2017).

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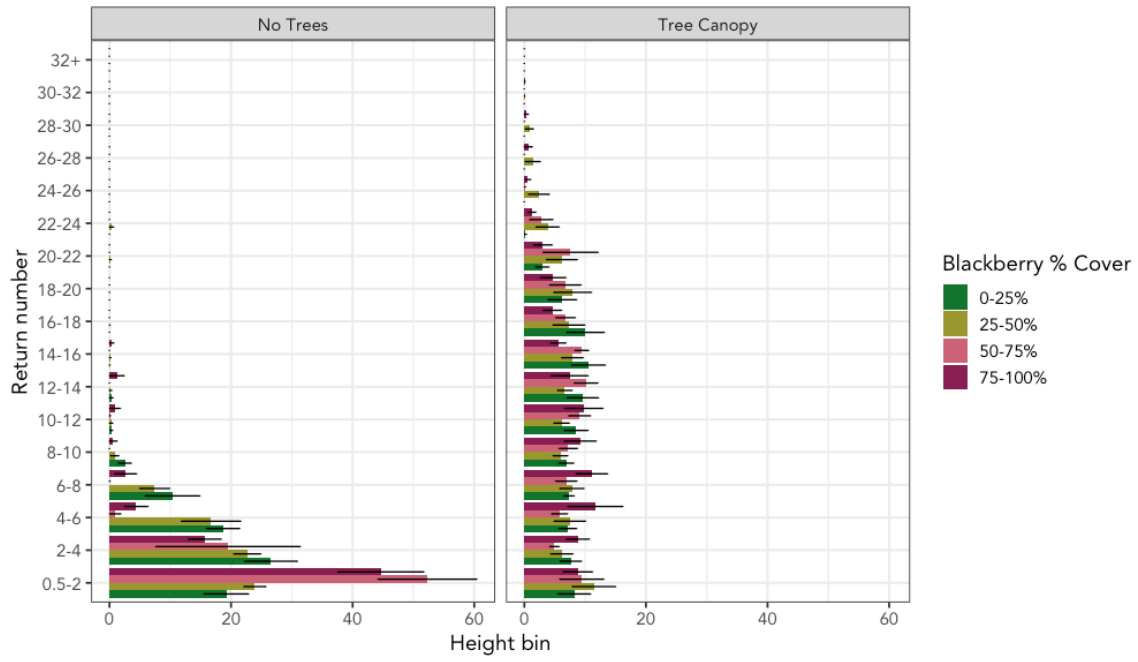
Appendix A. LiDAR visualizations

Figure A1. Comparing the distribution of LiDAR returns in height bins used to calculated Foliage Height Diversity between sites with and without a tree canopy for 4 categories of HBB % Cover

Appendix B. Species lists

Table B1. List of species observed during point counts in 30 m sections of hedgerow with varying levels of Himalayan Blackberry at Alasken National Wildlife Area and Serpentine Fen Wildlife Management Area. Four-letter codes were used in recording data. Species were later classified by main breeding season feeding guild.

Code	English	Latin	Guild	Consumer	Origin
Hummingbirds					
ANHU	Anna's Hummingbird	*Calypte anna*	Floral hover-gleaner	Y	Native
RUHU	Rufous Hummingbird	*Selasphorus rufus*	Floral hover-gleaner	Y	Native
Woodpeckers					
DOWO	Downy Woodpecker	*Picoides pubescens*	Bark gleaner	N	Native
Tyrant Flycatchers					
WIFL	Willow Flycatcher	*Empidonax traillii*	Insectivore	Y	Native
Corvids					
NOCR	Northwestern Crow	*Corvus caurinus*	Omnivore	Y	Native
Chickadees & allies					
BCCH	Black-capped Chickadee	*Poecile atricapillus*	Insectivore	Y	Native
BUSH	Bushtit	*Psaltriparus minimus*	Insectivore	Y	Native
Nuthatches & Creepers					
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	Bark gleaner	N	Native
BRCR	Brown Creeper	*Certhia americana*	Bark gleaner	N	Native
Wrens					
BEWR	Bewick's Wren	*Thryomanes bewickii*	Insectivore	Y	Native
MAWR	Marsh Wren	*Cistothorus palustris*	Insectivore	Y	Native
Thrushes					
AMRO	American Robin	*Turdus migratorius*	Omnivore	Y	Native
SWTH	Swainson's Thrush	*Catharus ustulatus*	Omnivore		Native
Starlings					
EUST	European Starling	*Sturnus vulgaris*	Omnivore	Y	Introduced
Waxwings					
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	Insectivore	Y	Native
Wood-warblers					
OCWA	Orange-crowned Warbler	*Oreothlypis celata*	Insectivore	Y	Native
YEWA	Yellow Warbler	*Setophaga petechia*	Insectivore	Y	Native
YRWA	Yellow-rumped Warbler	*Setophaga coronata*	Insectivore	Y	Native
COYE	Common Yellowthroat	*Geothlypis trichas*	Insectivore	Y	Native
WIWA	Wilson's Warbler	*Cardellina pusilla*	Insectivore	Y	Native
Tanagers & allies					
WETA	Western Tanager	*Piranga ludoviciana*	Omnivore	Y	Native
BHGR	Black-headed Grosbeak	*Pheucticus melanocephalus*	Omnivore	Y	Native

Sparrows					
SPTO	Spotted Towhee	*Pipilo maculatus*	Omnivore	Y	Native
SAVS	Savannah Sparrow	*Passerculus sandwichensis*	Omnivore	Y	Native
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*	Omnivore	Y	Native
SOSP	Song Sparrow	*Melospiza melodia*	Omnivore	Y	Native
Icterids					
BHCO	Brown-headed Cowbird	*Molothrus ater*	Omnivore	Y	Native
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*	Omnivore	Y	Native
BUOR	Bullock's Oriole	*Icterus bullockii*	Omnivore	Y	Native
Finches & Old World Sparrows					
PUFI	Purple Finch	*Haemorhous purpureus*	Granivore	N	Native
HOFI	House Finch	*Haemorhous mexicanus*	Granivore	N	Native
AMGO	American Goldfinch	*Spinus tristis*	Omnivore	Y	Native
HOSP	House Sparrow	*Passer domesticus*	Granivore	N	Introduced

Table B2. Tree and shrub species sampled during beat sheet surveys, including origin (native or introduced).

| Scientific Name	English Name	Origin
Alnus rubra	Red Alder	Native
Betula papyrifera	Paper Birch	Native
Cornus sericea	Red-osier Dogwood	Native
Crataegus douglasii	Black Hawthorn	Native
Crataegus laevigata	English Hawthorn	Introduced
Lonicera involucrata	Twinberry	Native
Malus fusca	Pacific Crabapple	Native
Oemleria cerasiformis	Indian-plum	Native
Populus trichocarpa	Black Cottonwood	Native
Prunus avium	Sweet Cherry	Introduced
Ribes sanguineum	Red-flowering Currant	Native
Rosa nutkana	Nootka Rose	Native
Rubus armeniacus	Himalayan Blackberry	Introduced
Rubus laciniatus	Cutleaf Blackberry	Introduced
Rubus spectabilis	Salmonberry	Native
Salix sp.	Willow	Native
Sambucus racemosa	Red Elderberry	Native
Spiraea douglasii	Hardhack Spirea	Native
Symphoricarpos albus	Snowberry	Native

Table B3. Arthropod groups found on foliage during beat sheet surveys (adapted from Hurlbert et al. 2019).

Common name	Scientific name	Taxonomic level	Distinguishing features
Ants	Formicidae	Family	Narrow waist, no wings; elbowed antennae.
Aphids, Psyllids	Sternorrhyncha	Suborder Order Hemiptera	Small (just a few mm); aphids are pear-shaped.
Barklice	Psocoptera	Order	Wings without many cross veins (Front and hind wings have similar texture, slope downwards at rest, not scaley or hairy. Mouthparts not in a rigid beak.)
Bees, Wasps	Hymenoptera (excluding Formicidae)	Order	2 pairs of wings with the hindwings smaller than the frontwings; wasps have narrow waists but bees do not.
Beetles	Coleoptera	Order	A straight line down the back where the two hard wing casings (elytra) meet.
Caterpillars	Lepidoptera (larvae)	Order	Soft, cylindrical body with 6 legs and up to 5 pairs of prolegs.
Daddy longlegs	Opiliones	Order	8 very long legs; they appear to have a single oval-shaped body.
Earwigs	Dermaptera	Order	Prominent "pincers" at the tip of the abdomen (cerci)
Flies	Diptera	Order	A single pair of wings.
Grasshoppers, Crickets	Orthoptera	Order	Usually with enlarged hind legs for jumping.
Harvestmen/Daddy Longlegs	Opiliones	Order	4 pairs of legs; Abdomen without distinct segments; Without "pincers," long and slender legs
Lacewing	Neuroptera	Order	Wings with many cross veins (Front and hind wings have similar texture, slope downwards at rest, not scaley or hairy. Mouthparts not in a rigid beak.)
Leafhoppers, Cicadas	Auchenorrhyncha	Suborder Order Hemiptera	Usually a wide head relative to the body; hoppers have wings folded tentlike over their back, while cicadas have large membranous wings.
Moths, Butterflies	Lepidoptera (adults)	Order	4 large wings covered by fine scales.
Pillbugs	Isopoda	Order	Seven pairs of tiny legs, some roll up into balls
Spiders	Araneae	Order	8 legs, with two distinct body segments: the cephalothorax and abdomen.
True Bugs	Heteroptera	Suborder Order Hemiptera	Semi-transparent wings which partially overlap creating a triangle or X shape on the back; often has pointy "shoulders"

Appendix C. Supplementary statistical methods

Appendix C provides arthropod biomass results and biomass distribution for comparison to arthropod abundance (Figure C1), and the length-weight regressions used to obtain the biomass figures (Table C1). It also includes correlation charts for several response variables, indicating significant relationships and their magnitude (Figure C2).
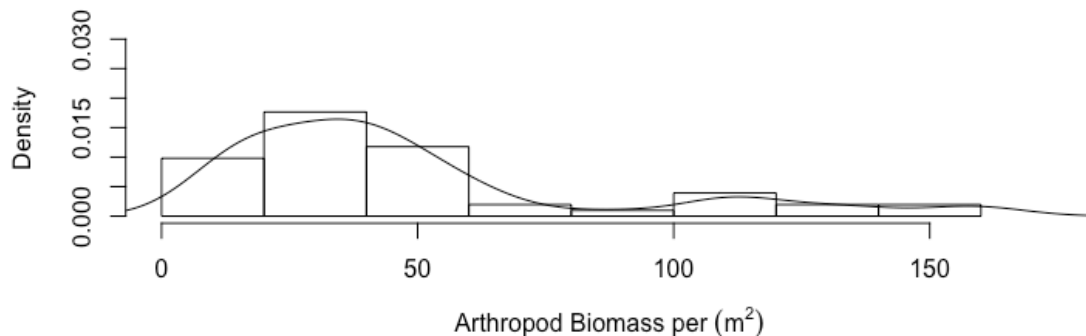
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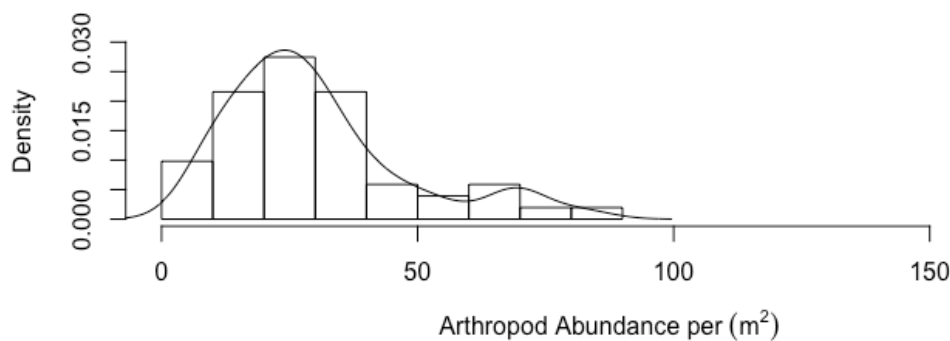
B)

Figure C1. Comparison of the distributions of A) arthropod abundance vs. B) arthropod biomass per unit leaf area. Total arthropod biomass was estimated for each branch and each site, but abundance was chosen as an index of food availability due to the highly skewed biomass distribution and uncertainty about the accuracy of regression calculations for biomass. I modeled Shannon songbird diversity (both overall and for arthropod-consumers) as a function of arthropod biomass. Similar to arthropod abundance, total bird diversity was not related to arthropod biomass (β = -0.01 ± 0.01, t = -1.1 p = 0.29). Shannon diversity of arthropod consumers was not affected by arthropod biomass (β = -0.004 ± 0.01, t = -0.3, p = 0.77). There was no relationship between arthropod biomass (β = 0.02 ± 0.01, t = 1.4, p = 0.16) and overall HBB % cover at each site. Like arthropod abundance, arthropod biomass also differed between plant groups ($\chi2$ = 24.62, df = 7, p<0.001; Figure 5B). Salmonberry (7.7 ± 0.4 mg) branches had a greater biomass of arthropods than

Himalayan Blackberry (4.9 ± 0.4 mg, p=0.002), Pacific Crabapple (4.5 ± 0.8 mg, p=0.04), and Willow sp. (2.2 ± 0.4 mg, p<0.001). Both Red Elderberry (4.6 ± 1.0 mg, p=0.05) and Red-osier Dogwood (5.5 ± 1.2 mg, p=0.05) had greater arthropod biomass than Willow.

Table C1. Biomass length-weight regressions (Rodenhouse 1986). Group-specific regression equations were used for taxa when available, and a general 'All Insect' equation was applied to other groups (Dermaptera, Opiliones, Isopoda, Orthoptera, Collembola, and Neuroptera).

| Group	Equation Type	Equation
Ant	Hymenoptera adult	Weight = $0.016(\text{length})^{2.55}$
Aphid	Homoptera, Hemiptera, Psocoptera	Weight = $0.024(\text{length})^{2.31}$
Beetle	Coleoptera	Weight = $0.082(\text{length})^{1.99}$
Bug	Homoptera, Hemiptera, Psocoptera	Weight = $0.024(\text{length})^{2.31}$
Caterpillar	Larval Lepidoptera	Weight = $0.004(\text{length})^{2.64}$
Collembola	Generic ("all-insect")	Weight = $0.024(\text{length})^{2.35}$
Dermaptera	Generic ("all-insect")	Weight = $0.024(\text{length})^{2.35}$
Fly	Diptera	Weight = $0.022(\text{length})^{2.42}$
Harvestmen	Generic ("all-insect")	Weight = $0.024(\text{length})^{2.35}$
Hopper	Homoptera, Hemiptera, Psocoptera	Weight = $0.024(\text{length})^{2.31}$
Hymenoptera	Hymenoptera adult	Weight = $0.016(\text{length})^{2.55}$
Isopod	Generic ("all-insect")	Weight = $0.024(\text{length})^{2.35}$
Lepidoptera	Lepidoptera	Weight = $0.014(\text{length})^{2.55}$
Neuroptera	Neuroptera	Weight = $0.024(\text{length})^{2.35}$
Orthoptera	Generic ("all-insect")	Weight = $0.024(\text{length})^{2.35}$
Psocoptera	Homoptera, Hemiptera, Psocoptera	Weight = $0.024(\text{length})^{2.31}$
Spider	Arachnida	Weight = $0.045(\text{length})^{2.93}$

A)

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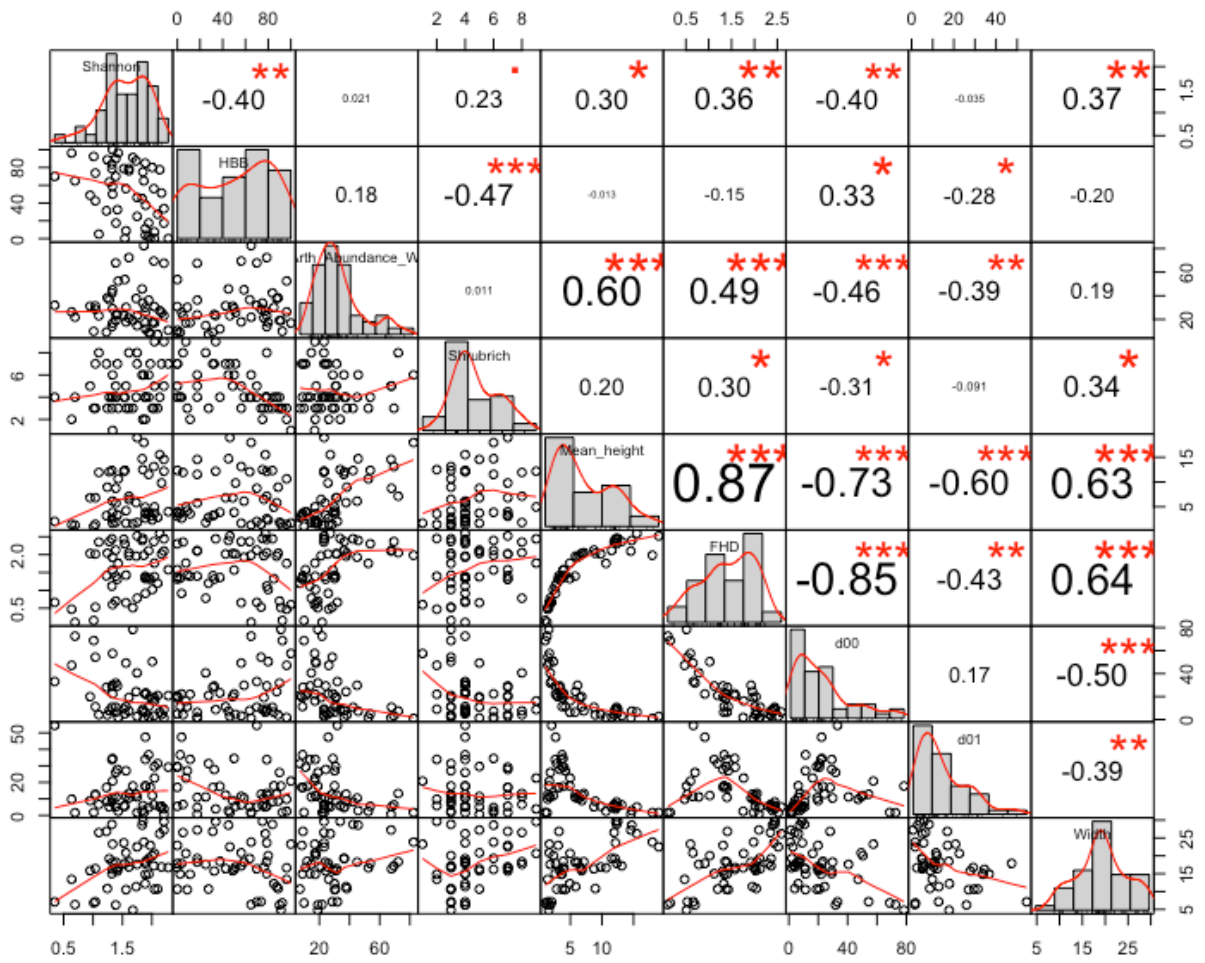
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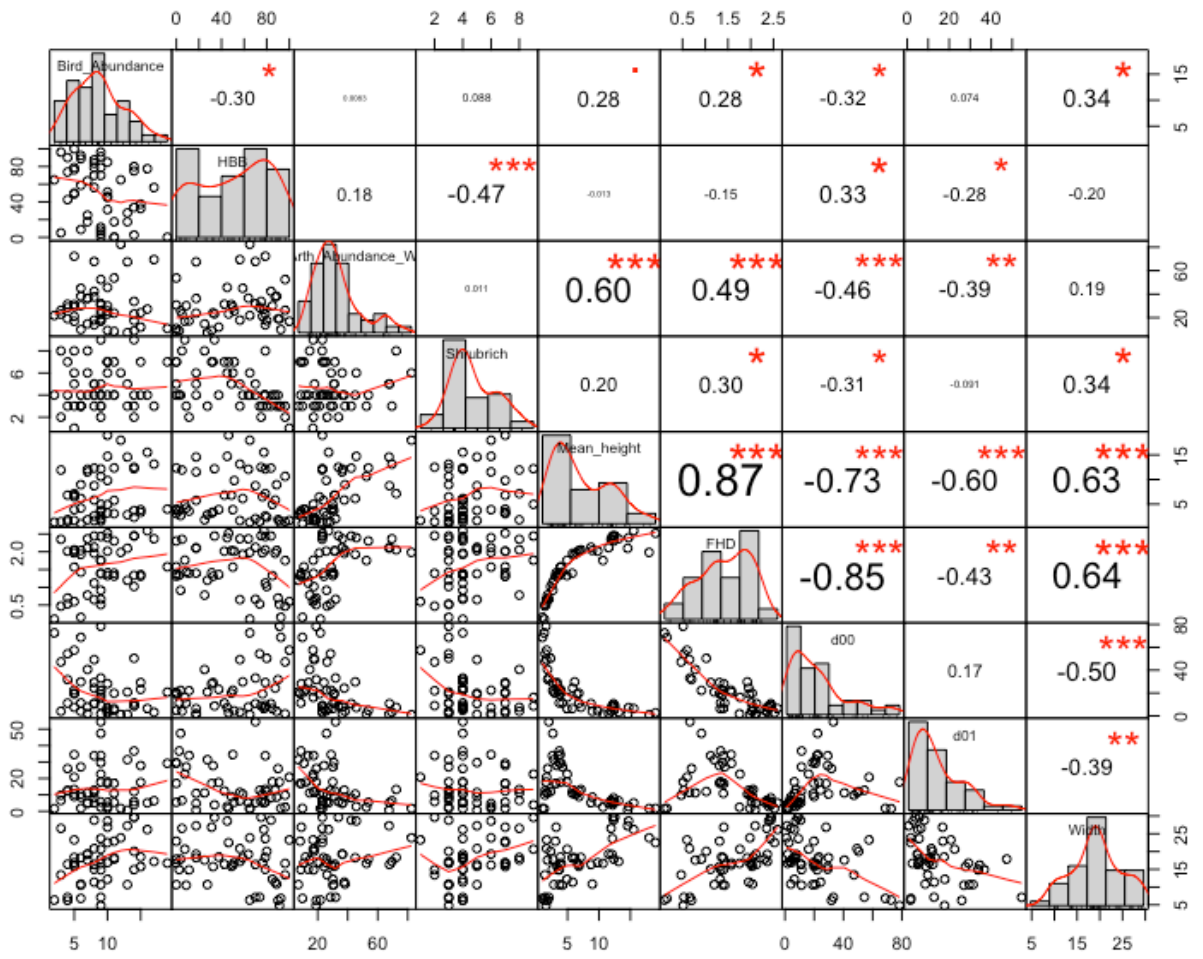
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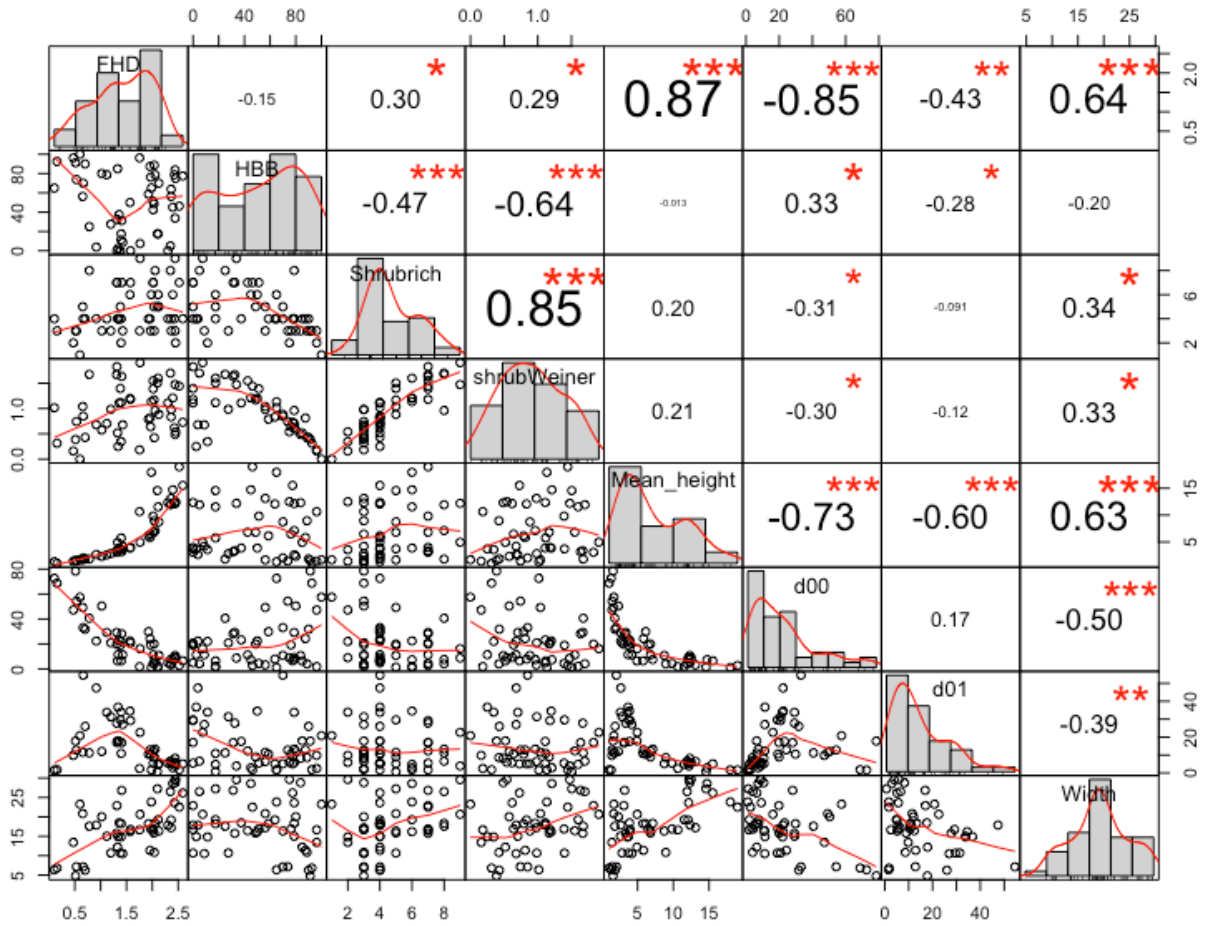
Figure C2. Correlation charts to explore significant relationships between bird metrics, arthropod abundance, and vegetation metrics in agricultural hedgerows at Alasken NWA and Serpentine Fen WMA. Red stars indicate significance, and the numbers in top right are R^2 values (absolute correlation) with the font size indicating the magnitude of the correlation. Plots on the bottom left are bivariate scatterplots with a fitted line. A) Correlation chart for Shannon index of bird diversity with HBB % cover, arthropod abundance per unit leaf area (Arth_Abundance_Wt), understory shrub species richness (Shrubrich), mean vegetation height (Mean_height), Foliage Height Diversity (FHD), density in the 0.5-2m layer (d00), the 2-4 m layer (d01), and hedgerow width (Width). B) Same chart for bird abundance. C) Correlation chart for FHD with HBB % cover, understory shrub species richness (Shrubrich), shrub species Shannon index (shrubWeiner), mean vegetation height (Mean_height), density in the 0.5-2m layer (d00), the 2-4 m layer (d01), and hedgerow width (Width).