

AN ABSTRACT OF THE THESIS OF

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Birds perform valuable ecological functions and are useful environmental indicators. Avian distributions and diversity are predicted to change over the next 50 years. Little information exists on the role of local and regional conditions in fluctuations of avian communities over time. Historic datasets present a legacy of information that helps to understand changes in avian community composition. This study utilizes a rare, highly detailed avian survey of sites in the Willamette Valley, Oregon from 1952 (Eddy 1953). Because they include counts for all species detected on each survey, these data are uniquely valuable to understanding how avian species assemblages in the Willamette Valley changed. I resurveyed sites in 2013 to quantify the nature and extent of avian community compositional change. I used aerial photographs and satellite imagery to quantify changes in land use and habitat cover between periods. I compared metrics of avian alpha, beta, and gamma diversity between survey periods on multiple spatial extents. I also tested for shifts in categorical species abundances. Data was ordinated along environmental gradients to determine important axes of change between historic and modern species assemblages. Nonparametric procedures identified indicator species for each survey era. Observed differences between historic and modern communities suggested substantial turnover; nearly 50% of species were replaced over 60 years. Species richness increased on both local and regional spatial extents. Modern avian communities tended towards bimodal, less even distributions of abundances. Ordination of survey sites in species space confirmed modern avian communities were different from

their historic counterparts. However, sites underwent relatively little change in vegetation and land use cover between survey eras. Indicator species characterized changes in regional abundances as well as differences in survey methodologies between eras. I took additional steps to confirm discrepancies in site location, survey effort, and detection probabilities did not influence analyses. These results suggest avian species assemblages are naturally dynamic. Complex processes outside of local habitat characteristics may influence community composition. Additional factors, such as vegetation structure and composition should be considered when modeling future shifts in species assemblage. Despite uncertainties in methodology, the historic data in this research provided unique, valuable insight into long-term changes in avian communities.

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60 Years of Avian Community Change in the Willamette Valley, Oregon

by
Jenna Curtis

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Jenna Curtis, Author

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60 Years of Avian Community Change in the Willamette Valley, Oregon

Chapter 1: General Introduction

Environments across the globe are dynamic, and experience many types of change both natural and anthropogenic. Several types of environmental change, including vegetation, climate, and precipitation are known to influence avian distribution (Crick 2004, McDonald et al. 2012, Root 1988, Thomas and Lennon 1999, Vale et al. 1982). Human activity also impacts avian communities, through environmental disturbances such as agricultural conversion, fire, forest fragmentation, grazing, and urbanization (Askins and Philbrick 1987, Haslem and Bennett 2008, Knick and Rotenberry 2000, Kotliar et al. 2007, Newmark 2006, Thibault and Brown 2008, Walther et al. 2002). Birds are frequently used as environmental indicators because of their relative ease of detection, high mobility and responsiveness to habitat change (Crick 2004, Temple and Wiens 1989).

An increased knowledge of bird distributions provides scientists with a better understanding of ongoing ecosystem processes. Restructuring of local bird communities can be indicative of changes in local habitat conditions (Brown et al. 2001, Knick and Rotenberry 2000, Rotenberry and Wiens 2009), or immigration and extinction at a regional level (Loreau and Mouquet 1999, Ricklefs 1987). Because of the valuable ecological functions birds provide, changes in avian communities can have serious consequences for ecosystem diversity and function (Sekercioglu 2006, Sekercioglu et al. 2004). Conservation biologists are challenged to preserve existing communities in the face of environmental change. Yet the drivers of avian community change remain difficult to ascertain. Information on how species assemblages vary over long periods is scarce. More research on long-term changes in community composition is needed to improve our understanding of the mechanisms driving such changes.

Given increasing pressures from anthropogenic disturbance and global climate change, there is a need to understand how avian biodiversity will respond on multiple geographic and temporal extents (Wiens et al. 2009). One of the best means to accomplish this is with long-term datasets. Historic and long-term datasets capture

variation within populations over an extended period of time and provide insight into ecological conditions at the time of data collection (Magurran et al. 2010). Historic datasets present a legacy of information, which modern researchers can use to enhance our understanding of bird distributions and long-term population cycles (Porzig et al. 2011). Short-term studies may be influenced by climate oscillations (Moritz et al. 2008), and some ecological processes are only evident after multiple decades (Collins 2001). Therefore, long-term datasets are necessary to gauge ecosystem change adequately.

Another way to enhance the value of long-term research is by collecting highly detailed biological or ecological information. Long-term monitoring programs that revisit sites annually provide the most precise depiction of population trends (Porzig et al. 2011). However, the majority of bird surveys are short-term investigations that substitute space for time; studies spanning multiple decades are rare (Marzluff et al. 2001). Examples of multi-decade bird monitoring programs in North America include the Christmas Bird Count (CBC) and Breeding Bird Surveys (BBS). However, the CBC aggregates surveys over large areas, and most BBS routes have been in operation for less than 50 years (Sauer et al. 2014). Other long term studies rely on sparse data from field notes, museum specimens, or pre-existing literature (Tingley and Beissinger 2009).

A challenge to scientists is many historic surveys lack adequate metadata to allow exact replication of surveys. Access to raw data from individual surveys is rare, and extrapolation is often necessary (Igl and Johnson 2005). Rigorous interpretation of trends over time is difficult. The less information the historic dataset provides, the more biases need to be accounted for when comparing against it (Tingley and Beissinger 2009). Notwithstanding such challenges, historic datasets provide a valuable perspective when compared against modern re-surveys. Yet few studies compare against historic data (see reviews in Igl and Johnson 2005 and Tingley and Beissinger 2009). Most existing historic comparisons are limited to a single site or geographic region and their conclusions are not widely applicable. Even fewer studies utilize historic data from the western United States or Canada (Diamond 1969, Kotliar et al. 2007, Martin et al. 2004, Rotenberry and Wiens 2009, Shultz et al. 2012).

This study incorporates a rare, highly-detailed historic avian dataset collected in 1952 by Richard Eddy for his Oregon State University master's thesis (Eddy 1953). No other avian dataset from this time is known to exist for the Pacific Northwest. The scope of these data is unique for the region, and is particularly valuable because Eddy reported raw data for repeated surveys of multiple sites. Repeated visits and estimates of abundance are essential for accurately estimating immigration, extinction, and site occupancy (Tingley and Beissinger 2009). This dataset makes a significant contribution towards understanding how avian communities in the Willamette Valley changed in the past 60 years. I resurveyed five of these sites in 2013 using methods that resemble Eddy's approach yet can also be exactly repeated by future studies.

My research is comprised of two chapters: the first investigates long-term variation in measures of avian community diversity across the different habitats surveyed by Eddy (1953). I evaluated trends in species diversity and assessed to what degree local community change matched regional trends. Observed changes in species assemblages were then evaluated in the context of three hypotheses of community compositional change. The second chapter is a comprehensive analysis of historic and modern avian communities using nonparametric permutation procedures. I tested for significant differences in species assemblages along environmental gradients. Indicator species analysis was used to identify species characteristic of each survey year. Finally, habitats were ordinated in species space to identify variables associated with observed changes in species assemblage. Overall, this study furthers our understanding of long-term changes in avian community composition and provides a more accurate depiction of variation in species assemblages of Willamette Valley birds over time.

Chapter 2: Sixty years of species turnover suggests complex structuring of Pacific Northwest avian communities

Abstract

Little information exists on the role of local and regional conditions in the fluctuations of avian communities over time. Historic datasets present a legacy of information useful for understanding changes in avian community composition. This study utilizes a rare, highly detailed avian survey of sites in the Willamette Valley, Oregon from 1952 (Eddy 1953). I resurveyed sites in 2013 to determine the nature and extent of community compositional change. Metrics of alpha, beta, and gamma diversity were compared between survey periods. I also tested for shifts in categorical abundances of species. Observed differences between historic and modern species assemblage indicated substantial community turnover. Nearly 50% of species were replaced over 60 years, with increased species richness and decreased evenness on both local and regional spatial extents. Measures of regional turnover agreed with local turnover, suggesting regional communities might influence species assemblages at smaller extents. Avian communities in the Willamette Valley appear to be dynamic over time with complex processes not driven by local factors alone.

Introduction

Characteristics of avian species communities are the result of many different processes, both species-specific and across populations. The degree to which communities are dynamic over time is influenced by immigration and extinction, and changes in vegetation structure, such as those driven by habitat succession and anthropogenic activity (Beissinger and Osborne 1982, Brown et al. 2001, Loreau and Mouquet 1999, Vale et al. 1982). Communities may also respond to regional factors, including climate cycles or precipitation regimes (Crick 2004, Davey et al. 2013, Devictor et al. 2008, Walther et al. 2002). Local and regional communities are thought to interact reciprocally, with regional communities establishing the species pools from which local assemblages are drawn and local communities driving the abundances of

species across regions (Harrison and Cornell 2008, Ricklefs 1987). Yet detailed, long-term data capable of quantifying community change remain rare. Relatively little information exists on how local and regional community diversities fluctuate after decades of environmental and species change.

Three hypotheses of community change currently prevail: stability, diversity decay, and turnover. Stability results when there are no changes in community composition, regardless of the degree of environmental change. The second hypothesis, diversity decay, suggests the number of species capable of inhabiting a given space is reduced over time, usually in conjunction with anthropogenic disturbance or urbanization (Beissinger and Osborne 1982, Catterall et al. 2010, Strohbach et al. 2014). The opposite of this hypothesis, that biodiversity increases over time, is rarely posited in scientific literature despite evidence that some urban environments support higher species diversity (Marzluff 2014).

The final hypothesis, turnover, is often divided into two forms. The first, community turnover, has been used to explain occasions when species composition changes without associated loss of richness and diversity (Catterall et al. 2010, Diamond 1969, Haney et al. 2001, Herkert 1995, Igl and Johnson 1997, Jones 2008, Rotenberry and Wiens 2009, Shultz et al. 2012). One form, called equilibrium turnover, requires habitat and environmental stability, with no outside forces acting upon species assembly (Diamond 1969, Lynch and Johnson 1974). A second type of turnover, known as community succession, occurs when a species assemblage changes in association with vegetation structure dynamics within the habitat (Etterson et al. 2007, Holmes and Sherry 1988, Lynch and Johnson 1974, Parody et al. 2001).

There remains some disagreement as to which of these hypotheses is likely to influence long-term changes in community composition. Some multi-decadal studies found urbanization was the driving force behind long-term declines in species richness (Strohbach et al. 2014) and community homogenization (Walcott 1974). While others reported half a century of high species turnover with minimal loss in diversity (Catterall et al. 2010, Shultz et al. 2012). Pronounced turnover of biological systems has been

observed across the globe (Dornelas et al. 2014), and is a common result of many extended studies, even after intensive anthropogenic influence (Brown et al. 2001, Parody et al. 2001). Different historic baselines for comparison may yield different observed results. Long-term avian monitoring on multiple geographic extents, coupled with assessments of habitat change, provides the best opportunity to observe community dynamics and determine which hypotheses apply to a given system.

I used a 60-year-old historic dataset to evaluate the nature of avian community change in the Willamette Valley, Oregon, and to characterize long-term variation in avian diversity between and among different habitats. I resurveyed five sites originally censused in 1952 (Eddy 1953) to determine how modern avian communities differed from historic communities. I compared alpha, beta, and gamma diversity, as well as species turnover and categorical abundance levels. Changes in land use and habitat were assessed using aerial photographs and satellite imagery. I then evaluated whether any hypotheses of community change were consistent with my results. Breeding Bird Survey data from Oregon and the surrounding geographic region were used to assess to what degree local differences between eras (alpha and beta diversity) matched changes to the regional community (gamma diversity).

Methods

Study Areas

In 1952 Richard Eddy conducted avian surveys at six sites within 50 km of Corvallis, Oregon (Eddy 1953). All sites were non-randomly selected to represent six primary habitat types (Figure 2.1). The coniferous site was a 14-hectare Douglas fir (*Pseudotsuga menziesii*) stand along the McDonald forest ridge. Eddy described the southern portion of the site as "burned over" and composed of primarily shrubs. The oak woodland site was a 14-hectare hillside covered in Oregon white oak (*Quercus garryana*) 1.6 km west of Corvallis, known today as Witham Hill. The 10-hectare Willamette River site was a floodplain forest located along a grassy riparian strip called "Murphy's Beach" 3.2 km south of Corvallis. The marsh site consisted of a 20-hectare portion of McFadden

Marsh in the William L. Finley National Wildlife Refuge. The mixed deciduous site was 8 hectares "just below and to the west of the Oak area" (Eddy 1953) clearly defined by the presence of agricultural lands on three sides. I could not relocate the historic "brushy" site, located along Peoria road in Linn County, and excluded it from modern surveys. Eddy did not measure vegetation, but he qualitatively described presence of dominant tree and shrub species (Appendix A).

To perform modern surveys, I first relocated each historic site as accurately as possible. Because the historic thesis did not include maps, each site was located using Eddy's site descriptions and aerial photographs of Benton County from 1956 (US Department of Agriculture, Farm Service Agency 1956; Appendix A). I used ArcGIS (ESRI 2013) to designate site boundaries and overlaid a 200m square grid aligned with the longest axis of the site. For sites where historic placement was uncertain, I designated "likely areas" adjacent to the selected survey area. These areas also met Eddy's site descriptions and may have been surveyed in 1952. I later compared sites to adjacent "likely areas" using paired t-tests to confirm site placement did not affect survey results (Appendix B).

Historic Avian Surveys

The purpose of Richard Eddy's avian censuses was to "satisfy the need for more detailed information of summer avifauna" (Eddy 1953). The original survey methods involved walking through a given site for two hours between 0500 and 1000, recording the number and species of birds observed. Eddy repeated this survey process 10 times for each site. Sites were visited approximately once per week between June 14 and August 24, with up to two sites surveyed in a single day. Eddy's research is unique in that he presented raw counts of individuals for each species on each site visit. This level of detail is rare for historic datasets, and allows for a more precise evaluation of community change compared to species lists from a single site visit with no associated effort data.

Eddy's methodology only specifies "two-hour observation periods" in which birds were observed using 8x25 power binoculars (Eddy 1953). Eddy's qualitative descriptions of each species only indicate birds as "seen". Birds that, in general, tend to

be detected through auditory means, such as American Bittern and Wilson's Snipe, are described as "very secretive and hard to flush" and "always seen after being flushed" (Eddy 1953; see Appendix C for scientific names). Additionally, Eddy failed to detect several common species including Hermit Warbler and Pacific Wren. These species were frequently detected in Breeding Bird Surveys from 1966 onward (Sauer et al. 2014), and it is likely they were present at sites in 1952. These species tend to reside high in the canopy or deep within underbrush, where it would be difficult to observe them visually. Given this information, it is likely Eddy's historic dataset contains only or mostly visual detections.

Historic surveys were performed June through August to obtain counts of resident "summer birds" (Eddy 1953). However, most summer breeding activity ends in early to mid-July, after which detectability of locally breeding birds declines (Ralph et al. 1998). Because my objective was to examine breeding season bird communities (May through July), it was necessary to restrict data comparisons to Eddy's first five visits to each site. Using paired t-tests, I evaluated if 10 site visits contributed significantly more information than the first five visits (Appendix B).

Modern Avian Surveys

To measure modern avian community composition, I spot mapped each of the five relocated sites five times during the 2013 breeding season beginning mid-May and ending the first week of July. I used the spot mapping protocol described in Bibby et al. (2000). Beginning within 10 minutes of sunrise, I systematically walked across each site from grid point to grid point until the entire area was surveyed. I used binoculars, field maps, and a compass to record the geographic locations, species, sex, number of individuals, detection method, and any relevant territorial or breeding behaviors for all birds encountered during a survey period. I did not conduct surveys on days with heavy rain.

Modern spot mapping surveys were between two and three hours long. Eddy (1953) specified each historic site visit was two hours long. To ensure I collected as much data as possible during each survey effort, I continued to spot map each site after the

initial survey period had ended, noting any new bird detections or relevant behaviors that occurred after the first 2-3 hours of surveying. I only considered observations made during the initial 2-3 hour survey period for statistical analysis.

Because spot mapping results may vary depending on the route and effort, and to improve the exact repeatability of surveys, I also conducted 4 to 5 unlimited-radius point counts within each site (Ralph et al. 1993, Reynolds et al. 1980). Point counts were located at each grid intersection falling within the site boundary. There were four point count locations within each site except the marsh site, which had five point counts. Upon reaching a predefined point count location during a morning survey, I counted the number of birds seen or heard within five minutes. The distance of the bird from the observer, as well as the methods of detection (flyover, singing, visual, etc.), was recorded. I surveyed each point count location five times during the breeding season. Point counts in designated “likely areas” were conducted one day before or after the adjacent site was spot mapped, weather permitting.

Regional Breeding Bird Surveys

To address questions regarding the spatial extent of changes observed in bird communities on the survey plots, I also evaluated patterns of community change on a regional level. The regional avian community was defined by ten Breeding Bird Survey (BBS) routes within the Willamette and northern Umpqua valleys selected for their geographic similarity to habitat surrounding Corvallis, Oregon. These routes (and BBS route number) were as follows: Tualatin (002), Umpqua (018), Days Creek (026), Adair (033), Scio (034), Dayton (040), Elkton (050), Canby (202), Salem (237), and Lorane (243). Individual route data was downloaded from the USGS Patuxent Wildlife Research Center FTP site (USGS Patuxent Wildlife Research Center 2013). All years of available data between 1966 and 2012 for a given route were used for analysis.

I also used species-specific BBS data from the surrounding region for an informal comparison of observed results and region-wide trends. The first level incorporated data from all BBS routes in the state of Oregon, including coastal, montane or shrub habitats not within the scope of this research. At the largest extent, I considered BBS data for the

entire Northern Pacific Rainforest bird conservation region (BCR). The Northern Pacific Rainforest BCR extends from the Willamette Valley north along the Pacific coast to southern Alaska. Species-specific regional data was obtained online courtesy Sauer et al. (2014).

Environmental Traits

To quantify changes in land use and vegetation cover between historic and modern surveys, I scanned high-resolution digital images of 1956 aerial photographs from Benton County (US Department of Agriculture, Farm Service Agency 1956). These images were brought into geospatial software and overlaid onto a 1m high-resolution satellite photograph of Oregon from 2012 (US Department of Agriculture, Farm Service Agency 2012). I visually classified all habitat cover within 150m of each site for both survey eras based on observable physical characteristics of the vegetation. Rather than pre-determined 5m pixels, I drew freehand polygons to mark the boundaries between vegetation classes (Appendix D). This provided a higher level of detail than would be possible with pre-determined pixel sizes. Each polygon was classified down to the Macrogroup level using the US National Vegetation classification system (US Geological Survey 2012). For cases where the vegetation class for a given area was unclear, landscape data from the US Gap Analysis Project (US Geological Survey 2012) was consulted to help determine the most likely classification for that polygon. The mean elevation, exact area in square meters, and percent cover of each land use and vegetation classification for each site were calculated using ArcGIS (ESRI 2013). I compared percent cover values between years to identify any changes in habitat cover for each site.

Statistical Analysis

All statistical analyses were performed in program R (R Core Team 2013). Species richness estimates, accumulation curves, and diversity indices were obtained using the package “vegan” (Oksanen et al. 2013). Alpha diversity confidence intervals and test statistics were obtained using PAST Paleontological Statistics version 3.0 (Hammer et al. 2001). I calculated beta diversity using the program R code provided by

Chase et al. (2011). It was necessary to remove non-visual detections from the modern data to make it comparable to the historic dataset. When comparing only visual detections between survey periods, raw counts of individuals from the modern data were imprecise. Therefore, when applicable, I used both datasets including and omitting non-visual detections for statistical analyses.

Species Diversity Comparisons

I compared several measures of avian richness and diversity between 1952 and 2013. Alpha diversity is a metric of species variety on an individual, site-specific basis. It is often represented by species richness or, more frequently, a compound diversity index that accounts for both richness and evenness (Stirling and Wilsey 2001). I measured alpha diversity using estimates of species richness and Simpson's diversity index. I calculated species richness as the total number of species detected at a site across the entire survey era. It is assumed that heterogeneous species detection probabilities result in some species being overlooked during a survey period (Boulinier et al. 1998). Thus, the observed species pool is an underestimation of the actual species pool. To account for non-detected species, I estimated actual species richness using Chao's first estimator ("Chao 1"; Chao 1984). Chao 1 estimates richness based on the number of observed species and the number of species seen only once or twice during a survey period. While several other nonparametric estimates of species richness are available, Chao 1 was used because it was found to be comparatively more precise for abundance-based avian community data (Chao 1984, Walther and Martin 2001).

I limited my diversity index analyses to birds detected at least twice during a survey year. Species that were detected only once across all 25 surveys for a single year were likely not residing within any site during the breeding season. Removing these rare species reduced the amount of noise in the data and provided a more reliable representation of how the breeding avian community changed over time. I calculated compound alpha diversity for the total number of individuals of each species observed at a given site during a survey era using the inverse Simpson's diversity ($1/D$) index. Simpson's inverse measures how likely two randomly chosen individuals will be of the

same species. This index of diversity tends to be influenced by species evenness and the presence of dominant species, rather than changes in species richness or rare species (McCune et al. 2002). 95% confidence intervals for the inverse of Simpson's diversity were obtained by percentile bootstrapping data from a given site and survey period for 9999 iterations (Hammer 2013). Inverse Simpson's indices between survey periods were compared using paired t-tests under the null hypothesis that the modern community diversity of a site was not significantly different from the historic diversity (Brower et al. 1998, Hammer 2013).

Beta diversity is a useful way of investigating similarities among multiple communities separated by space and/or time (Anderson et al. 2011, Chase et al. 2011). Unlike alpha diversity, beta diversity uses metrics of dissimilarity to compare community composition between different sites. I quantified beta diversity using the modified Raup-Crick method (β_{RC} ; Chase et al. 2011). Unlike many measures of beta diversity, β_{RC} is independent of changes in alpha diversity and does not depend on the number of species within each community (Anderson et al. 2011). This approach evaluates whether pairs of communities for a given time period are more or less different than chance. Calculations are based on the number of species in each site and in the regional pool, as well as the proportional occupancy of each species. The resulting matrix of β_{RC} values suggests whether mechanisms structuring ecological communities are similar across sites or over time.

To identify significant differences in beta diversity among non-random pairs of communities, it was necessary to compare against null communities generated by chance. To derive null communities, I randomly sampled a number of species from the entire species pool equal to the number of species for a given pair of sites. I estimated the probability that the observed number of shared species in a pair of communities was equal to or lower than the null expectation. This probability was re-scaled to a metric ranging from -1 to 1, where communities with lower values are less dissimilar than expected, and communities with higher values are more dissimilar than expected (Chase et al. 2011). To compare beta diversity for communities between years, I calculated

pairwise dissimilarity matrices for all sites within a given year then tested for differences in mean dissimilarity values using paired two-sample t-tests.

Turnover is an important metric of community diversity that represents the instability of a species pool over time. Many measures of turnover fail to account for non-detected species that may immigrate or go extinct from the local species pool between years (Boulinier et al. 1998). For this study, species turnover was defined as the complement of the estimated total number of species shared between two time periods (i and j) conditioned on the estimated total number of species during time j (Nichols et al. 1998). The number of shared species was estimated with the Chao 1 richness estimator using the abundance data from time i only for species also detected during time j . Because Chao 1 approximates actual species richness, including an estimate of species missed by the surveyor, the result is a conservative estimate of shared species richness that accounts for non-detected species. This value was divided by Chao's estimate of species richness for time j to produce the probability that any given species at time j was a species present during time i . The complement of this was the estimated probability that a species is "new", or not present during the initial surveys. I calculated turnover for each site as well as the entire study area between survey years. Estimates of standard error were obtained by standard nonparametric bootstrapping of the data for 1000 iterations using the "boot" package in program R (Canty and Ripley 2014).

Due to the structure of the regional BBS data, it was necessary to use Chao's estimate, rather than observed richness, when examining species turnover on larger spatial extents. The estimated number of shared species across all BBS routes was frequently as large as or larger than the observed richness for the second year. To reduce bias, the denominator on which the estimate of richness is conditioned must be representative of the relevant species pool (Cam et al. 2000). Because the area represented by the regional species pool was so large, there was a considerable discrepancy between observed and estimated species richness. Conditioning upon the estimated regional species richness for the second survey period produced a less biased

estimate of turnover more appropriate for examining large-scale regional gamma diversity.

To investigate changes in gamma diversity, I first defined the regional species pool from which immigrations into the local sites might occur. Regional species data consisted of ten BBS routes closest in geographic similarity to the local survey sites. I summed species abundances for all routes conducted during a given year to produce a single regional dataset for each year from 1968 to 2013. Annual species richness was estimated using Chao 1, one of several robust methods that account for heterogeneous species detection probabilities (Chao 1984, Nichols et al. 1998, Walther and Martin 2001). I calculated yearly regional species turnover using a method similar to the same method as local turnover.

Changes in Abundance

Modern abundances were approximately two times larger than historic abundances. This was likely an artifact arising from including non-visually detected birds in the modern dataset. It was necessary to account for the fact that historic estimates of abundance are not directly comparable to modern estimates. To detect large shifts in abundances, I organized species into categorical levels of abundance. I based categories on the mean number of individuals per visit to a site for a given year. Species were classified as follows (mean number of individuals per visit provided in parentheses): “rare” (up to 1.5 individuals per visit), “uncommon” (between 1.5 and 4.5 individuals per visit), “common” (between 4.5 and 10 individuals per visit), and “abundant” (over 10 individuals per visit). Species not observed at a given site during one of the survey eras were classified as “not detected” (0 individuals per visit) for that period.

Species were also categorized based on the observed change in abundance between years (Appendix E). I based trend classifications on both the direction and magnitude of the shift in abundance category. Species that retained their historic abundance classification were classified as “no change”. I tested for shifts in the distribution of species among abundance categories between years using Chi-square tests under the null hypothesis that the distribution of species within categories was not

different between 1952 and 2013. When the assumptions of the Chi-square test were not met, Fisher's exact tests were used instead. I compared any species considered to be strongly increasing or decreasing in abundance against calculated Breeding Bird Survey trends for the surrounding region. Trends were obtained from Sauer et al. 2014, who use a hierarchical model to produce annual indices of abundance (Sauer et al. 2014). I considered possible explanations for notable changes in abundances, as well as disagreements between local and regional trends.

Results

I addressed several challenges associated with comparing against historic datasets (Appendix B). I limited my analyses to the breeding season to improve the reliability of species detections. There was no evidence the last five visits to each site in the historic dataset contributed significantly more information than the first five visits. Comparisons of species accumulation curves and detection probabilities showed historic and modern survey efforts encountered species at similar rates and with similar thoroughness (Appendix F). I addressed the issue of uncertainty in site placement by comparing point counts within and adjacent to sites where location was unclear (Appendix B). There was no evidence that changing site placement would significantly influence modern surveys. By addressing the challenges with this historic dataset, the reliability of my results are improved.

Land Use and Vegetation Cover

To determine if environmental conditions at survey sites shifted, I quantified the amount of change in the percent cover of different vegetation and land use classes. The amount and direction of habitat change varied among sites (Table 2.1; Appendix D). In general, most sites experienced a small increase in urban land use and anthropogenic development. However, this was not true of the Willamette River site, which decreased in urban land use. The Willamette River site experienced some of the greatest overall changes in percent cover of habitat. Historically this site was nearly 50% wetland and approximately 30% open water. By 2013, floodplain forest dominated the site with 85%

cover. Similar developments were seen in the coniferous site, which went from over 15% disturbed vegetation (primarily in the burned region) to less than 1% disturbed and almost entirely contiguous upland coniferous forest. Both the mixed deciduous and oak woodland sites experienced some degree of transition between forest types. The mixed deciduous site changed from primarily riparian forest to a mixed forest/pasture habitat with nearly 50% deciduous cover. Similarly, the oak woodland site lost almost 15% deciduous cover to expanding coniferous forest. Overall, there were no prevailing trends in the direction of cover change across sites.

Species Diversity

I evaluated changes in species richness and diversity in the context of prevailing community change hypotheses. Some hypotheses, such as stability and turnover, predict species richness will remain the same, while diversity decay predicts richness will decrease. Observed species richness was 2 to 27 species higher in modern study sites compared to the historic surveys (Table 2.2). The marsh site contained the highest species richness, while the coniferous site had the lowest. 13 rare species were removed from historic dataset and 18 from the modern dataset, 14 of which were visually detected. After removing non-visual detections from the modern surveys, observed species richness remained between 4 and 17 species higher than historic richness, except for the coniferous site, which decreased in richness. Estimates of species richness accounting for rare and undetected species showed significant increases in richness for the marsh and oak woodland sites, regardless of detection type. I detected more species with only one individual during a given survey (84 instances, 63 visually detected; compared to 40 historic instances; Table 2.2).

Alpha diversity is linearly related to species richness, and should exhibit a similar response as richness under each hypothesis of community change. After removing rare species, alpha diversity was 0.5 to 7 higher for modern sites (Table 2.3). Across all sites, the inverse of Simpson's diversity ($1/D$) experienced a statistically significant increase between years (all detections: $t = 19.316$, $p < 0.001$; visual detections: $t = 16.168$, $p < 0.001$). There was no evidence of changes in diversity for the mixed deciduous and

Willamette River sites. The only significant diversity increase regardless of detection type occurred at the marsh site (all detections: $t = 23$, $p < 0.001$; visual detections: $t = 20.905$, $p < 0.001$), which increased from 3.14 to 10.89 for all detection types (9.62, visual detections only). The coniferous and oak woodland sites both showed significant decreases in diversity considering only visual detections (coniferous: $t = -6.55$, $p < 0.001$; oak woodland: $t = -3.76$, $p < 0.001$). The coniferous site was the only location to decrease in diversity for both detection types. However, the significance of these changes was lost after accounting for non-visual detections. There was evidence removing non-visual detections had the general effect of decreasing modern diversity to below historic values. This is notable, considering richness was still higher in the modern era after removing non-visual detections.

Beta diversity, a measure of community dissimilarity among sites, should remain constant under the hypotheses of stability and turnover, and decrease under the hypotheses of diversity decay. Beta diversity did not significantly differ between years (all detection types: $t = 2.188$, $p = 0.117$; visual detections only: $t = 1.895$, $p = 0.154$). Accounting for differences in species richness, mean among-site beta diversity for the historic period was 0.61, while mean among-site beta diversity for the modern period was 0.180 (0.193 visual only). Both survey periods showed less among-site similarity than expected by chance (Appendix G). While modern sites were more similar in community composition than their historic counterparts were, this change was not significant.

I evaluated the hypothesis of community turnover by quantifying the probability of species replacement between survey periods. Species turnover between 1952 and 2013 was high (Table 2.4). After removing rarities, only 48 out of a total pool of 102 species (39 out of 91 species, visual detections only) were present across all sites for both survey periods. There was a nearly 40% chance that a given species was new to the species pool during the modern surveys (48% considering visual detections only). Turnover among individual sites was higher than turnover across the entire study area. Variation in the degree of turnover among sites was moderate, ranging between 55 and 75%. The oak woodland site had the highest values of species turnover: over 70% for both detection

types. Removing visual detections generally increased turnover values, with the exception of the Willamette River site.

I compared local community results to regional community change using BBS data. Trends in regional gamma diversity based on selected BBS routes matched local results quite well (Figure 2.2). Overall species richness across 10 Willamette Valley routes significantly increased from an estimated 85 species in 1968 (SE = 7.71) to 135 species in 2012 (SE = 14.32). Estimated species richness ranged between 83 in 1969 to 152 in 2011. These results were proportional to an increase in survey effort over time. The estimate of overall regional turnover was similar to local turnover, with a 48% probability of species replacement over time. Annual turnover rates were lower than total species turnover, averaging 17% over the entire 34-year period. Estimated turnover between pairs of years ranged from 0 (no difference in species assemblage between years) to 40% turnover (between 1970 and 1971). Linear trend lines fitted to annual estimates of richness and turnover showed species richness increased in conjunction with a slightly, though non-significantly decreasing rate of turnover (Figure 2.2). There was more variation in early values of richness and turnover, likely due to proportionally fewer BBS routes surveyed between 1968 and 1980.

Abundance Comparisons

Some hypotheses of community change predict avian abundances to decrease in the face of urbanization or habitat loss. Considering all detection types, the majority of species in this study were increasing or strongly increasing (40 and 17 species, respectively, out of a total pool of 102 species; Table 2.5; 0). Another 17 species did not change in categorical abundance over time. 23 species were decreasing in abundance. However, after removing non-visual detections, more birds were decreasing or strongly decreasing in abundance (34 and 8 out of 91 visually observed species, respectively). Only 38 visually detected species increased in abundance to any degree. 11 species did not change in categorical abundance based on visual detections.

The distribution of species among abundance categories shifted significantly over time (all detections: $\chi^2 = 10.35$, $p = 0.035$; visual detections only: $\chi^2 = 9.54$, $p = 0.049$).

There was variation in the degree to which abundance distributions changed for each individual site. The coniferous and oak woodland site both showed significant shifts in categorical avian abundances regardless of detection type (coniferous site: all detections $p = 0.026$, visual detections $p = 0.002$; oak woodland site: all detections $p = 0.030$, visual detections $p = 0.0003$). When all detection types were considered, the Willamette River site also experienced significant shifts in avian abundances ($p = 0.007$). In general, the distribution of modern abundances was bimodal, with more species in the “rare” and “abundant” categories compared to historic abundances. As suggested by observed species richness, more bird species tended to be “not detected” during historic surveys when all detection types were included. However, when examining only visual detections, modern surveys identified more “rare” and “not detected” species.

Discussion

In 1952, Richard Eddy conducted detailed avian surveys at five sites in Benton County, Oregon. I resurveyed those sites 60 years later to evaluate how and to what extent avian community composition changed. After accounting for differences in methodology and observer skill, results remained complex and not easily characterized. Species turnover was high, and there is strong evidence nearly half of species within modern avian communities were not present historically. On a local scale, richness appeared to increase. Community turnover and increasing species richness were also evident on a regional extent. These results paint a dynamic picture of species and community change that is difficult to find among current literature abound with hypotheses of population declines and range contractions.

These conclusions are limited by uncertainties associated with the datasets. Given the small sample size in this research ($n = 5$) the strength of these conclusions is limited. There remains the possibility some changes were the result of methodological differences or changes in detectability, rather than actual ecological changes. I addressed these issues by closely approximating historic efforts. Removing non-visually detected species provided a conservative estimate of modern avian diversity. I confirmed different

detection probabilities and site placement were unlikely to influence comparisons. To account for differences in methodology, I performed analyses with and without modern visual detections. Finally, because raw abundances were unreliable, I compared categorical abundances instead. While insufficient historic vegetation data and limitations associated with the interpretation of Eddy's data restrict the precision of these conclusions, I nevertheless found strong indications of change across the surveyed avian communities.

Changes in Richness and Diversity

Species richness increased over time across four of the five study sites. The observed low richness estimate for the coniferous site may be an artifact of survey methodology, as modern richness values were considerably higher when non-visual detections were included. Local and regional estimates of "true" species richness agree with these observations. Chao's estimates of richness and confidence intervals may be lower for the historic surveys because Eddy detected fewer species with only one individual during a given survey.

Though richness increased, evenness and diversity both decreased, in some cases to a statistically significant degree. Historic communities had more species of intermediate abundance (common, uncommon), while modern species tended to be either rare or abundant. This suggests higher species richness can be associated with a decrease in community diversity when abundances vary over time. Previous research suggests increasing species richness can occasionally be negatively associated with evenness through a disproportionate distribution of abundances (La Sorte and Boecklen 2005a). Simpson's index of diversity is sensitive to changes in evenness. An uneven distribution of individual abundances should result in lower calculated species diversity, even if species richness increased over the same period. My results support these conclusions.

In this study, beta diversity did not significantly change across sites over time. Long-term trends in beta diversity are mixed. Some extensive studies found beta diversity to be increasing globally (Dornelas et al. 2014). Yet several other long-term comparisons of avian communities observed temporal declines in beta diversity (Catterall et al. 2010,

Davey et al. 2013, Shultz et al. 2012). Because species richness was stable or increasing, these researchers concluded ubiquitous species were colonizing multiple sites simultaneously, homogenizing the regional community pool (La Sorte and Boecklen 2005b). Increases in species richness are frequently associated with decreases in beta diversity because larger species pools share more species between sites (Davey et al. 2013). After removing non-visual detections, beta diversity did slightly decrease between survey periods. However, this is likely because I encountered the same non-visually detected species across sites during the modern surveys. If the same species (e.g. species whose behaviors or physical characteristics made them difficult to see) consistently failed to be visually observed at every site, then their removal should increase the heterogeneity of the remaining visually detected species across sites.

Environmental and Regional Influences

There was some degree of vegetation change during this study not characterized by changes in percent cover of habitat type. Variations in vegetation structure and volume may explain, to some extent, the observed changes in species assemblages and abundances at these study sites (Holmes and Sherry 1988, Seavy and Alexander 2011, Vale et al. 1982). The oak woodland and Willamette River sites experienced some of the most pronounced changes in vegetation and land use cover. Nearly a third of the oak woodland site is now coniferous forest. An increase in coniferous-associated species at this site, including Pacific-slope Flycatcher and Pacific Wrens, may be attributed to changes in forest cover type (Hagar et al. 1996). The Willamette River site transitioned from primarily urban-adjacent open grass and wetlands (Eddy 1953), to a dense, closed-canopy flooded forest. This site also had one of the largest increases in species richness as well as the highest turnover rate.

At the marsh site, the elimination of grazing and changes in water management provided more standing water for birds including Pied-billed Grebes, Wood Ducks, and Tree Swallows. Likewise, species historically detected at the coniferous site - including Western Bluebird, MacGillivray's Warbler, and Ruffed Grouse - exhibited decreasing abundances following vegetation growth and canopy closure in the area of the site that

was formerly burned (Eddy 1953). Though Western Bluebirds and Ruffed Grouse are increasing regionally (Sauer et al. 2014), local declines in these species, as well as MacGillivray's Warblers, may be associated with a loss of non-coniferous habitat (Hagar 2007). It may be that some species presences or absences may be associated with changes in the surrounding vegetation community, as suggested by previous studies (Holmes and Sherry 2001, Seavy and Alexander 2011, Vale et al. 1982), even if the fine details of such change are difficult to see in this study given limited historic vegetation data.

It is generally suggested that local community composition is regulated by site-specific characteristics rather than large-scale influences (Knick and Rotenberry 2000, Rotenberry and Wiens 2009). While I detected some environmental change in this study, overall land use and vegetation cover remained stable among survey sites. This supports the idea that regional community composition is important in structuring local diversity (Ricklefs 1987). A large regional species pool provides a greater assortment of individuals capable of being recruited into local communities (Brown et al. 2001). I found changes in regional gamma diversity complemented local changes in richness and species composition. Indeed, local richness exhibited a positive linear relationship with regional richness; a characteristic of communities in which local species are proportionally sampled from a larger regional pool (Lawton 1999). Given that relatively little environmental changes occurred on a small scale, regional forces might be one of the driving factors behind observed changes in community diversity at these five study sites.

Local and Regional Population Trends

Overall, local abundance trends reflected regional population trends. Species with strongly decreasing local populations included Chipping sparrow, House Sparrow, Nashville Warbler, and Northern Rough-winged Swallow. All of these species were common or abundant in 1952 but not detected during modern surveys. Other birds originally detected but not observed during resurveys include Ring-necked Pheasant, Northern Bobwhite, MacGillivray's Warbler, and Common Nighthawk. Statewide BBS trends for these species are all negative and, in the case of Chipping Sparrow, Northern

Bobwhite, and Northern Rough-winged Swallow, population declines are quite strong (Sauer et al. 2014).

Many species with strongly increasing populations on a local scale are also increasing regionally (Sauer et al. 2014). It has been suggested that as species richness increases, dominant species, or species with proportionally large numbers of individuals, also increase (La Sorte and Boecklen 2005a). In this study, several previously unobserved species are now community dominant with high categorical abundance. New species, including European Starling, House Finch, and Brown-headed Cowbird, are some of the most common species in the Willamette Valley (Hennings and Edge 2003). Species not detected historically but frequently observed during modern surveys included House Finch, Anna's Hummingbird, and Acorn Woodpecker. The remaining new species tended to be categorically rare, either because they were not yet well established in the area, or because they are now slightly easier to detect than historically.

Hypotheses of Community Change

Avian community diversity at five sites in the Willamette Valley, Oregon changed over the course of 60 years, but the nature of this change was complex and not easily characterized. Which hypothesis of community change best represents these results? Most hypotheses of stability assume resilience to environmental changes, balanced abundances, and resistance to local extinctions (McCann 2000; Morgan Ernest and Brown 2001). However, given the degree of change in assemblage, richness and diversity across sites, it is unlikely surveyed avian communities fit the paradigm of stability. Likewise, the hypothesis of diversity decay can be dismissed. Though observed losses in species diversity and evenness may be suggestive of such decay, these data do not reveal similar losses in species richness. There was no evidence for loss of non-urban habitats, increasing anthropogenic influence, or reduction in vegetation complexity at any site.

Out of all paradigms of community change, my results best resemble the hypothesis of community turnover. Increases in species richness contrasted decreases in species evenness and diversity, but by far the largest change was in species composition. I observed less than half of historically occurring species during modern surveys.

Turnover estimated across sites was a conservative measure of assemblage change because species extirpated from one area may still have been detected at another site. Estimates of turnover at individual sites were even higher; the odds of species persisting within the local assemblage at any given site were between 40 and 25%. These values agree with those from other research. After 50 years of study, Parody et al. (2001) reported only 30% of species remained the same. Diamond (1969) found species turnover rates of 50-60% after nearly half a century of community change. Likewise both Catterall et al. (2010) and Shultz et al. (2012) determined turnover was the driving force of community change over time, as neither species richness nor diversity significantly differed between years. Across the globe, communities may undergo significant assemblage changes without systematic loss of diversity (Dornelas et al. 2014).

Conclusion

Global environmental and climate change are driving shifts in species distributions (Brommer 2004, Moritz et al. 2008, Thomas and Lennon 1999). Novel, no-analog communities are likely as species adjust to changing habitat conditions (Williams and Jackson 2007). There is concern the resulting communities will possess altered ecosystem functionalities and challenge species' abilities to adapt (Stralberg et al. 2009). There is an underlying implication that communities would otherwise remain static, or that the current species assemblage is comparatively more "natural" than those influenced by climate change and anthropogenic disturbance. However, it is difficult to say how much species assemblage variation could be expected even under "normal" conditions (Magurran et al. 2010). This study suggests communities are constantly in a state of flux and may dramatically "re-shuffle" even with little environmental impetus. While climate change may drive species to assort themselves in novel ways, the precision of such predictions are limited by normal background variation in community composition.

The emphasis of many community-based predictive models has been climate or vegetation (Seoane et al. 2004, Wiens et al. 2009). Much has been said about the influence of site-specific conditions on observed community composition (Knick and Rotenberry 2000, Rotenberry and Wiens 2009). However, my results reflected the

importance of regional community turnover in association with environmental change at smaller scales. The drivers of community change may not always relate to climate, vegetation, or human disturbance exclusively. This study demonstrates the natural dynamism of species assemblages. The avian community did not remain constant, nor were all species replaced with a second, discrete community. Instead, diversity, richness, and evenness all changed in contrasting ways, suggesting a continuous process influenced by multiple factors. The dramatic community turnover observed in this study demonstrates the long-term unpredictability of species composition.

There is no strict “end point” to predicted species shifts, after which communities are fixed. Even no-analog communities will likely continue to change under future conditions. Community turnover is an ecologically important result, and can be a major source of variation in future avian communities. There is reason for conservationists to be concerned about the effect of human activity on community composition (Stralberg et al. 2009). However, rather than focusing on species assemblage itself, research efforts may be better directed towards associated changes in ecosystem functionality, taxonomic diversity, and evenness. Long-term species turnover rates can be used to better understand the underlying mechanisms structuring local communities (Chase et al. 2011, Mikkelsen et al. 2011). The connection between functional diversity and species turnover also remains relatively unstudied.

This study suggests some interesting and potentially beneficial avenues for future research. It has been hypothesized that the presence of dominant species within a community tends to regulate turnover and enhance stability (Diamond 1969, Sasaki and Lauenroth 2011). My results indicate increasing species richness may be associated with an increasing number of common or abundant species. On a regional extent, there was suggestive evidence that rates of turnover decreased as community richness increased. It would be interesting to test whether this relationship also exists on a local scale.

Despite the limitations of this study, I remain confident my comparisons of community diversity are ecologically relevant. The best way to understand how biodiversity changes over time is by analyzing long-term data (Igl and Johnson 2005,

Tingley and Beissinger 2009). When continuous long-term datasets are unavailable, as is the case in many regions, independent historic datasets are a useful alternative. Richard Eddy's (1953) dataset is the only one of such detail currently known for the entire Pacific Northwest, and provides us with a look at historic avian communities that would not exist otherwise. Studies like this paint a complex picture of the associations between environmental change, diversity and species assemblages. Historic data reminds us that biological communities are always in flux and may not be easily characterized by a few seasons of data collection. As more researchers seek ways to conserve biodiversity in the face of global climate change, historic datasets present an essential perspective on how community diversity varies over time.

Tables and Figures



Figure 2.1. Map of study site locations in relation to cities in Benton County, Oregon. Survey sites are filled in red and labeled with their four-letter identification codes. Site names (and four-letter codes) are as follows: Coniferous (CONI), Marsh (MARS), Mixed Deciduous (MIXD), Oak Woodland (OAKW), and Willamette River (WILL). See Appendix A for site descriptions and location methods.

Table 2.1. Amount of change in vegetation and land use classes at each study site. Values represent the difference between modern and historic percent cover. Negative values indicate a decline in that cover type since 1952, and positive values an increase since 1952. Sites were visually classified using aerial photos and satellite imagery based on

categories developed by the US National Vegetation classification system (US Geological Survey 2012).

	Site				
	Coniferous	Marsh	Mixed Deciduous	Oak Woodland	Willamette
Vegetation Classes					
Cool forest	9	0	0	22	0
Warm forest	4	-1	36	-13	-2
Flooded forest	0	1	-33	0	83
Grassland	0	0	-2	-11	0
Wet meadow	0	-5	0	0	-42
Agricultural	0	0	-3	-1	0
Developed	2	3	4	3	-13
Disturbed	-15	0	0	0	0
Water	0	1	0	0	-25
Land Use Classes					
Deciduous forest	0	-1	36	-13	-2
Evergreen forest	-6	0	0	37	0
Mixed forest	4	0	0	-15	0
Woody wetlands	0	1	-33	0	83
Shrub/Scrub	0	0	-2	-11	0
Grassland/Herb	0	2	0	0	0
Emergent wetland	0	-5	0	0	-42
Pasture	0	-2	-3	-1	0
Urban	2	3	4	3	-13
Water	0	1	0	0	-25

Table 2.2. Species richness (S) values for historic and modern surveys. Observed species richness is the total number of species detected during five survey efforts. Chao's estimate of S and standard error are calculated using Chao 1 estimator of the total species pool (Chao 1984). Values for the modern data were calculated for the entire dataset as well as for the data after removing non-visual detections to better replicate historic survey methods. * indicates a significant increase in estimated richness compared to historic values.

Year	Richness Measure	Site					
		All Sites	Coniferous	Marsh	Mixed Deciduous	Oak	Willamette
1952	S Observed	79	32	34	32	25	27
	Chao1 S	87	33	35	33	25	29

	Chao1 95% CI	(79–99)	(32–40)	(34–40)	(32–36)	(25–28)	(27–43)
2013 (All Detections)	S Observed	101	36	61	43	52	46
	Chao1 S	116	46	69	46	58	48
	Chao1 95% CI	(101-134)*	(36–78)	(61–83)*	(43–53)*	(52–72)*	(46–53)*
2013 (Visual Only)	S Observed	85	19	51	36	31	36
	Chao1 S	109	24	55	42	37	39
	Chao1 95% CI	(85–137)	(19–58)	(51–62)*	(36–57)	(31–51)*	(36–45)

Table 2.3. Calculated Simpson’s diversity values (1/D) for historic and modern survey eras. 95% confidence intervals are provided below each value. * indicates significantly different modern diversity compared to historic values (Paired t-test, $p < 0.05$). I calculated indices for the modern data before and after removing non-visual detections from the data.

Site	1952	2013 (All Detections)	2013 (Visual Only)
Overall	9.28 (8.66 – 9.93)	30.90 * (29.62 – 31.91)	23.47 * (22.04 – 24.58)
Coniferous	15.93 (13.51 - 17.33)	13.95 (12.64 – 14.93)	7.15 * (6.01 - 8.10)
Marsh	3.14 (2.97 – 3.33)	10.89 * (10.14 – 11.66)	9.63 * (8.84 – 10.42)
Mixed Deciduous	12.24 (10.51 – 13.66)	12.92 (11.44 – 14.26)	11.11 (9.45 – 12.5)
Oak	11.12 (9.63 – 12.21)	12.19 (10.67 – 13.7)	7.55 * (6.54 – 8.6)
Willamette	12.69 (11.34 – 13.41)	12.08 (10.93 – 13.14)	10.73 (9.15 – 12.06)

Table 2.4. Local species turnover between 1952 and 2013. Standard error provided in parentheses. Turnover was calculated using a conservative approach that accounts for non-detected species (Nichols et al. 1998). Estimates represent the probability that a randomly selected species was “new” to the species pool during the modern survey period. Standard errors were derived from nonparametric bootstrapping methods.

Site	All Detections	Visual Only
Overall	39.30 (6.21)	48.26 (6.66)
Coniferous	55.65 (10.69)	68.32 (3.50)
Marsh	63.63 (12.27)	64.04 (7.27)
Mixed Deciduous	58.12 (4.96)	59.10 (4.48)
Oak Woodland	70.15 (6.54)	75.17 (2.95)
Willamette	58.90 (8.13)	54.10 (6.92)

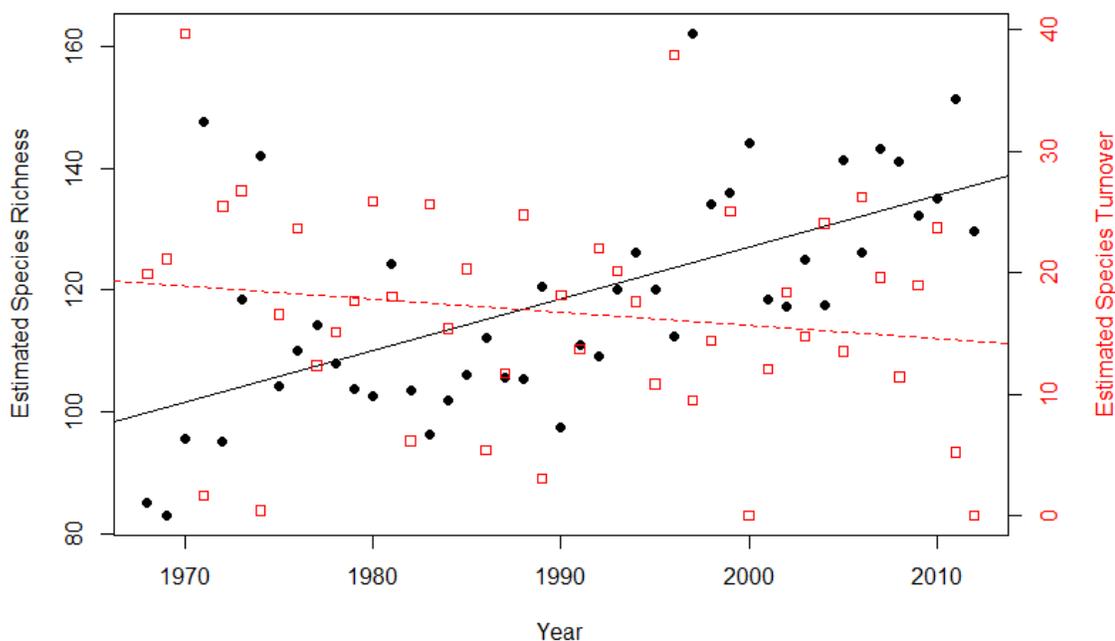


Figure 2.2. Estimates of regional species richness and turnover between 1968 and 2012. Estimates based on 10 Willamette Valley BBS routes selected to represent the regional species pool. Species richness estimates are represented by filled black dots, while turnover estimates (based on equations in Nichols et al. 1998) are represented by empty red squares. Linear trend lines were fitted to the data, using a black line for species richness ($R^2 = 0.3618$) and a dashed red line for species turnover ($R^2 = 0.0024$).

Table 2.5. Trends in species abundance across all sites over time based on all detections. Species were sorted into abundance categories based on average number of individuals detected per visit regardless of site (see Table 3). Trends were classified based on the size of the shift in abundance categories between years. For species classified as “No Change”, (A) indicates species were generally abundant both years, while (R) indicates species were generally rare both years. Species marked with an asterisk (*) were not visually detected.

Population Trend	Species
No Change (A)	American Crow
	American Robin
	Black-capped Chickadee
	Bewick's Wren
	Bushtit
	Cliff Swallow
	Downy Woodpecker
	Lazuli Bunting
	Red-winged Blackbird
	Song Sparrow
	Spotted Towhee
	Steller's Jay

No Change (R)	Yellow Warbler Hairy Woodpecker Killdeer Pileated Woodpecker Townsend's Warbler
Increasing	Acorn Woodpecker American Goldfinch Anna's Hummingbird Bald Eagle Belted Kingfisher Black Phoebe Cedar Waxwing Cinnamon Teal Cooper's Hawk * Common Merganser * Common Raven Common Yellowthroat Dark-eyed Junco Great Blue Heron Great Horned Owl Great Egret Hairy Flycatcher * House Wren * Lesser Goldfinch Mallard Marsh Wren Mourning Dove Northern Flicker Northern Pygmy-owl * Orange-crowned Warbler Osprey * Pied-billed Grebe Purple Finch Red-breasted Sapsucker Red-tailed Hawk Rufous Hummingbird Sora * Spotted Sandpiper Swainson's Thrush Warbling Vireo Western Scrub-jay Western Wood-pewee Willow Flycatcher * Yellow-headed Blackbird *
Decreasing	American Kestrel Barn Swallow Brewer's Blackbird Band-tailed Pigeon Black-throated Gray Warbler California Quail Cassin's Vireo Golden-crowned Kinglet Gray Jay MacGillivray's Warbler Northern Bobwhite Olive-sided Flycatcher Pine Siskin Ring-necked Pheasant

	Ruffed Grouse
	Violet-green Swallow
	White-breasted Nuthatch
	White-crowned Sparrow
	Western Bluebird
	Western Meadowlark
	Western Tanager
	Yellow-breasted Chat
Strongly Increasing	Brown-headed Cowbird
	Black-headed Grosbeak
	Brown Creeper
	Chestnut-backed Chickadee
	European Starling
	Evening Grosbeak
	Hermit Warbler *
	House Finch
	Pacific Wren
	Pacific-slope Flycatcher
	Red-breasted Nuthatch
	Red Crossbill
	Tree Swallow
	Virginia Rail
	Wilson's Warbler
	Wood Duck
Strongly Decreasing	Chipping Sparrow
	House Sparrow
	Nashville Warbler
	Northern Rough-winged Swallow
	Turkey Vulture

Chapter 3: Structural instability of avian communities along gradients of environmental change

Abstract

Avian biodiversity is predicted to shift over the next 50 years. Yet the models used to predict these shifts may overlook the natural dynamism of species assemblages. Historic datasets are a valuable means of understanding real-world changes in avian communities. In 2013, I revisited sites from a unique highly detailed avian survey of Benton County, Oregon conducted in 1952 (Eddy 1953). My objectives were to quantify and describe the extent of avian community change; relate observed species assemblages to changes in environmental variables; and identify species with specific associations to either survey era. Nonparametric permutation procedures identified both habitat and year as significant factors defining communities. Ordination of survey sites in species space confirmed modern avian communities were significantly different from their historic counterparts. However, sites underwent relatively little change in vegetation and land use cover between survey eras. Indicator species characterized changes in regional abundances as well as differences in survey methodologies between eras. These results suggest avian communities are naturally dynamic even in areas with relatively stable habitat conditions. Additional factors, such as vegetation structure and composition should be considered when predicting future shifts in species assemblages.

Introduction

Scientists use bioclimatic niche models, known as species distribution models (SDMs), to anticipate how future climatic and vegetation changes may drive range shifts in birds. These models are based on individual species' climatic requirements, which are assumed to be a derivative of that species' fundamental niche (Hutchinson 1957). SDMs have wide variety of functions, and are used to predict range shifts, habitat relationships, and community composition (Araújo et al. 2004, Azeria et al. 2006, Huntley et al. 2008, Lawler et al. 2009, Moritz et al. 2008, Pearson et al. 2004, Rotenberry and Wiens 2009, Stralberg et al. 2009, Thomas et al. 2004). While useful, SDMs simplify ecological

processes and often fail to account for species interactions or incomplete occupancy of an environment (see Pearson and Dawson 2003 and Sinclair et al. 2010). Even the best fitting models can fail to predict observed long-term changes in species distributions (Araújo et al. 2005, Rotenberry and Wiens 2009).

One major assumption of predictive models is that the relationship between species and habitat characteristics is static. It is assumed species have a fixed set of environmental requirements and conditions in which they can persist, and that species will continue to occupy their observed niche into the future. Yet there is little evidence that the limited range of “suitable” environmental conditions assumed by SDMs do not change over time (Guisan et al. 2002). Historic habitat conditions, site tenacity, and changes in food supply or nesting site availability all influence species responses to environmental change (Devictor et al. 2008, Hitch and Leberg 2007, Knick and Rotenberry 2000). Most models ignore behavioral and niche plasticity: the ability to occupy different, even novel environmental conditions over space and time. Behavioral plasticity has been observed in a wide variety of taxa, from fish (Werner and Hal 1976) to lizards (Schoener 1975), and even birds (Alatalo et al. 1986, Diamond 1969).

Given some plasticity in the way species associate with their environment, it may be inappropriate for predictive models like SDMs to assume niches are fixed. Recent evidence indicates a complex mix of ecological and biological factors create dynamic, individualistic responses to habitat change that are frequently unpredictable (Beale et al. 2008, Kokko and López-Sepulcre 2006). Species expected to shift ranges in response to habitat change may fail to do so under certain circumstances (Schoener 1975). Biological communities may change even with little to no environmental variation (Curtis 2014, Parody et al. 2001, Shultz et al. 2012). The assumption that species-habitat relationships do not vary temporally requires further testing using empirical datasets for both individual species and entire communities.

Historic datasets provide a means of examining changes in species-environment relationships over time. Paired with past climate data and vegetation characteristics, historic datasets expand our understanding of how birds distribute themselves within

environments. Historic datasets provide a longer temporal baseline for comparisons of community change, and – with enough detail – can even be used to validate assumptions of predictive models (Tingley and Beissinger 2009). Modern nonparametric ordination techniques allow us to test whether different groups of species distribute themselves differently within the environmental space along gradients of time and/or space. Nonparametric comparisons of species assemblages grouped by year allow a holistic, similarity-based assessment of changes in community composition between historic and modern periods. Contemporary indicator species analysis identifies species characteristic of a given survey period. Differences in indicator species between years may exemplify larger shifts in community structure and composition. Together, historic data and modern statistical methods can begin to assess whether the ecological assumptions of SDMs are appropriate.

This study aims to evaluate the nature of avian community compositional change along environmental and temporal gradients using a rare, highly detailed historic avian dataset (Eddy 1953). This dataset is uniquely valuable to understanding how avian communities in the Willamette Valley changed in the past 60 years. My objectives were: 1) to quantify and describe the extent of avian community change between 1952 and 2013, 2) relate observed changes to changes in environmental variables, and 3) identify indicator species with specific associations to either survey era. Using advanced nonparametric ordination techniques, I assessed whether the distribution of the avian community within the environmental space varied temporally. Indicator species analysis was used to identify species that differentiate historic and modern surveys across all sites. I also explored the effects of detection type and rare or poorly detected species on the observed species assemblages. Ultimately, this research provides insight into long-term variation in avian communities in the face of environmental change and anthropogenic activity.

Methods

Study Area and Data Collection

In 1952 Richard Eddy, a master's student in the Oregon State University department of zoology, conducted avian surveys at six sites within 50km of Corvallis, Oregon (Eddy 1953). These habitats were as follows: coniferous, marsh, mixed deciduous, oak woodland, and Willamette River (Appendix A). One site representing “brushy” habitat could not be relocated and was omitted from modern surveys and analysis. Eddy non-randomly selected six survey sites to represent six primary habitats in the region and ranged from 10 to 20 hectares (Table 3.1). The original methods involved walking through a given site for two hours between 0500 and 1000, recording the number and species of birds visually observed. Eddy repeated this process 10 times for each of the six sites. Because surveys 6-10 for each site occurred after the breeding season, when detection probabilities decline, these data are unreliable. Paired t-tests confirmed the last five visits to each site did not contribute significant additional data to the dataset (Appendix B). Therefore, I omitted the last five historic surveys to each site from analysis.

Modern Avian Surveys

I relocated each survey site as accurately as possible using Eddy’s site descriptions and aerial photographs of Benton County taken in 1956 (US Department of Agriculture, Farm Service Agency 1956; Appendix A). I used ArcGIS (ESRI 2013) to designate site boundaries and overlaid a 200m square grid aligned with the longest axis of the site. For sites where historic placement was uncertain, I designated “likely areas” adjacent to the selected survey area. These areas met Eddy’s site descriptions and may have been surveyed in 1952. “Likely areas” were later used to confirm site placement did not unduly influence results. Using a protocol derived from Bibby et al. 2000, I spot mapped each of the five sites five times during the 2013 breeding season (mid-April to mid-July). The number, species, behavior, and location of each bird detected (visually or aurally) was recorded on a site map, and then entered onto digital maps using ArcGIS. I implemented a secondary point count protocol to enhance reproducibility of these surveys and to compare within-site avian communities to those of the “likely areas” (Appendix B).

Differences in observer ability and changing survey conditions may influence the probability of detecting species (Tingley and Beissinger 2012). To evaluate changes in detection probabilities between survey eras, I used package “unmarked” (Fiske and Chandler 2011) in program R (R Core Team 2013) to calculate simple estimates of detection probability for each species using only the historic dataset (Appendix F). I identified the best fitting model based on historic species abundances across all site visits. The first was a basic model with no covariates. The second detection model included a single covariate for survey date, and the third included a single covariate for habitat. Unfortunately, more advanced models of detection probability with multiple covariates were unviable due to the small number of study plots. I used package unmarked’s (Fiske and Chandler 2011) model selection tool in Program R to choose the best detection probability model for each species based on AIC values. The selected best-fitting model was then used to estimate the detection probability of that species for both modern and historic survey periods. I did not adjust abundances by detection values, though probabilities were used to confirm there were no salient differences in species detectability between years.

Environmental Variables

I also collected supplementary environmental data for each site (Table 3.2). Eddy (1953) provided information regarding general location, size, and vegetation characteristics for each site (Appendix A). The percent cover of different land use and vegetation classes were calculated for each site based on visual classification using the National GAP Analysis Program’s classification system (US Geological Survey 2012; Appendix D). Classification of historic habitat cover values was conducted using high-resolution APFO aerial photographs from 1956 (US Department of Agriculture, Farm Service Agency 1956). Modern habitat classification was performed using imagery from the National Agriculture Imagery Program (NAIP; US Department of Agriculture, Farm Service Agency 2012). The mean elevation, exact area in square meters, and percent cover of each land use and vegetation classification for each site were calculated using

ArcGIS (ESRI 2013). Percent cover values were compared between years to identify any changes in habitat cover for each site.

Statistical Analysis

My response variable was the mean abundance of each species per site visit for a given year. Mean species abundance per visit ranged from 0.1 to 213.4 (Red-winged blackbirds; see Appendix C for scientific names). The initial species dataset contained response variables for all species visually detected at 10 sampling units (5 historic sites, and 5 modern resurveys). A secondary species dataset contained the mean abundances for species at the 10 sampling units observed using all detection types. Because species with low or abnormal detection probabilities were believed to have unreliable abundances and could influence conclusions, I created a tertiary dataset where species with detection probabilities of less than 0.05 or equal to 1 were removed. Such very rare and very common species are poorly fit by the models, and may distract from species whose abundances changed over time due to factors other than detection probability. The matrix of environmental variables contained values for mean elevation, area in square meters, and percent cover of each vegetation and land use class, as well as categorical variables for year and site.

Before proceeding with analysis, I transformed the data to meet the assumption of linearity inherent in many statistical tests. Data transformations and analyses were conducted in PC-ORD 6.12 (McCune and Mefford 2011). Examination of the initial species matrix revealed a high degree of variation in the data ranging from a few highly abundant species to several species with very low abundances. Rare species, defined as those species detected in less than two surveys for a given year, were removed. This reduced noise produced by species that likely did not occupy the study sites during the breeding season. I then performed square root transformations on the response variable to reduce the influence of species with particularly high abundances. The square root transformation was more appropriate than a log transformation because even the highest abundance values did not need strong adjustment, and I did not wish to modify the relatively large number of zero values in my dataset. These zero values would be

undefined in a log transformation and require special treatment (McCune et al. 2002). Relativizations were considered but not performed on the dataset because the differences in abundance between common and rare species were considered important biological information

To identify potentially influential outliers among the sampling units, I examined the average distances of sampling units from the grand mean of distances between sampling units using several distance measures. One sampling unit was identified as having distances more than two standard deviations from the grand mean using Euclidean Distance (1952 marsh site, approximately 2.5 standard deviations from the mean). Visual inspection of the ordered main matrix showed this site had relatively little overlap in species composition with other sites and contained several species with high abundances that were not encountered elsewhere during the study. There was no reason to suspect this sampling unit would have undue influence on the ordinations, nor was it outside the normal range of variation in abundances. I retained this sampling unit for analysis.

Multi-response Permutation Procedures (MRPP; Mielke 1984) were used to test for differences in species composition across sites between groups, where each group was a study year (1952 or 2013). The A-statistic derived from MRPP is a value of within-group chance corrected homogeneity, a useful measure of overall group similarity (McCune et al. 2002). High A-values indicate that members of a group are more similar to each other than to members of other groups. This suggests the system used to group communities of species is appropriate. I performed MRPP analysis using the Sørensen distance measure, which considers differences between units based on proportional abundances. To test for within-site differences between years, I used Permutational Multivariate Analysis of Variance (PerMANOVA; Anderson 2001) using the Sørensen distance measure, the fixed group as year, a random factor for sites as blocks (randomized block design), and 4999 permutations. PERMANOVA provides quantitative measures for the effects of site and year in nonparametric data via pseudo-F statistics and p-values from permutation tests. Because of the small size of these data, I decided to verify the PerMANOVA results using a similar test: Blocked MRPP (MRBP). Blocked

MRPP answers the same questions as PerMANOVA, but uses a different procedure structured around MRPP analysis. Blocks were defined by sites, and groups were defined by year. For MRBP, I selected median alignment in order to investigate correlations between sites outside of exact matches. Since Sørensen distance is not compatible with the negative values produced by median alignment, Euclidean Distance was used (McCune et al. 2002).

Indicator Species Analysis was performed to assess species-specific associations across sites for a particular survey year (Dufrêne and Legendre 1997). Indicator Species Analysis utilizes proportional species abundances and frequencies within a priori groups. Results include indicator values (IV) between 0 and 1 for each species in the community. These IV scores reflect the strength of association between species and groups based on species abundance and overall prevalence. I similarly used Blocked Indicator Species Analysis to identify species that best represented individual sites within groups of years. To test the statistical significance of the IV scores, I performed analyses for 4999 random permutations and obtained a p-value obtained for each IV. Species with high observed IV scores and significant p-values (< 0.05) were considered indicative of that survey year.

Species and sites were ordinated in species space using Non-metric Multidimensional Scaling (NMS). NMS is an iterative ordination procedure that seeks monotonic, or “low stress”, configurations based on ranked distances among sampling units (Kruskal 1964). Unlike Principal Component Analysis, NMS does not assume linear relationships between species responses and environmental gradients (McCune et al. 2002). I performed NMS using the Sørensen distance measure on random starting configurations for 50 runs on both real and randomized data. Ties were not penalized. The Sørensen distance measure was selected because it provides a fixed maximum distance value for sampling units that have no species in common; this is considered a biologically intuitive and useful attribute (McCune et al. 2002). A randomization procedure was included to test if the axes extracted in the final configuration were stronger than those obtained by chance. I extracted R^2 values for each axis in the final configuration to represent the correlation between distances in the original and resulting

k-dimensional ordination spaces. Pearson and Kendall correlation coefficients were also calculated among environmental variables and the ordination axes.

Finally, to quantify the effect produced on ordinations by omitting non-visual detections and species with poor detection probabilities, I compared NMS ordination scores among the primary dataset and two supplementary datasets (those with non-visual and poorly detected species removed) using the Mantel's asymptotic approximation method (Mantel 1967). The standardized Mantel statistic (r) ranges from 0 to 1, with higher values indicating stronger correlation structures between matrices (i.e. between distance matrices for data including rare species and data omitting rare species). A randomization test provided a p-value for the Mantel test statistic.

Results

I used NMS to define the environmental space in which the historic and modern avian communities were oriented. NMS results help illustrate the relationship between species composition and environmental variables. The NMS ordination of species abundances converged on a stable, 2-dimensional solution (final stress = 4.46, final instability = 0.0000) with a cumulative R^2 of 0.86 (Figure 3.1). Environmental variables associated along axis 1 included cool montane forest, higher elevation, and evergreen trees on one end, and wetlands and grasslands on the other. Thus, axis 1 represented an environmental gradient of vegetation from lower elevation wetlands and marshes to higher elevation coniferous forests. Year had a strong positive correlation with axis 2 ($R = 0.886$), such that more recent surveys were higher on the axis. This axis also defined a slight gradient along percent cover grass and shrub vegetation, though these variables were not strongly correlated with any axis. Axis 1 accounted for 63.7% of the variation in the species ordination space, while axis 2 accounted for another 22.2% of the variation. Both axes exhibited convincing evidence of correlation with the data stronger than what was expected by chance (p-values = 0.02). Table 3.3 contains a summary of Pearson and Kendall correlations between environmental variables and the final ordination axes.

There were notable differences in the ordination of sites based on species composition between years. Each site occupied a different area of the species ordination space, with some overlap near the center (Figure 3.1). Historic survey areas tended to be more associated with grass/shrub type habitats. Higher elevations and montane evergreen forests characterized the coniferous site. By contrast, the marsh site was best characterized by wetland and, to a small degree, grass cover. Modern site conditions tended to be similar to historic habitat conditions, as evidenced by the relatively vertical orientation of temporal lines connecting historic and modern sampling units (Figure 3.1). The marsh, mixed deciduous, and Willamette River sites experienced a small amount of land use and vegetation cover change over the 60-year period. The modern mixed deciduous site was less associated with shrub and forested habitat. Both the modern marsh and Willamette River site shifted along the first axis in the opposite direction; in modern surveys, these sites experienced a decrease in percent cover of grass. The coniferous site experienced the largest amount of change in species assemblage, followed closely by the oak woodland site.

My primary objective was to quantify the extent of avian community change between 1952 and 2013. I tested for significant differences in avian communities between survey eras using MRPP. There was convincing evidence of differences in species assemblages between historic and modern surveys ($p = 0.045$, $A = 0.0472$). PerMANOVA found suggestive evidence for differences in species composition between years after accounting for variation among sites ($F = 3.41$, $p = 0.061$). There was also strong evidence for differences between sites after accounting for year ($F = 2.68$, $p = 0.016$). The variation among sites was comparable to the variation among years (Site mean sum-of-squares = 0.348, Year mean sum-of-squares = 0.443). Because the p-value for the effect of year on community composition was close to the 0.05 significance threshold, I chose to report the MRBP results as well. Blocked MRPP found significant differences in species composition between years when considering paired sites ($p = 0.018$, $A = 0.0744$). This supported PerMANOVA results that individual site

characteristics were important to observing differences in community composition between years.

My final objective was to identify species that distinguished historic and modern survey periods. Indicator Species Analysis identified several species that significantly differentiated across-site communities for each survey era (Table 3.4). Species identified as indicators were common and found in all habitat types. Turkey vulture, White-breasted nuthatch, and Western tanager were indicative of the historic surveys. Indicator species for the modern surveys were Rufous hummingbird, Brown-headed cowbird, Black-headed grosbeak, and House finch. These species were ubiquitous and abundant both locally and regionally for the eras in which they were identified as indicators. When I performed Blocked Indicator Species Analysis among sites grouped by year, I found no statistically significant indicator species (those with $p < 0.05$). However, several species had large observed indicator values that approached significance (Table 3.4). For the historic period, these were Spotted Towhee and Turkey Vulture. Indicators species approaching significance for modern surveys included American Goldfinch, Rufous Hummingbird, and Black-headed Grosbeak. Blocking appears to reduce the statistical power of the analysis and may be partially responsible for the lack of significant indicator species in this small dataset.

Finally, I compared NMS scores to confirm removing poorly detected species and non-visual detections did not influence results. Mantel tests for three comparisons of NMS scores found strong correlation between ordinations. Ordinations were highly redundant, indicating strong overlap in configuration. Between transformed matrices including and omitting non-visual detections, the percent redundancy was 91.4 and the Mantel statistic of similarity was 0.956. Between the transformed matrix of visual detections and the same matrix with poorly detected species removed, the percent redundancy was 91.6 and the Mantel statistic was 0.957. There was convincing evidence these correlations were stronger than expected by chance ($p < 0.001$). I concluded that omitting rare species, poorly detected species, and non-visual detections did not significantly influence NMS results. Among NMS ordinations, the configuration derived

from average abundances for visual detections with rare species removed had the lowest final stress (final stress = 4.904, $p = 0.02$), therefore I used that species matrix to draw conclusions.

Discussion

Avian community composition in Benton County, Oregon changed significantly between 1952 and 2013, despite relatively little changes in habitat characteristics. Species assemblages were different across time as well as between habitats. Observed groupings of species within the ordination space agreed with their general habitat associations. NMS clustered birds around appropriate habitat and environmental variables within the ordination space, with marsh and wetland birds on one end of the axis, and coniferous forest birds on the other end. However, the communities associated with each of these habitats were dynamic; 60 years after the original surveys, different groupings of birds were associated with each site.

The underlying drivers of such community dynamism include changes in abundance, the arrival of new species, and species turnover. Multiple indicator species distinguished each survey year because they were comparatively more prevalent for one survey period than the other. These species may be representative of an overall change from one species assemblage to another. Widespread changes in abundance as formerly common species – such as Chipping Sparrow, Nashville Warbler, and House Sparrow – became rare, shifted modern communities away from their historic counterparts. Furthermore, I observed several new species, including Brown-headed Cowbird, European Starling, and House Finch, across most habitats. These species further differentiated modern and historic communities.

I identified indicator species to help characterize historic and modern avian communities. Many of these indicator species demonstrate notable changes in abundance between survey years locally and regionally. Historic indicator species, including Turkey Vultures and White-breasted Nuthatches, are known to be in decline today (Sauer et al. 2014). Conversely, American Goldfinches, Brown-headed Cowbirds, and House Finches

– all indicators of modern avian communities – are increasing regionally (Sauer et al. 2014). The remaining indicator species may be the result of differences in survey methodology. Western Tanagers and Spotted Towhees were identified as historic indicator species. However, these species were also common during modern surveys (Curtis, unpublished data). Their status as indicators likely arises because they were not frequently visually detected in 2013. Likewise, Black-headed Grosbeaks and Rufous Hummingbirds were ubiquitous, abundant indicator species for the modern surveys. It is likely these species were as abundant in 1952 (Sauer et al. 2014), but not commonly visually detected by Richard Eddy. Despite these few indicator species resulting from survey differences, the majority still represent a shift in avian species assemblage over the past 60 years.

Species Distributions in Environmental Space

It is not always necessary that physical changes in the environment precede changes in species distributions. In this study, avian communities at each site were significantly different along a temporal gradient, but sites did not vary along the environmental gradient. Survey areas tended to remain in the same environmental space, though species did not. Sites with the largest amounts of community change along a temporal gradient, such as the oak woodland and coniferous areas, experienced relatively little change along an environmental gradient. The marsh and Willamette River sites experienced greater changes in habitat cover (represented by shifts along the first ordination axis), but had less distance between communities along the temporal gradient. Species distribution models that assume species distributions are driven by climate, urbanization, or habitat availability might predict communities in these areas to remain unchanged, given little change to the surrounding environment. Such predictions would not match observed patterns in community composition

One goal of this study was to evaluate whether species associations with the environment do not change over time. Predictive models of species distributions take for granted that species will continue to inhabit the same ecological niches decades into the future. This assumption is necessary in order to predict how changes in climate or

vegetation will alter future species distributions or community structure (Guisan et al. 2002). However, the way species actually distribute within their environment can be plastic and not easily predicted (Beale et al. 2008, Kokko and López-Sepulcre 2006). For example, given stable ecosystem productivity, species turnover may result in reduced competition and allow species to expand into novel habitats (Alatalo et al. 1986, Blondel et al. 1988). Species may occupy different niches simply due to the presence or absence of other species (Werner and Hal 1976), or may exhibit differential responses to environmental change based on physical and life history characteristics (Hill et al. 1999, Sol and Price 2008).

Some of the observed variation in species assemblage may be attributed to vegetation growth and canopy closure. In 1952, the lower portion of the coniferous site was burned and possessed a relatively open canopy (Eddy 1953). However, by 2013 mature Douglas fir trees covered almost the entire site. The canopy grew and matured over 60 years while the overall percent cover of environmental variables was remained stable. For the oak woodland site, the relative percent covers of different vegetation and land use classes were similar over time, but tree growth and canopy closure altered vegetation structure, likely changing the avian species assemblage. An additional factor to consider for the oak woodland site is the encroachment of urban development. In 1952 the oak site was almost a mile from the nearest residential development. By 2013, nearly half the survey area was directly adjacent to apartment complexes. This recent urban development likely influenced the species composition even if within-site habitat remained unchanged.

This study does not take into account changes in vegetation structure, density, or complexity. It is possible that these unmeasured vegetation variables are more closely associated with community changes than land use and vegetation class (Seavy and Alexander 2011). Even though the marsh and Willamette site experienced greater changes in percent habitat cover than the oak and coniferous sites, their overall vegetation structure or complexity may have remained relatively stable. Meanwhile, the oak and coniferous sites experienced vegetation structure change, which may have influenced the

observed differences in avian community composition over time. It is difficult to test this without detailed historic vegetation data. While extensive LiDAR data exists for modern landscapes, historic vegetation data is scarce.

Methodological Differences

I took several steps to reduce the uncertainty associated with the historic dataset (Appendix B). When site boundaries were uncertain, I used two-sample t-tests comparing within-site diversity to adjacent areas to ensure site placement did not influence survey results. Sample-based species accumulation curves showed historic and modern surveys were equally thorough at documenting species assemblage (Appendix B, Figure B.1). There was little evidence additional surveys would contribute meaningful information to the modern dataset. Though I assumed constant detection probabilities, the effect of changing detection probabilities on the data is unknown. However, Mantel tests of similarity confirmed removing poorly detected species or species whose abundances may have been influenced by detection type had little effect on results. When non-visual detections were included in the ordination, each underwent a similar amount of community change over time. Given the limitations of this dataset, it may not be possible to determine conclusively the driving factors behind the observed changes in avian community composition. Yet the results remain clear: changes in vegetation type and land use do not match observed changes in avian communities. Other drivers of community change should be considered.

After accounting for potential differences in methodology, several remaining factors could influence observed species assemblages. It is possible interspecific competition, changes in regional community composition, and vegetation structure and assembly contributed to the observed differences between historic and modern avian communities. Future studies should incorporate these additional factors into analyses to determine their influence on community composition over a long temporal scale. Another consideration may be whether species that show less affiliation to certain habitat types (i.e. habitat generalists) contribute more to community changes over time. Species capable of inhabiting a broader range of habitats types may expand their ranges

comparatively more quickly, producing community turnover as they move into new areas. These factors are not accounted for in species distribution models (Pearson and Dawson 2003, Sinclair et al. 2010, Wiens et al. 2009). Their effects may vary among individual species and along different spatial extents. This would produce communities different from those predicted based on associations with vegetation cover alone.

Conclusion

While it has been established that avian communities experience high levels of change over time, relatively few datasets are able to quantify community change across more than two or three decades, much less across multiple habitat types (Parody et al. 2001, Shultz et al. 2012). This study was able to examine over 60 years of changes in bird communities in five different habitats. Site-specific avian communities were different over time, but did not appear to shift along an environmental gradient, as would be expected if vegetation or land use change were driving differences in species assemblage. Many ecologists rely on species distribution models to predict future species distributions (Araújo et al. 2005, Huntley et al. 2008, Lawler et al. 2009, Thomas et al. 2004, among others) or community composition (Stralberg et al. 2009). However, these models assume the way species distribute themselves within the environment is fixed and directly linked to vegetation type, which does not appear to be true for this research. Results from this study suggest further investigation into the drivers of community change is needed.

Despite the limitations of this study, the observed changes in avian community composition are ecologically important. Historic datasets provide an important avenue towards understanding long-term changes in biodiversity, and Richard Eddy's (1953) dataset is uniquely valuable to understanding historic avian communities in the Pacific Northwest. Historic datasets present an excellent resource for scientists attempting to predict how communities will change under the influence of global climate change. This study creates a complex picture of the associations between species assemblages and their environment, demonstrating how dynamic and difficult to characterize biological communities can be over long periods.

Tables and Figures

Table 3.1. Overview of study sites. Table includes primary habitat type, area in hectares, and both historic and modern species richness. Species richness is the total number of species observed across five survey visits using visual detections only.

Site	Primary Habitat	Area (hectares)	Historic Richness	Modern Richness
Coniferous	Coniferous forest	14	32	19
Marsh	Emergent wetland vegetation	20	34	51
Mixed Deciduous	Open mixed-species deciduous forest (oak and beech)	8	32	36
Oak Woodland	Oak forest with some conifers	14	25	31
Willamette	Flooded riparian forest	10	27	36

Table 3.2. Abbreviations and descriptions of environmental variables used. “Type” indicates whether the variable referred to a specific land use or vegetation class, or was a general quantitative variable.

Abbreviation	Type	Description
Year	General	Year of survey
Habitat	General	Categorical variable of habitat type (one per site)
Elev	General	Mean elevation in feet
Size	General	Area of site in acres
Deciduous	Land Use	% cover of deciduous forest
Evergreen	Land Use	% cover of evergreen forest
Mixed	Land Use	% cover of mixed forest types
Grass	Land Use	% cover of grass vegetation
Shrub	Land Use	% cover of shrub-type vegetation
Wetland	Land Use	% cover of marsh, swamp, and/or wetland
Pasture	Land Use	% cover of land used for livestock grazing purposes
Water	Land Use/Veg	% cover of open water, both running and still
Urban	Land Use/Veg	% cover of urban development (buildings, roads, etc.)
WarmForest	Vegetation	% cover of warm, temperate, and lowland forest
CoolForest	Vegetation	% cover of cool, upland and coniferous forest
FloodForest	Vegetation	% cover of riparian and flooded forest
GrassShrub	Vegetation	% cover of mixed grassland and shrub
Agri	Vegetation	% cover of land used for agricultural crops
Disturbed	Vegetation	% cover of recently disturbed open land

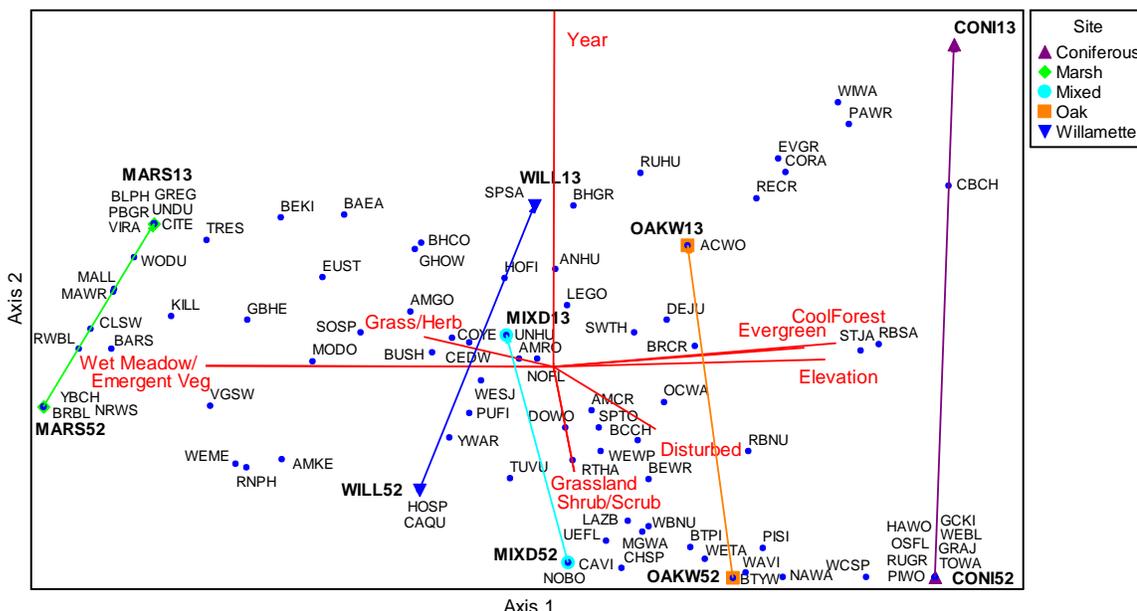


Figure 3.1. NMS ordination of species and sampling units in species space. Species are represented by blue dots and sampling units by colored icons. Numbers after the four letter site codes indicate survey year. Temporal lines colored by site connect historic and modern surveys. The length of these lines corresponds to the degree of avian community compositional change between years. Sites and species near the bottom of the graph are more associated with historic surveys. Environmental variables with r^2 values > 0.2 are displayed as a joint bi-plot with vector lengths corresponding to correlation strength along that axis. Vectors adjacent to each axis indicate the gradient in environmental variables with strongest correlations for that axis. See Appendix C for species common and scientific names and codes.

Table 3.3. Strongest Pearson and Kendall correlation coefficients. Correlation coefficients calculated between environmental variables and the 2-dimensional NMS configuration of sampling units in species space.

Variable	Axis	r	r ²	tau
CoolForest	1	0.788	0.621	0.762
Elevation	1	0.773	0.597	0.707
Evergreen	1	0.743	0.552	0.609
Wetland/Emergent Veg	1	-0.874	0.764	-0.835
Grass	1	-0.533	0.284	-0.365
Year	2	0.886	0.784	0.745

Table 3.4. Indicator species and blocked indicator species results for species with high observed indicator values and p-values. P-values should be interpreted with caution given the low statistical power of analyses on small datasets such as this.

Type of ISA	Species	Year of max. association	Percent indicator value	p-value
Unblocked	Turkey vulture	1952	83.9	0.0072
Unblocked	Western tanager	1952	80.0	0.0486
Unblocked	White-breasted nuthatch	1952	69.6	0.0486
Unblocked	Black-headed grosbeak	2013	100.0	0.0072
Unblocked	Rufous hummingbird	2013	100.0	0.0072
Unblocked	Brown-headed cowbird	2013	80.0	0.0424
Unblocked	House finch	2013	80.0	0.0424
Blocked	Turkey vulture	1952	86.1	0.0614
Blocked	Spotted towhee	1952	72.1	0.0614
Blocked	Black-headed grosbeak	2013	100.0	0.0614
Blocked	Rufous hummingbird	2013	100.0	0.0614
Blocked	American goldfinch	2013	80.4	0.0614

Chapter 4: General Conclusion

Preserving Data Functionality

In this research, I investigated long-term changes in avian communities using a historic dataset from 1952 (Eddy 1953). Igl and Johnson (2005) list a number of criteria to consider when repeating historic surveys. The original survey methods and study design should be followed as closely as possible. While historic documentation may not allow for exact repetition of survey methods or accurate relocation of survey sites, approximating them as closely as possible minimizes bias associated with the resurveys. Modifications to the study objectives or methodology can be considered so long as they do not compromise comparisons between the two datasets (Igl and Johnson 2005). In this research, I made efforts to replicate both Richard Eddy's survey efforts and study sites. When sites could not be accurately relocated, I compared within-site diversity to diversity in similar, "likely areas" to confirm that incorrect site placement did not influence results. Some degree of bias is still to be expected due to uncontrollable differences in observers and conditions between survey periods (Igl and Johnson 2005, Tingley and Beissinger 2009). Because I took precautions to maximize the strength of comparisons between years, concerns about long-term conclusions based on two data points in time can be assuaged.

We have more ecological data now than we could possibly have imagined 60 years ago. New technology and well-developed survey protocols allow us to better understand and appreciate complex ecosystems. As years pass, the amount of accessible scientific data will grow exponentially. Even the most cutting-edge data will eventually be historic and useful for long-term study. Therefore, it is necessary to implement methods that will extend these data's accessibility for as long as possible. I made efforts to improve the scientific strength of this study for future generations. While Eddy (1953) implemented an area search protocol, I chose to spot map sites instead. Spot mapping collects the same abundance data as that of Eddy (1953), but also records the geographic location of birds within each site. Future researchers can examine whether or not birds shift their distribution within each site on a fine scale. A secondary point count protocol

further enhances the reproducibility of this research. Point count protocols are exactly repeatable and points can be precisely relocated using latitudinal and longitudinal coordinates (Ralph et al. 1998). Where point counts were difficult to access, a potential problem confronting future surveyors, I designated additional point count locations located on publicly accessible trails and paths.

One challenge to identifying and utilizing historic data is the rapid rate at which scientific data becomes lost. A recent study suggests the odds of biological data remaining extant and available decreases by 17% each year after publication (Vines et al. 2014). After 20 years, nearly 80% of biological data was inaccessible due to technologically obsolete storage devices or outdated contact information. Stringent data archiving policies vastly improve the odds of finding accessible scientific data (Vines et al. 2013). Metadata, or supplementary “data about data”, is a crucial element that allows future researchers to understand content and structure of a dataset. Well-documented metadata extends the temporal usefulness of a dataset to future researchers. All information collected in conjunction with this research, including metadata, will be digitally archived with a high level of detail (Appendix I). By incorporating historic data into new research, we bring it into a context where it can be revisited by future generations.

Sixty Years of Avian Community Change

Sixty years ago, Richard Eddy repeatedly surveyed avian communities at five sites in the Willamette Valley. The detail and geographic scope of his project is unique; no other dataset of this nature is known to exist in the Pacific Northwest. Without Eddy’s historic dataset, we have scant knowledge of past avian communities in the Willamette Valley. Using Eddy’s (1953) data as a baseline, I analyzed the nature and extent of changes to the avian community over time. The results tell a rich story of species turnover and community transformation. Species composition changed dramatically over time; less than half of the species observed today were reported during the historic surveys. However, this is not necessarily cause for alarm. Some researchers express

concern that global climate change will result in novel communities with different ecosystem functionalities (Stralberg et al. 2009). Yet reports of anthropogenic causes of declining biodiversity often fail to report the amount of uncertainty associated with normal background variation in species assemblages (Magurran et al. 2010). There is evidence species assemblages are undergoing systematic change, rather than widespread loss (Dornelas et al. 2014). Species assemblages are constantly in a state of flux and may arrange into novel ways even without environmental pressure. Ordination of species in environmental space showed some species were associated with modern communities even though sites experienced little change along a gradient of land use and vegetation cover. This research is a valuable example of how strong background changes in species composition can be over the course of time.

Historic datasets are fraught with problems that make them difficult to accurately compare against (Igl and Johnson 2005, Magurran et al. 2010, Tingley and Beissinger 2009). Richard Eddy (1953) recorded visual detections only, and it is impossible to estimate how many birds he missed because he could not physically see them or identify their species. The sample size of this study is small ($n = 5$). Statistical analyses of small datasets frequently fail to reject the null hypothesis when real differences exist within the community. It is not possible to determine the causes of observed changes in community diversity and species composition, though this would be an interesting opportunity for further research. Environmental data from 1952, including vegetation structure and composition, and local climate, are lacking. It is possible that any number of unmeasured factors caused the avian community at one or more sites to change. This study provides a general indication of change and incentive for continuing research.

Despite these problems with differing methodologies, species detections, and observer bias between years, this is still a meaningful study. To omit historic data because it lacks scientific rigor is to ignore a valuable perspective into actual past conditions. It is better to accept the inherent uncertainties of historic data and account for them than it is to ignore these data entirely. Access to historic raw data is rare (Igl and Johnson 2005). To ignore Eddy's (1953) dataset because it lacks scientific rigor is to

ignore a valuable perspective into actual past conditions on a level of detail that would not exist otherwise. While conclusions may not be as precise, even general estimates of trends for a subset of historically well-detected species provides valuable information to modern ecologists and wildlife managers.

Given the growing threats of climate change, habitat fragmentation, and urbanization, it is important to understand how ecosystems change in relation to the environment. Though many large-scale, long-term population monitoring programs such as the North American Breeding Bird Survey are now in place, their spatial and temporal scopes are limited (Igl and Johnson 2005). Even the best modeled predictions and back-casting are still only estimates that require empirical data to substantiate. Only historic data provides an adequate temporal baseline for understanding long-term ecological change. This research provides an empirical example of long-term interactions between bird communities and their environment on a time scale that most existing data cannot depict. My results indicate how complex real-world community changes can be. Future research should turn to historic data to evaluate the nature and causes of avian community change over the long periods used by predictive modelling. The assumptions on the nature of species and community relations to environmental variables need to be further tested using empirical data.

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APPENDICES

Appendix A - Site Descriptions

Coniferous site (CONI)

The coniferous site is a 14-hectare plot located 4.8km west of Lewisburg, OR along a "forested ridge" in the McDonald forest (Eddy 1953). Richard Eddy's description of the site states that the southern portion of the site was "burned over" and composed of primarily shrubs. Dominant vegetation in 1952 included Douglas fir, deciduous big-leaf maple (*Acer macrophyllum*), and an understory of vine maple (*Acer circinatum*), thimbleberry (*Rubus parviflorus*), and various *Salix* willow species. The shrub species in the burned portion of the coniferous site included trailing blackberry (*Rubus ursinus*) and elder (*Sambucus* sp.).

I placed the modern site at the intersection of Sulphur Springs Road and an unmarked forest road, which provided easy access to a patch of established coniferous trees. This intersection is exactly 4.8km west of Lewisburg, Oregon. A topographical map of Benton County confirms that the McDonald forest ridge begins within the western quadrant of this intersection and continues south adjacent to the unmarked forest road. A 1956 aerial photograph of the region showed a sparsely treed area that could have been burned in the years prior to the 1952 surveys. This burned area spanned approximately 0.4 to 0.8km along the unmarked forest road. The 1956 aerial photograph indicates a patch of dense old-growth conifers stretching from the edge of this burned patch north/north-east with its westernmost boundary crossing Sulphur Springs Road approximately 0.5km north from the aforementioned intersection with the forest road. I defined the southeastern and northeastern boundaries of the site as the unmarked forest road and Sulphur Springs road, respectively, and the edge of the old growth patch formed the western boundary. This created a triangular site approximately 14.5 hectares in size. Because there were no other areas along the McDonald forest ridge 4.8km from Lewisburg with a burned area at the southern end, I am reasonably confident about the general placement of this site. Nevertheless, there remains some uncertainty about exact site boundaries and whether the site should be extended further west or north along the forest road.

Marsh site (MARS)

The marsh site is located at McFadden Marsh in the Finley National Wildlife Refuge. In 1952, one side of the site was lined with Oregon white oak, Big-leaf maple, and Oregon ash (*Fraxinus latifolia*). Herbaceous vegetation at the marsh site included cattails (*Typha latifolia*), bulrush (*Seirpus californicus*), and sedges (*Carus oregonensis*). Fortunately, the name of this site has not changed since 1952. McFadden Marsh is approximately 18.5km south of Corvallis, and 1.3km west from Highway 99 along Bruce Road. In 1952, 20-hectare section of this marsh was surveyed, of which 2 hectares were open water. McFadden marsh extends both north and south of Bruce Road, however only the northern section has a large enough patch of open water to match the 1952 site description. A berm stretches across the marsh 0.8km north of Bruce Road and is visible in 1956 both aerial photographs and today. Agricultural fields border the marsh to the east and a walking path along mixed oak and riparian woodlands borders it to the west. These oak woodlands contain a marshy stream also reported by Eddy in 1952. The area of McFadden marsh between the northern berm and Bruce Road is approximately 22.6 hectares. While this is larger than Richard Eddy's estimate, based on the 1956 aerial photographs it is hard to determine a specific 20-hectare portion of the marsh that he would have surveyed. It is more likely that he made a general estimate of the survey area and was off by 2 or 3 hectares. I am very confident about this site placement because it meets the 1952 descriptions, is well defined on all sides by geographic features, and has retained its name from the original surveys. No other site nearby met these requirements.

Mixed Deciduous site (MIXD)

This is an 8-hectare site "just below and to the west of the oak area" (Eddy 1953). Eddy describes "a small stream [running] through the center of the area". The mixed deciduous site had a variety of canopy trees including Oregon white oak, Big-leaf maple, willows, alder (*Alnus* sp.), wild cherry (*Prunus emarginata*), and hawthorn (*Crataegus douglasii*). The primary shrub species for the mixed deciduous site were wild rose and poison oak. Two such sites meet that description, one south of Harrison Blvd. almost directly to the south of the oak woodland site. The other is on the north side of Harrison

Blvd., to the west of the OSU poultry facilities and almost adjacent to the oak woodland site. The southern site has Oak Creek running through it, while the northern site contains an unnamed stream, which becomes a moist, marshy area before it meets Oak Creek. Eddy depicts the site as "surrounded on three sides by pasture land, and on one side by a typical oak woodland." (Eddy 1953). According to 1956 aerial photographs, only the northern site meets this description; the southern site had farmlands on all four sides. The mixed deciduous woodlands are clearly defined by the presence of agricultural lands. Where the site meets the oak woods to the north and northwest, the 1956 aerial photographs show a clear transition from low, sparse trees and shrubs to established oaks. Today 53rd street runs through this northern section and divides approximately 2.4 hectares from the rest of the site. These two sections together create an area that would have been approximately 8.9 hectares in 1956. I am very confident about this site placement because there is no other woodland that matches the description given in Richard Eddy's thesis.

Oak Woodland site (OAKW)

This is a 14-hectare site 1.6km "west of Corvallis on a hillside behind and to one side of a Turkey farm along Harrison Street" (Eddy 1953). Along with Oregon white oak, the oak woodland site included both poison oak (*Toxicodendron diversilobum*) and wild rose (*Rosa* sp.). The modern Oregon State University poultry facilities are 1.9km west of the university campus along Harrison Boulevard, so it is likely this was the turkey farm referred to in the original thesis. A hillside begins approximately 0.8km directly north of the poultry facilities. Dense oak woodlands cover area, known as Witham Hill. An aerial photograph of this area shows that oaks covered only the eastern half of the hill in 1956; a distinct property line runs between the middle of the hillside, dividing older, dense oak woods on the right, and a sparse, shrubby area on the left. Using the 1956 aerial photograph as a guide to select only the oak woodlands on the western portion of the area (and extending southeast at the bottom of the property line) produces a zone approximately 14.6 hectares in size. This zone of established oaks is therefore the likely location of the "oak woodland" site surveyed in 1952. Because this area was the only oak

woodland within 3km of Corvallis in 1956, and happens to be on a hillside behind a poultry farm, I am confident about the placement of this site. There is a possibility that some of the shrubby eastern portion of the hill may have been surveyed.

Willamette River site (WILL)

In 1952, the Willamette River site was located at a place called "Murphy's Beach", though no such site exists with that name today. Richard Eddy describes the 10-hectare site as 3.2km south of Corvallis with a "ten to fifteen foot gravel shore between the bank and the water". However, it is difficult to determine whether Eddy was referring to the entire site with this description. "Most of the area was covered in tall grass" during the historic survey period (Eddy 1953). The Willamette site possessed a dominant canopy of Douglas fir and Big-leaf maple, and a shrub layer of red alder (*Alnus rubra*), elder, wild rose, and evergreen blackberry (*Rubus laciniatus*), as well as herbaceous thistles (*Cirsium* sp.). The Crystal Lakes Sports complex and Kendall Natural Area is approximately 4km south of Corvallis. According to 1956 aerial photographs, the more northerly area of this riverbank was a grassy floodplain with a 3-3.5m bank and a border of established forest along the eastern edge. The southern area was almost entirely oak woodlands with a distinct 3m gravel bank. An examination of Eddy's 1952 species detections shows a number of grass-associated birds such as Lesser and American Goldfinches, but not as many forest-associated birds like Swainson's Thrush. Therefore, I assume that the site with more grass (the northern option) is the likely candidate. It is probable the southern option would not have produced the same assortment of species observed in 1952. The northern site had an access road running along the western edge, with a boat ramp near the top. Using the river and access road as boundaries produced a site 10.1 hectares in size, supporting my site placement.

Brushy Area site

I omitted this site from the modern surveys because I could not identify a single likely location for the site. Richard Eddy describes the site as a 12 hectare region 9.6km "south-east of Corvallis along the Peoria road". In 1952, a "small swampy creek" ran

along the southern boundary of the site (Eddy 1953). Unfortunately, there are several such creeks along Peoria road and all brushy areas adjacent to creeks appear equally likely site candidates. 1956 aerial photographs show the vast majority of Peoria road was lined with agricultural farmlands. Most of the areas not farmed in 1956 are farmed now, and the rest of the area has been subject to successional vegetation changes. The brushy site is likely to have experienced more changes compared to the other five sites, and therefore any associated avian community developments may be considered outliers. Because any potential plots have undergone farming or natural succession in the past 60 years, and because I could not locate a single candidate area for the site location, I did not survey the brushy site in 2013.

Tables and Figures

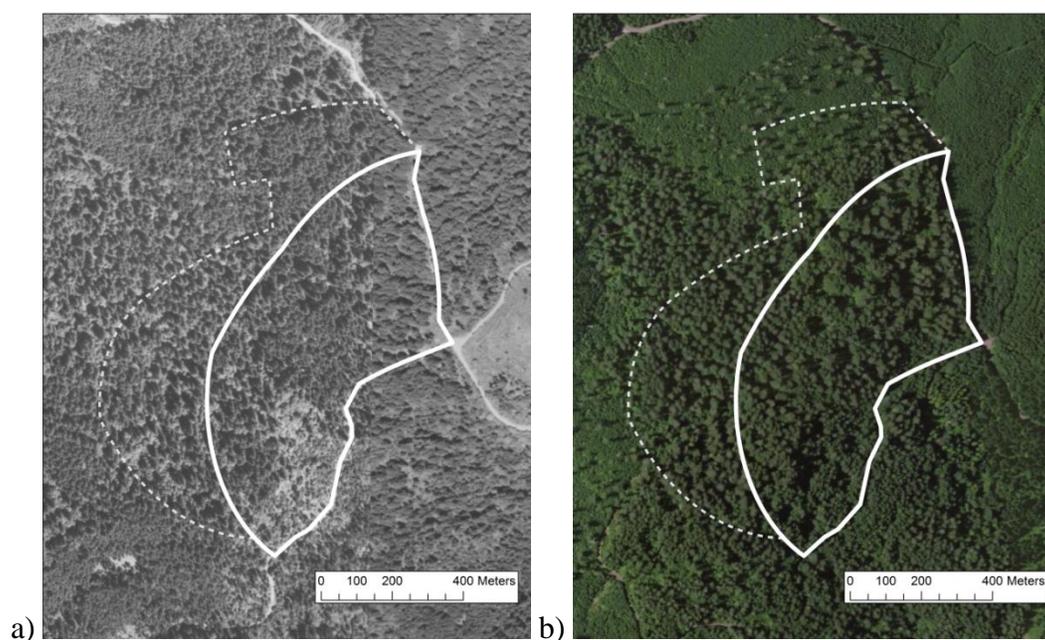


Figure A.1. Map of the coniferous survey site. Imagery from (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 14-hectare survey site is marked in white. I used a white dashed line to indicate the adjacent “likely area” in which the historic site boundaries may have occurred. (Sources: US Geological Survey 1956, Google Earth 2012.)

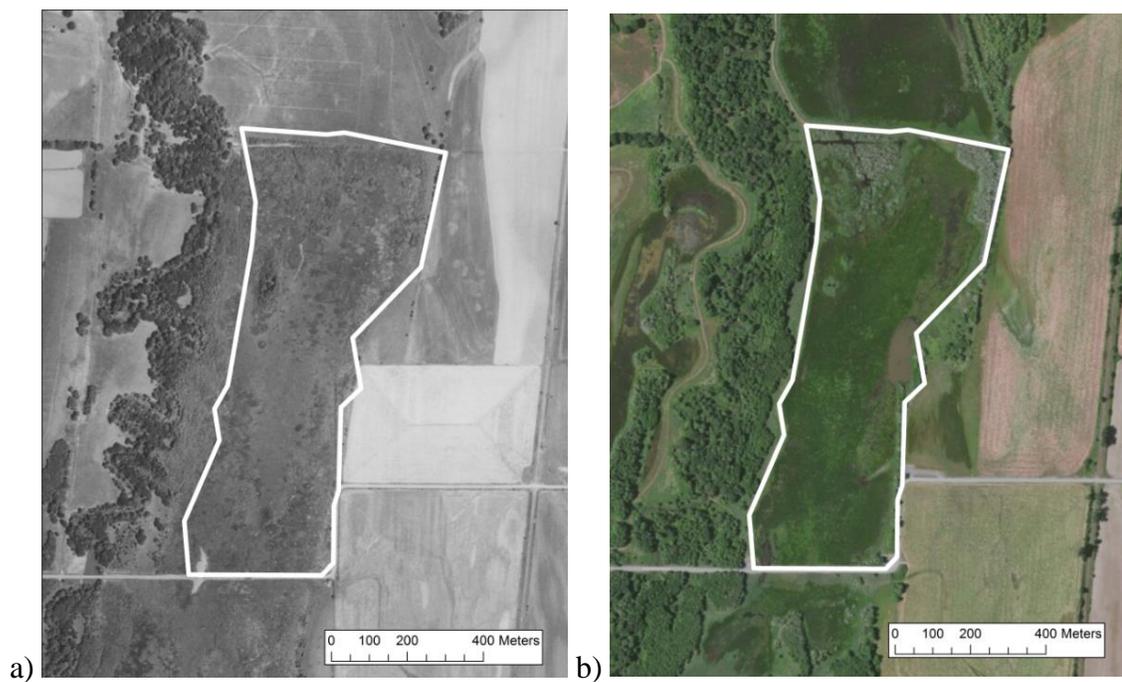


Figure A.2. Map of the McFadden marsh survey site. Imagery from (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 20-hectare survey site is marked in white. (Sources: US Geological Survey 1956, Google Earth 2012.)

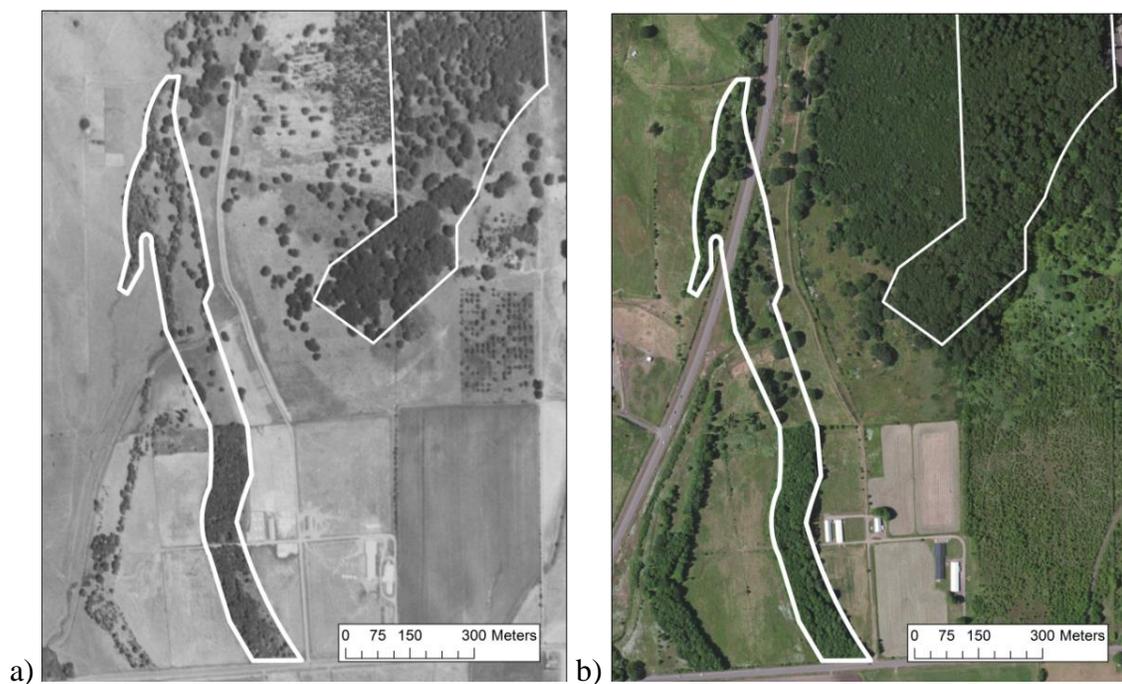


Figure A.3. Map of the mixed deciduous survey site. Imagery from (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 8-hectare survey site is marked in white. The partial boundary in the upper right hand corner of the figure is a portion of the oak woodland site. (Sources: US Geological Survey 1956, Google Earth 2012.)

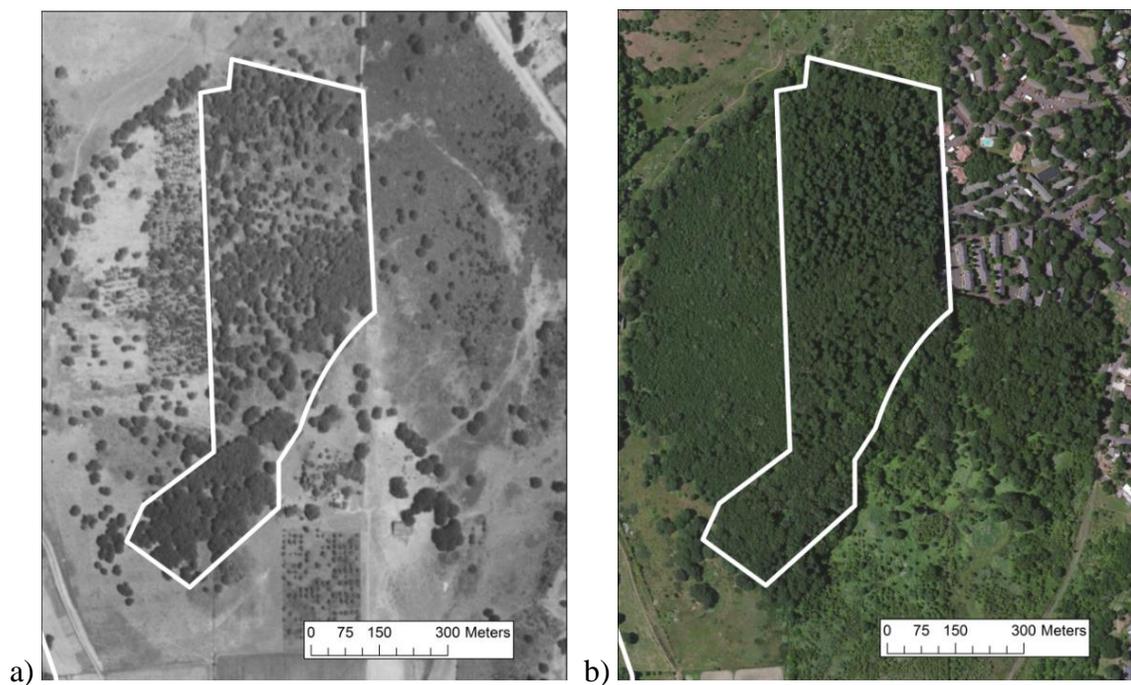


Figure A.4. Map of the oak woodland survey site. Imagery from (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 14-hectare survey site is marked in white. (Sources: US Geological Survey 1956, Google Earth 2012.)

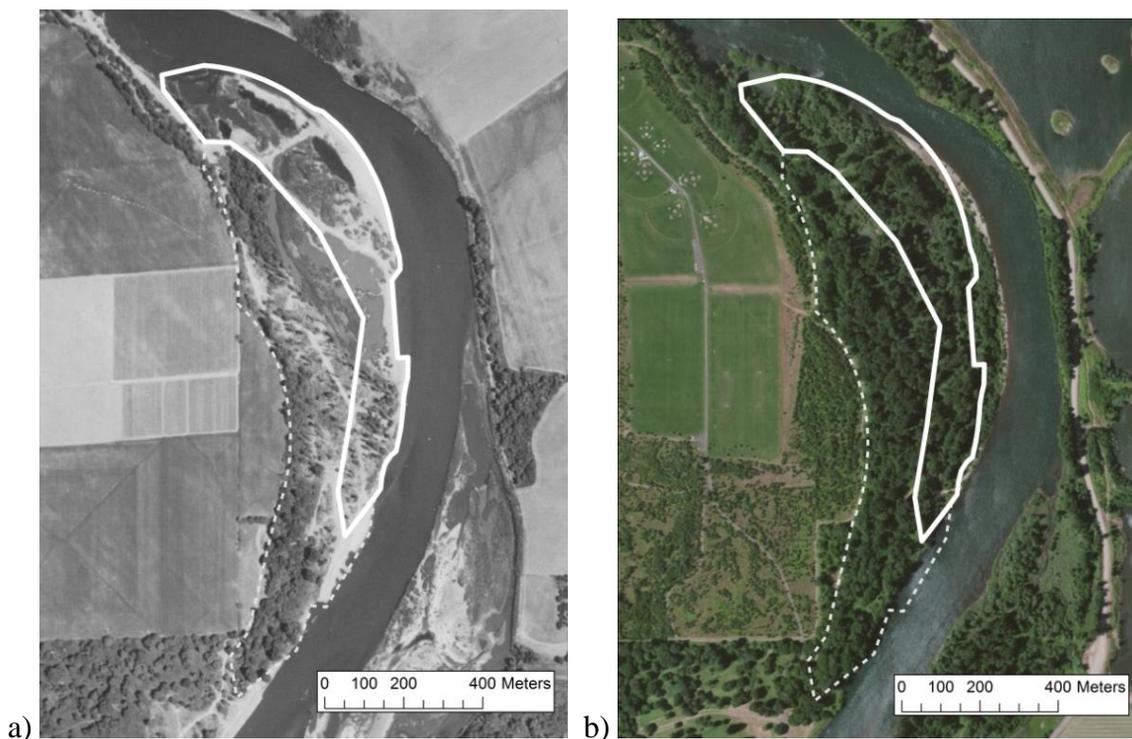


Figure A.5. Map of the Willamette River survey site. Imagery from (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in white. I used a white dashed line to indicate the adjacent “likely area” in which the historic site boundaries may have occurred. (Sources: US Geological Survey 1956, Google Earth 2012.)

Appendix B - Supplementary Methods and Statistical Analyses

Comparing 5 vs. 10 Survey Visits:

Given my desire to restrict surveys to within the breeding season, I tested the need for 10 visits per site. Several sources (Bibby et al. 2000, Ralph et al. 1993) recommend a minimum of eight spot mapping visits per site to obtain an accurate depiction of breeding territory size. However, defining breeding territories was not an objective of this study. Furthermore, it was likely the last five visits to each historic site contained unreliable count data. To determine if data from five site visits would be sufficient for this study, I examined the rate of new detections for six common territorial songbird species detected at each site in 1952: Black-capped chickadee, Bewick’s wren, Orange-crowned warbler, Western tanager, Spotted towhee, and Song sparrow. I charted the number of new

individuals detected at each site (i.e. the number of additional individuals detected when the total abundance for a visit was higher than previous surveys) against the date at which those individuals were observed. I tested the null hypothesis that there was no difference in the mean calculated density of all species encountered between the first five visits and all 10 visits using two-sample Student's t-tests. I obtained calculated density by dividing the total number of individuals detected for each species by the number of surveys conducted (either 5 or 10). A non-significant result (*i.e.* $p > 0.05$) suggests that 10 site visits does not contribute statistically different species densities compare to densities observed after five site visits.

An examination of Richard Eddy's data showed new detections of common territorial songbirds tapered off by the fifth or sixth visit to a site. This suggests birds were occupying study sites for the early part of the survey season, but were not as commonly detected during the latter half of the season. Brief jumps in new detections were observed late in the season for some species. These were likely fledgling birds or early migrants moving through the sites. Because neither fledglings nor migrant birds are considered breeding season occupants to a site, including their counts would be inappropriate for measuring breeding bird abundance. To confirm that the latter half of the survey season did not produce significantly different data from the first five surveys, I compared mean avian densities between five and ten visits. For each of the six sites surveyed in 1952, 10 visits did not produce significantly different mean densities compared to the first five visits (Table B.1; two-sample t-test, $p > 0.1$). I concluded that data from five surveys would be sufficient for comparing historic and modern breeding season avian abundances.

Testing the Need for Multiple Survey Seasons:

There is some concern about the statistical validity of comparing two data points separated by several decades. It has been recommended that multiple repeats of a historic survey be conducted to encompass normal variation between individual survey years (Igl and Johnson 2005). To determine the relative benefits of surveying sites for one breeding season versus multiple seasons, I evaluated the most recent 20 years of Breeding Bird

Survey (BBS) data for the ten selected “regional” routes (USGS Patuxent Wildlife Research Center 2013). Only those years in which at least eight of the ten routes were surveyed were considered for this part of the analysis. The result was 16 years of eligible data collected between 1993 and 2012. Using methods derived from Heath and Ballard 2003, I calculated Shannon-Wiener diversity indices (H') for each BBS route during each year. I then performed paired t-tests to compare mean values of H' across routes between random pairs of years under the null hypothesis that the mean species diversity was not different between any two random years. Out of ten comparisons, no Shannon diversity indices significantly differed between random pairs of years (all values of $p > 0.1$). I concluded there was little evidence that a second survey year would produce community diversity measures different from the first. Because of this small sample size ($n = 5$), only one year is necessary to capture an accurate depiction of the avian communities in the surveyed areas.

Species Accumulation Curves:

To evaluate how thoroughly each survey era detected the number of species within each site, I created smoothed sample-based species accumulation curves for historic and modern data (Oksanen et al. 2013, R Core Team 2013). This process plots the rate at which new species are found within a community as a function of sampling effort. As effort - the number of sites sampled - increases, the number of new species encountered increases. When the majority of species have been added, the accumulation curve forms a plateau and one can conclude the community has been sufficiently surveyed. I plotted cumulative species number as a function of five visits to a given site with sample accumulation order randomized for 1000 iterations without replacement. The means and standard deviations for resulting values were plotted as a rarefaction curve. Sample-based species accumulation curves were compared between historic and modern data to determine if there were observable differences in thoroughness of community sampling given similar effort during each sampling period.

An examination of smoothed, sample-based species accumulation curves showed little difference in the rate of new species detections between historic and modern survey

efforts (Figure B.1). Confidence intervals were narrower for the modern species accumulation curves. This is likely because I encountered new species at a more consistent rate than Richard Eddy. In the historic surveys, new species were detected at irregular intervals not always in proportion to survey effort. Because sites are selected at random to produce accumulation curves, irregular rates of species detections (i.e. some visits with many new species, some visits with no new species) will produce a wider variety of curve shapes, and, by extension, larger confidence intervals after repeated permutations. The modern surveys had narrower confidence intervals because new species were detected more uniformly in relation to survey effort. Species detection rates also tended to be slightly higher for the modern surveys, as evidenced by steeper slopes cumulating in higher total species richness. These small differences in species detections are most likely due to differences in observer skill. With equal effort, I was able to detect more species more efficiently than Richard Eddy. However, because modern and historic surveys had similar accumulation curves with overlapping confidence bands, I concluded both survey periods documented avian communities with similar thoroughness.

Influence of Site Placement:

Because Eddy's (1953) site descriptions were not precise, there was a possibility I incorrectly positioned the coniferous and Willamette sites. Differences in site placement could affect results if modern sites included geographic areas that were not part of the historic survey areas. To account for error in site placement, I identified "likely areas" adjacent to the proposed sites that also met Eddy's descriptions and could possibly have been surveyed in 1952. The 200m grid established within sites was extended into the likely areas, and four additional "likely area" point count locations were established at each intersecting grid point.

I tested whether site placement could influence modern results by comparing avian communities between the within-site and "likely area" point count data for each of those two sites. Using the same methods as when comparing randomly paired years of BBS data, I calculated Shannon-Wiener diversity among five visits for each of the within-site point count locations. I repeated this for each of the likely area point count

locations for that same site. I then used a Student's t-test to evaluate the null hypothesis of no difference in mean species diversity within the designated site compared to nearby areas. A significant p-value could indicate that changing the placement of the site would result in a different species assemblage, possibly influencing comparisons between historic and modern avian communities.

Comparisons of diversity between within-site and likely area point counts failed to reject the null hypothesis of differences in mean diversity depending on site placement. There was no evidence that placing the site in the likely area rather than the selected region would result in a different avian community for either the coniferous or Willamette site ($p = 0.5748$ for coniferous and $p = 0.9374$ for Willamette). Even if modern site boundaries were not exactly the same as the historic sites, these differences were not enough to influence community comparisons between years.

Tables and Figures

Table B.1. Comparison of mean calculated density between 5 and 10 surveys at a single site. Calculated using a Student's two-sample t-test comparing mean total individuals of all species divided by number of visits. The unusually large standard deviations for the McFadden Marsh site are likely due to high numbers of swallows during earlier surveys. These birds migrated and were not observed at later visits to the site, creating a large variation in abundance.

Site Name	5 Visits		10 Visits		5 vs. 10 visits	
	Density	SD	Density	SD	p-value	D.F.
Coniferous	1.884	2.124	1.834	1.882	0.580	37
Oak Woodland	3.133	3.553	3.530	4.130	0.156	26
Brushy	2.131	2.486	2.156	2.346	0.764	31
Willamette	2.276	2.764	2.467	2.982	0.358	33
McFadden Marsh	9.814	34.550	9.477	30.697	0.623	42
Mixed Deciduous	2.537	3.561	2.332	3.433	0.197	37

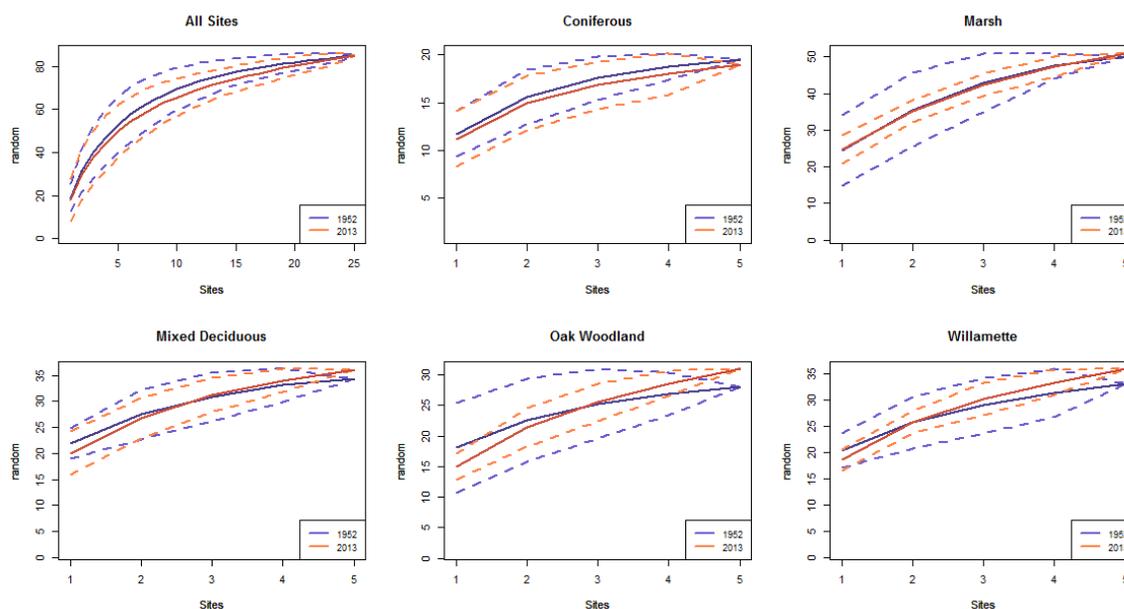


Figure B.1. Smoothed, sample-based species accumulation curves for overall modern and historic survey efforts as well as for each individual site. Curves plot the total number of unique species encountered on the vertical axis against the number of surveys conducted. Because confidence intervals overlap for both survey periods, it can be concluded that both historic and modern avian surveys were similar in thoroughness.

Appendix C - Species List

Table C.1. Common names, scientific names, and 4-letter codes for all bird species observed at survey sites. List arranged in alphabetic order by common name. Codes obtained from: Pyle, P. and D. DeSante. "List of North American Birds and Alpha Codes according to American Ornithologists' Union Taxonomy Through the 54th AOU Supplement," 2014.

Common Name	Scientific Name	Code
Acorn Woodpecker	<i>Melanerpes formicivorus</i>	ACWO
American Bittern	<i>Botaurus lentiginosus</i>	AMBI
American Coot	<i>Fulica americana</i>	AMCO
American Crow	<i>Corvus brachyrhynchos</i>	AMCR
American Goldfinch	<i>Spinus tristis</i>	AMGO
American Kestrel	<i>Falco sparverius</i>	AMKE
American Robin	<i>Turdus migratorius</i>	AMRO
Anna's Hummingbird	<i>Calypte anna</i>	ANHU
Barred Owl	<i>Strix varia</i>	BADO
Bald Eagle	<i>Haliaeetus leucocephalus</i>	BAEA

Bank Swallow	<i>Riparia riparia</i>	BANS
Barn Swallow	<i>Hirundo rustica</i>	BARS
Black-capped Chickadee	<i>Poecile atricapillus</i>	BCCH
Belted Kingfisher	<i>Megaceryle alcyon</i>	BEKI
Bewick's Wren	<i>Thryomanes bewickii</i>	BEWR
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	BHGR
Black Phoebe	<i>Sayornis nigricans</i>	BLPH
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	BRBL
Brown Creeper	<i>Certhia americana</i>	BRCR
Band-tailed Pigeon	<i>Patagioenas fasciata</i>	BTPI
Black-throated Gray Warbler	<i>Setophaga nigrescens</i>	BTYW
Bushtit	<i>Psaltriparus minimus</i>	BUSH
Canada Goose	<i>Branta canadensis</i>	CANG
California Quail	<i>Callipepla californica</i>	CAQU
Cassin's Vireo	<i>Vireo cassinii</i>	CAVI
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	CBCH
Cedar Waxwing	<i>Bombycilla cedrorum</i>	CEDW
Chipping Sparrow	<i>Spizella passerina</i>	CHSP
Cinnamon Teal	<i>Anas cyanoptera</i>	CITE
Cliff Swallow	<i>Petrochelidon pyrrhonota</i>	CLSW
Cooper's Hawk	<i>Accipiter cooperii</i>	COHA
Common Merganser	<i>Mergus merganser</i>	COME
Common Nighthawk	<i>Chordeiles minor</i>	CONI
Common Raven	<i>Corvus corax</i>	CORA
Common Yellowthroat	<i>Geothlypis trichas</i>	COYE
Dark-eyed Junco	<i>Junco hyemalis</i>	DEJU
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO
Eurasian Collared-Dove	<i>Streptopelia decaocto</i>	EUCD
European Starling	<i>Sturnus vulgaris</i>	EUST
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	EVGR
Fox Sparrow	<i>Passerella iliaca</i>	FOSP
Great Blue Heron	<i>Ardea herodias</i>	GBHE
Golden-crowned Kinglet	<i>Regulus satrapa</i>	GCKI
Great Horned Owl	<i>Bubo virginianus</i>	GHOW
Gray Jay	<i>Perisoreus canadensis</i>	GRAJ
Great Egret	<i>Ardea alba</i>	GREG
Green Heron	<i>Butorides virescens</i>	GRHE
Greater Yellowlegs	<i>Tringa melanoleuca</i>	GRYE
Green-winged Teal	<i>Anas crecca</i>	GWTE
Hammond's Flycatcher	<i>Empidonax hammondii</i>	HAFL
Hairy Woodpecker	<i>Picoides villosus</i>	HAWO

Hermit Warbler	<i>Setophaga occidentalis</i>	HEWA
House Finch	<i>Haemorhous mexicanus</i>	HOFI
House Sparrow	<i>Passer domesticus</i>	HOSP
House Wren	<i>Troglodytes aedon</i>	HOWR
Hutton's Vireo	<i>Vireo huttoni</i>	HUVI
Killdeer	<i>Charadrius vociferus</i>	KILL
Lazuli Bunting	<i>Passerina amoena</i>	LAZB
Lesser Goldfinch	<i>Spinus psaltria</i>	LEGO
Lewis's Woodpecker	<i>Melanerpes lewis</i>	LEWO
Mallard	<i>Anas platyrhynchos</i>	MALL
Marsh Wren	<i>Cistothorus palustris</i>	MAWR
Merlin	<i>Falco columbarius</i>	MERL
MacGillivray's Warbler	<i>Geothlypis tolmiei</i>	MGWA
Mourning Dove	<i>Zenaida macroura</i>	MODO
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	NAWA
Northern Bobwhite	<i>Colinus virginianus</i>	NOBO
Northern Flicker	<i>Colaptes auratus</i>	NOFL
Northern Harrier	<i>Circus cyaneus</i>	NOHA
Northern Pygmy-Owl	<i>Glaucidium gnoma</i>	NOPO
Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>	NRWS
Orange-crowned Warbler	<i>Oreothlypis celata</i>	OCWA
Olive-sided Flycatcher	<i>Contopus cooperi</i>	OSFL
Osprey	<i>Pandion haliaetus</i>	OSPR
Pacific Wren	<i>Troglodytes pacificus</i>	PAWR
Pied-billed Grebe	<i>Podilymbus podiceps</i>	PBGR
Peregrine Falcon	<i>Falco peregrinus</i>	PEFA
Pine Siskin	<i>Spinus pinus</i>	PISI
Pileated Woodpecker	<i>Dryocopus pileatus</i>	PIWO
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	PSFL
Purple Finch	<i>Haemorhous purpureus</i>	PUFI
Red-breasted Nuthatch	<i>Sitta canadensis</i>	RBNU
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>	RBSA
Red Crossbill	<i>Loxia curvirostra</i>	RECR
Red-necked Phalarope	<i>Phalaropus lobatus</i>	RNPH
Red-tailed Hawk	<i>Buteo jamaicensis</i>	RTHA
Ruffed Grouse	<i>Bonasa umbellus</i>	RUGR
Rufous Hummingbird	<i>Selasphorus rufus</i>	RUHU
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	RWBL
Savannah Sparrow	<i>Passerculus sandwichensis</i>	SAVS
Sora	<i>Porzana carolina</i>	SORA
Song Sparrow	<i>Melospiza melodia</i>	SOSP
Spotted Sandpiper	<i>Actitis macularius</i>	SPSA

Spotted Towhee	<i>Pipilo maculatus</i>	SPTO
Sharp-shinned Hawk	<i>Accipiter striatus</i>	SSHA
Steller's Jay	<i>Cyanocitta stelleri</i>	STJA
Swainson's Thrush	<i>Catharus ustulatus</i>	SWTH
Townsend's Warbler	<i>Setophaga townsendi</i>	TOWA
Tree Swallow	<i>Tachycineta bicolor</i>	TRES
Turkey Vulture	<i>Cathartes aura</i>	TUVU
Unidentified Empidonax Flycatcher	<i>Empidonax (sp)</i>	UEFL
Unidentified Duck	<i>Anatinae (gen, sp)</i>	UNDU
Unidentified Flycatcher	<i>Tyrannidae (gen, sp)</i>	UNFL
Unidentified Hummingbird	<i>Trochilidae (gen, sp)</i>	UNHU
Unidentified Warbler	<i>Parulidae (gen, sp)</i>	UNWA
Violet-green Swallow	<i>Tachycineta thalassina</i>	VGSW
Virginia Rail	<i>Rallus limicola</i>	VIRA
Warbling Vireo	<i>Vireo gilvus</i>	WAVI
White-breasted Nuthatch	<i>Sitta carolinensis</i>	WBNU
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	WCSP
Western Bluebird	<i>Sialia mexicana</i>	WEBL
Western Meadowlark	<i>Sturnella neglecta</i>	WEME
Western Scrub-Jay	<i>Aphelocoma californica</i>	WESJ
Western Tanager	<i>Piranga ludoviciana</i>	WETA
Western Wood-Pewee	<i>Contopus sordidulus</i>	WEWP
Willow Flycatcher	<i>Empidonax traillii</i>	WIFL
Wilson's Snipe	<i>Gallinago delicata</i>	WISN
Wilson's Warbler	<i>Cardellina pusilla</i>	WIWA
Wood Duck	<i>Aix sponsa</i>	WODU
Wrentit	<i>Chamaea fasciata</i>	WREN
Yellow-breasted Chat	<i>Icteria virens</i>	YBCH
Yellow Warbler	<i>Setophaga petechia</i>	YWAR
Yellow-headed Blackbird	<i>Xanthocephalus xanthocephalus</i>	YHBL

Appendix D - Vegetation and Land Use Classifications

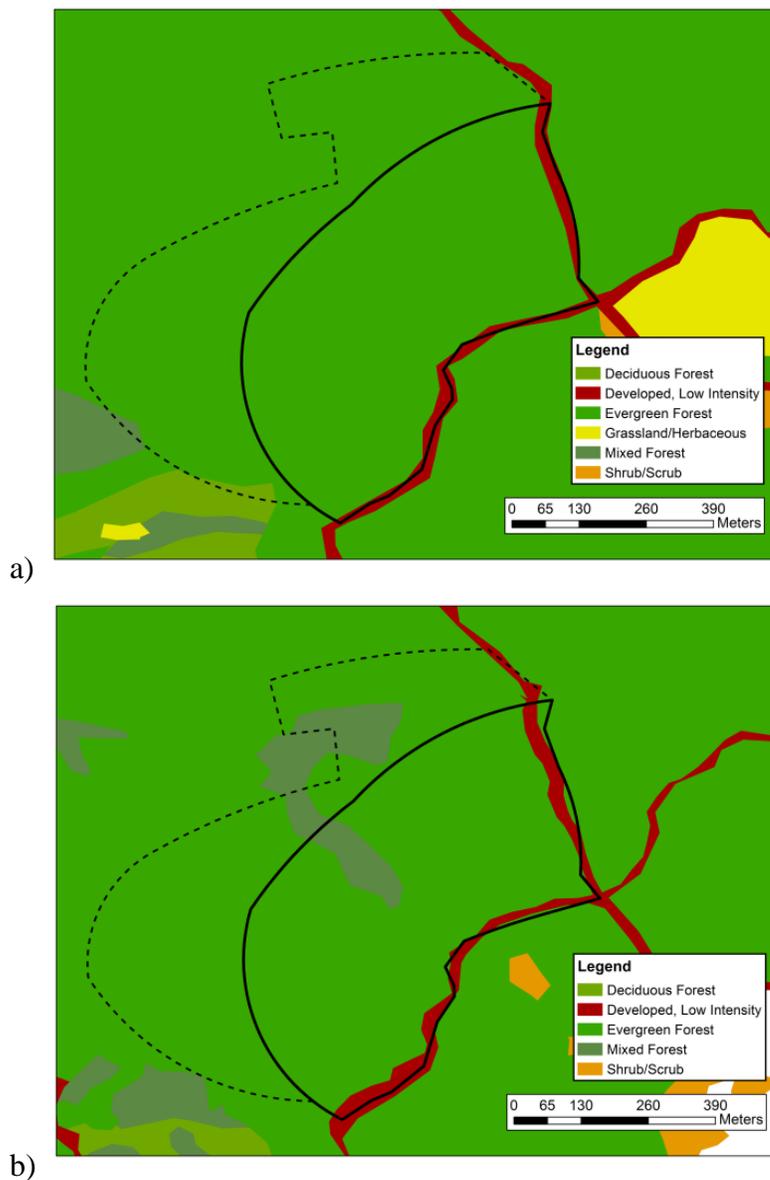


Figure D.1. Map of visually classified land use categories for the coniferous site. Classifications based on (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in black. The adjacent “likely area” in which the historic site boundaries may have occurred is indicated with a black dashed line. Land use categories derived from National Gap Analysis Program (GAP) (US Geological Survey 2012).

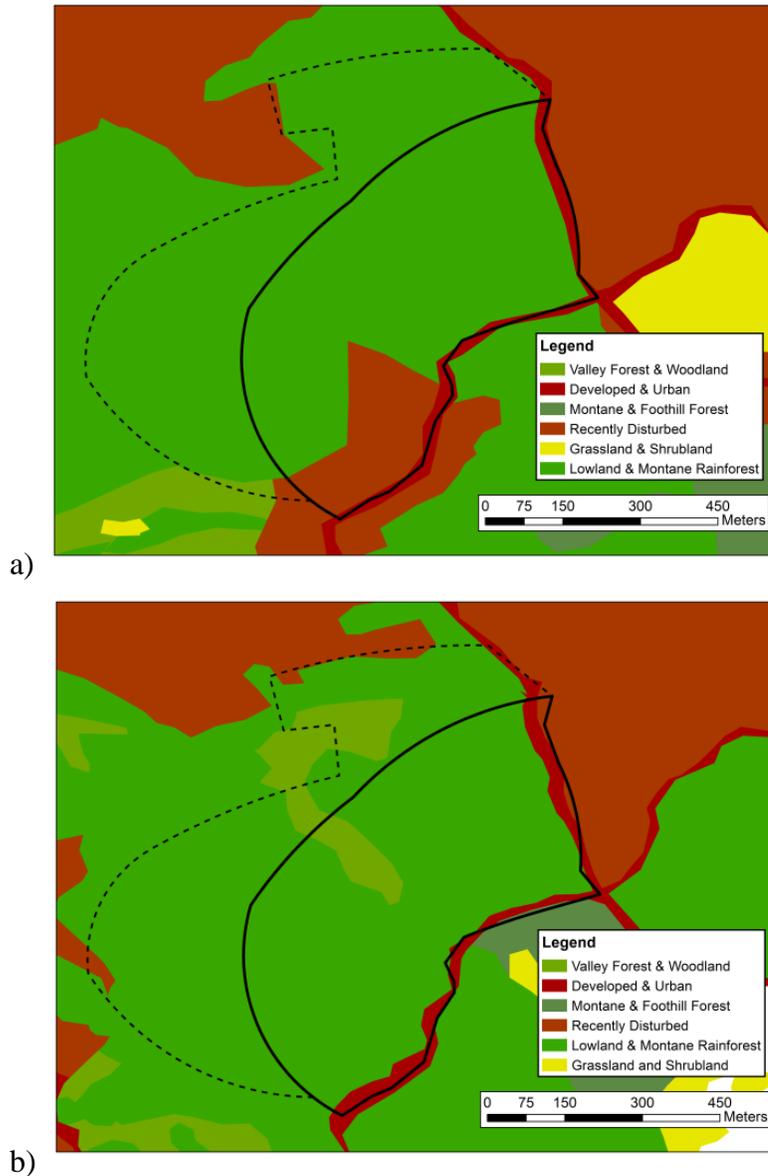


Figure D.2. Map of visually classified vegetation categories for the coniferous site. Classifications based on (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in black. The adjacent “likely area” in which the historic site boundaries may have occurred is indicated with a black dashed line. Vegetation system categories derived from NVC levels in the National Gap Analysis Program (GAP) (US Geological Survey 2012).

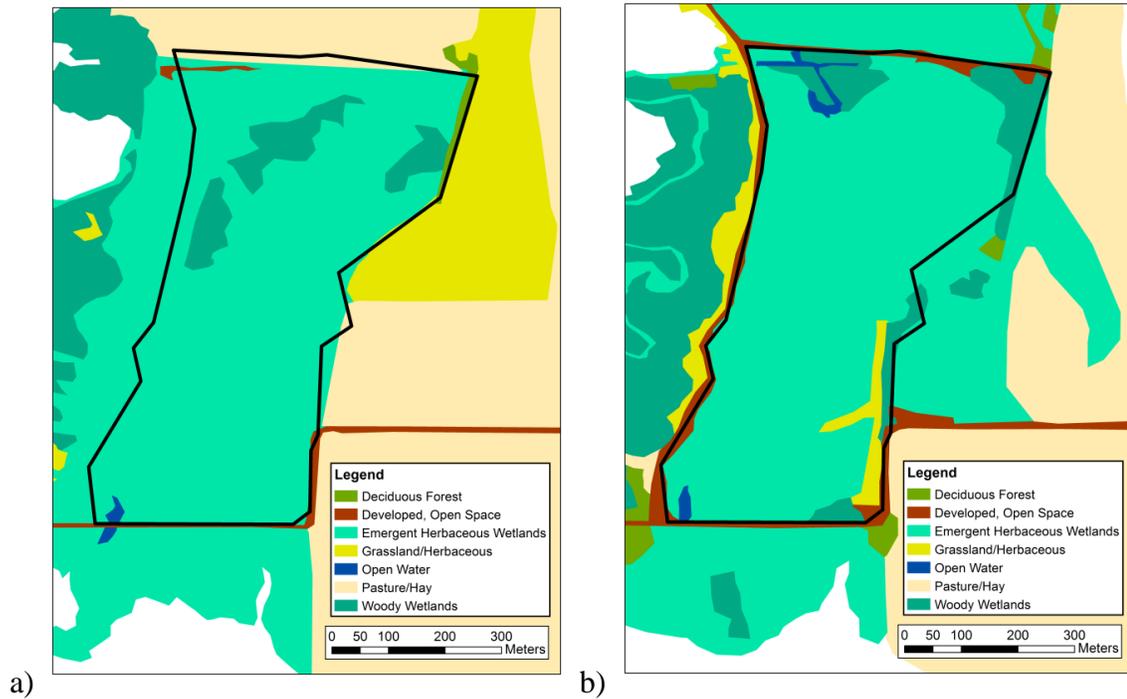


Figure D.3. Map of visually classified land use categories for the marsh site. Classifications based on (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in black. Land use categories derived from National Gap Analysis Program (GAP) (US Geological Survey 2012).

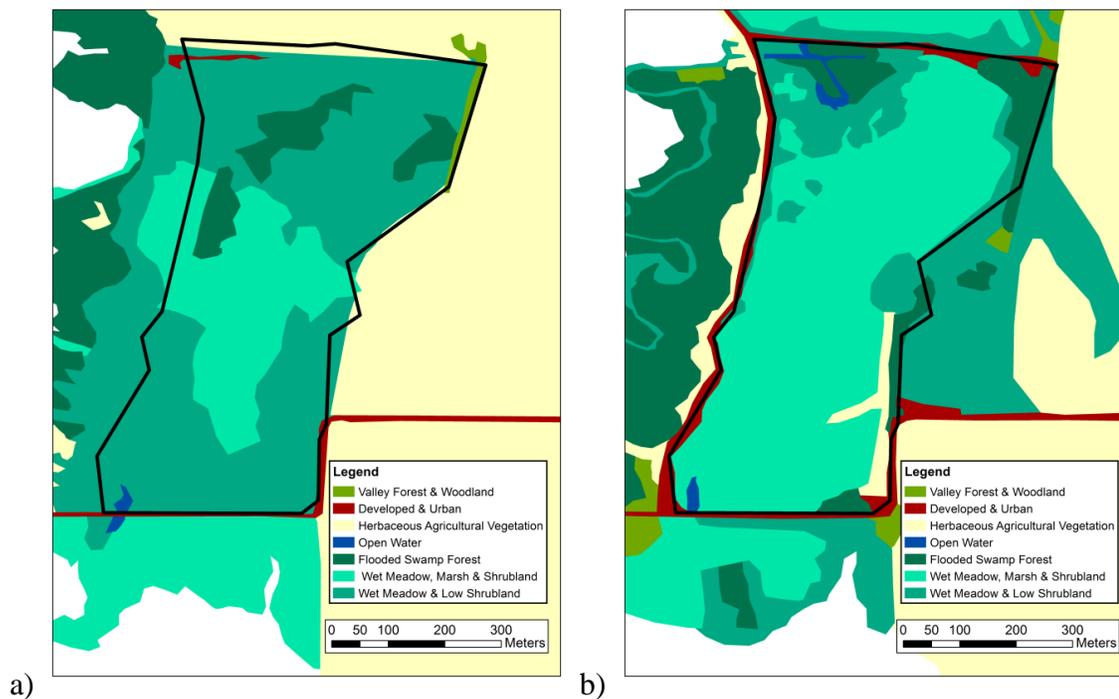


Figure D.4. Map of visually classified vegetation type categories for the marsh site. Classifications based on (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in black. Vegetation system categories derived from NVC levels in the National Gap Analysis Program (GAP) (US Geological Survey 2012).

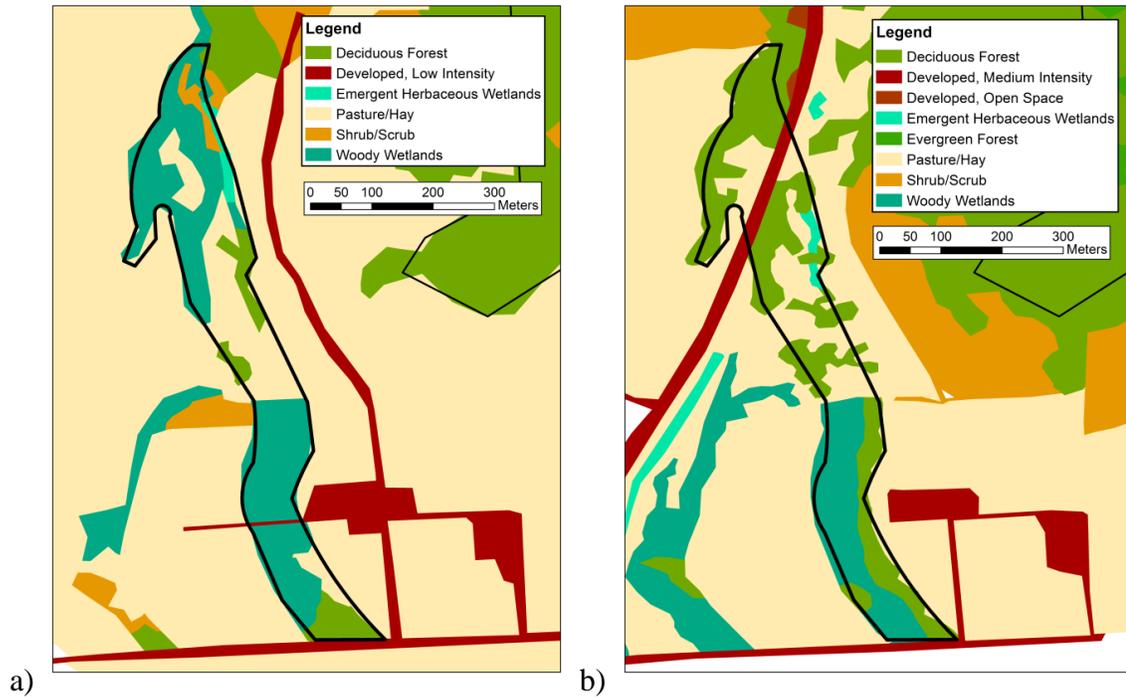


Figure D.5. Map of visually classified land use categories for the mixed deciduous site. Classifications based on (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in black. Land use categories derived from National Gap Analysis Program (GAP) (US Geological Survey 2012).

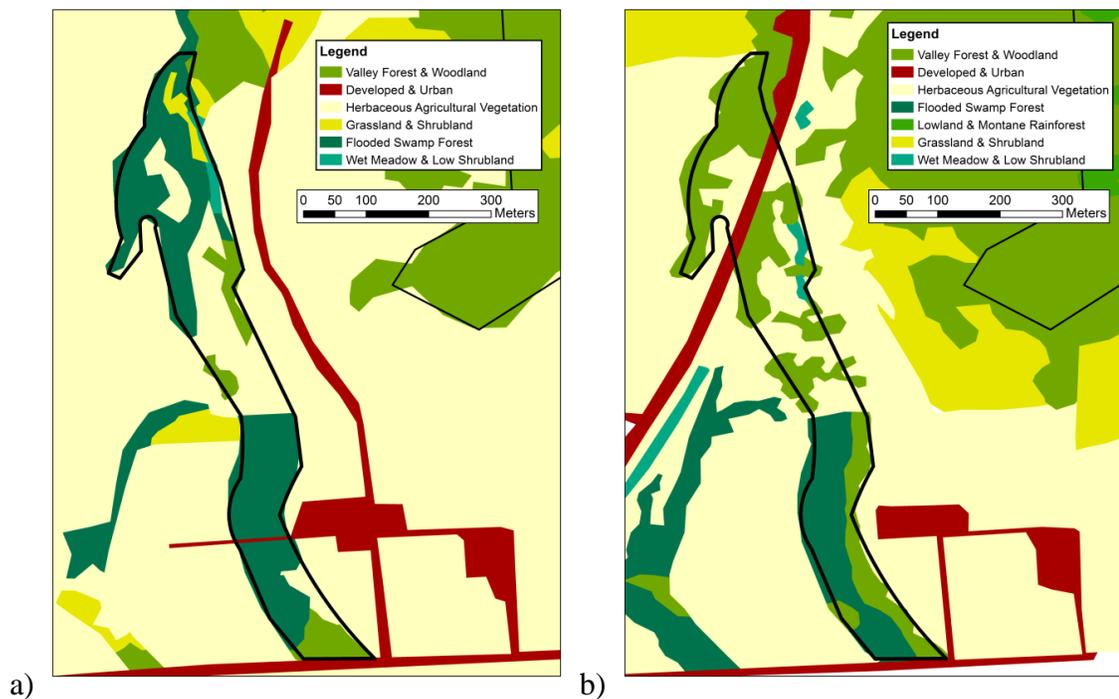


Figure D.6. Map of visually classified vegetation type categories for the mixed deciduous site. Classifications based on (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in black. Vegetation system categories derived from NVC levels in the National Gap Analysis Program (GAP) (US Geological Survey 2012).

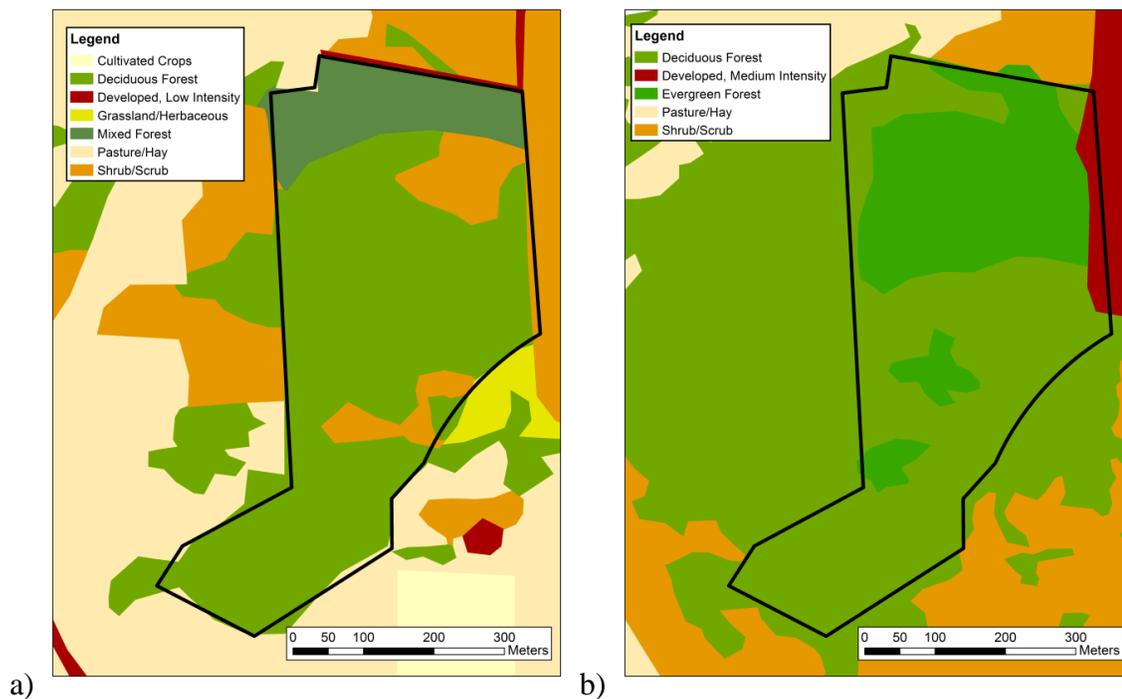


Figure D.7. Map of visually classified land use categories for the oak woodland site. Classifications based on (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in black. Land use categories derived from National Gap Analysis Program (GAP) (US Geological Survey 2012).

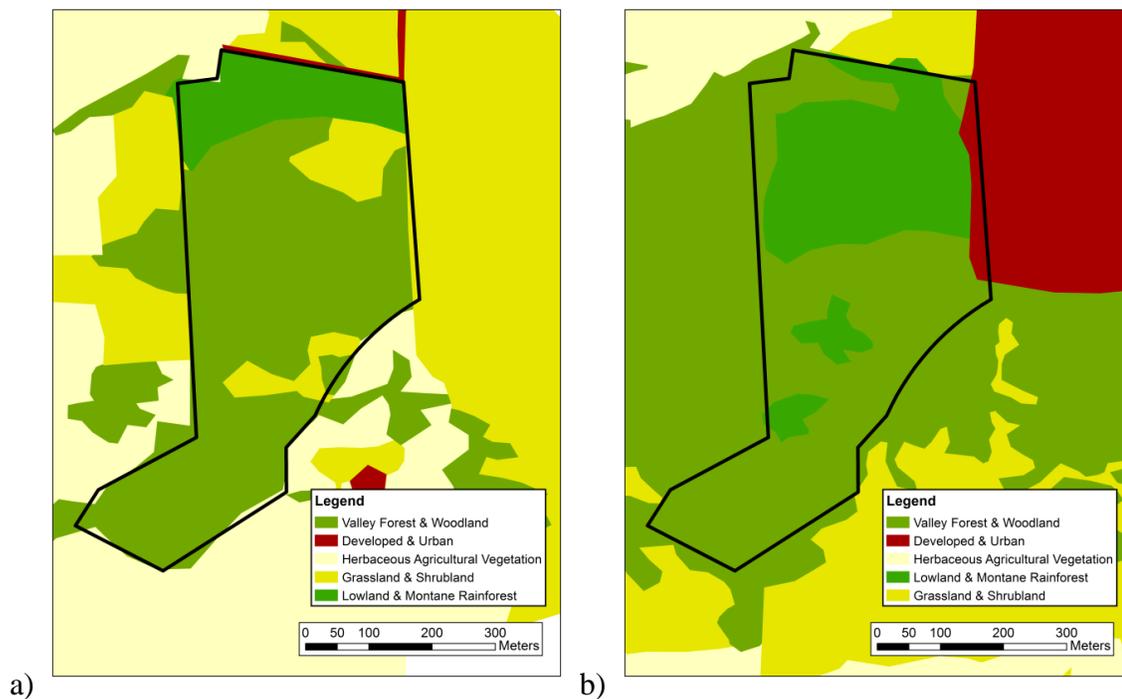


Figure D.8. Map of visually classified vegetation type categories for the oak woodland site. Classifications based on (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in black. Vegetation system categories derived from NVC levels in the National Gap Analysis Program (GAP) (US Geological Survey 2012).

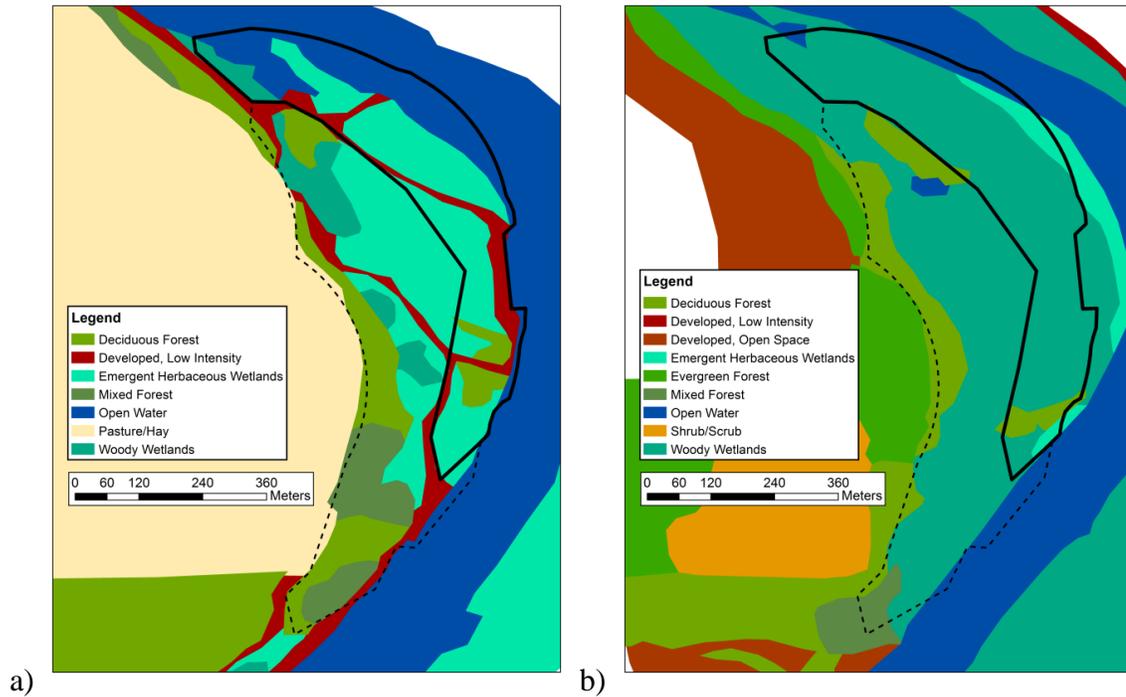


Figure D.9. Map of visually classified vegetation type categories for the Willamette River site. Classifications based on (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in black. The adjacent “likely area” in which the historic site boundaries may have occurred is indicated with a black dashed line. Vegetation system categories derived from NVC levels in the National Gap Analysis Program (GAP) (US Geological Survey 2012).

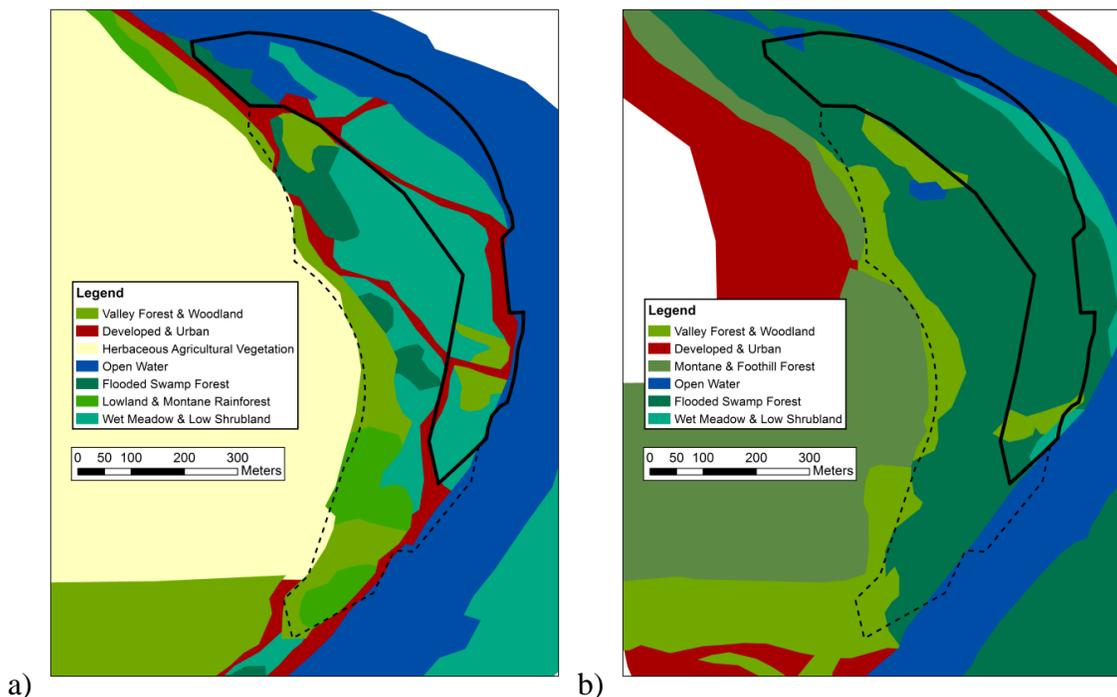


Figure D.10. Map of visually classified land use categories for the Willamette River site. Classifications based on (a) 1956 aerial photographs and (b) 2012 satellite imagery. The boundary of the 10-hectare survey site is marked in black. The adjacent “likely area” in which the historic site boundaries may have occurred is indicated with a black dashed line. Land use categories derived from National Gap Analysis Program (GAP) (US Geological Survey 2012).

Appendix E - Abundance Categories

Table E.1. Matrix of population trend categories. Categories based the magnitude and direction of change between historic and modern abundance categories. The thresholds of average number of individuals counted per survey used to define abundance categories are provided in parentheses in the second column.

		Modern Abundance Category				
		Abundant	Common	Uncommon	Rare	Not Detected
Historic Abundance Category	Abundant (> 10)	No Change	Decreasing	Decreasing	Strongly Decreasing	Strongly Decreasing
	Common (4.5 - 10)	Increasing	No Change	Decreasing	Decreasing	Strongly Decreasing
	Uncommon (1.5 - 4.49)	Increasing	Increasing	No Change	Decreasing	Decreasing
	Rare (< 1.5)	Strongly Increasing	Increasing	Increasing	No Change	Decreasing

Not Detected (0) Strongly Increasing Strongly Increasing Increasing Increasing No Change

Appendix F - Detection Probabilities

Table F.1. Detection probabilities for modern and historic survey periods. Probabilities calculated using the best fitting model based on historic species abundances across all site visits. The best fitting model for each species was selected from three options based on AIC values using package unmarked (Fiske and Chandler 2011). M1 refers to a basic model with no covariates; m2 includes a single covariate for survey date; m3 includes a single covariate for habitat.

Species Code	Best Model	1952		2013	
		Detection Probability	1952 SE	Detection Probability	2013 SE
AMBI	m1	0.04011	0.0404	0.0007	NA
AMCR	m1	0.79974	0.1269	0.4206	0.1235
AMGO	m2	0.94396	0.0878	0.7200	0.0898
AMKE	m1	0.20432	0.1666	0.0007	NA
AMRO	m3	0.79952	0.0895	0.9601	0.0391
BARS	m1	0.99987	0.0051	0.5933	0.1612
BCCH	m1	0.84992	0.0799	0.7995	0.0895
BEKI	m2	0.96507	0.2039	0.2043	0.1666
BEWR	m2	0.99729	0.0134	0.4670	0.1289
BRBL	m1	0.59333	0.228	0.0007	NA
BRCR	m1	0.20432	0.1666	0.6977	0.1452
BTPI	m2	0.29109	0.2268	0.0007	NA
BTYW	m1	0.59333	0.228	0.0007	NA
BUSH	m3	0.26596	0.1141	0.5000	0.1118
CAQU	m3	0.80000	0.1789	0.0401	0.0404
CAVI	m2	0.04240	0.38	0.0007	NA
CBCH	m3	0.80028	0.1788	1.0000	0.0018
CEDW	m1	0.79974	0.1036	0.7995	0.0895
CHSP	m1	0.89999	0.0949	0.0007	NA
CLSW	m1	0.99987	0.0051	0.5933	0.228
COME	m3	0.19968	0.1789	0.1997	0.1789
CONI	m1	0.04011	0.0404	0.0007	NA
COYE	m1	0.48121	0.1713	0.6638	0.1244
DEJU	m3	0.66611	0.1218	0.7323	0.1153
DOWO	m3	0.86714	0.0876	0.5000	0.1118
FOSP	m2	0.00000	0	0.0007	NA

GBHE	m2	0.99704	0.0141	0.7997	0.1269
GCKI	m3	0.80028	0.1788	0.0007	NA
GHOW	m3	0.19959	0.1788	0.1604	0.0761
GRAJ	m3	0.39982	0.2191	0.0000	0
HAWO	m2	0.00000	0	0.1996	0.1788
HOSP	m3	0.80000	0.1789	0.0007	NA
HOWR	m2	0.97127	0.1795	0.0401	0.0404
KILL	m2	1.00000	0	0.0801	0.0544
LAZB	m2	1.00000	0	0.3555	0.2494
LEGO	m2	0.99995	0.0013	0.2665	0.1142
MALL	m2	1.00000	0	0.9999	0.0051
MAWR	m1	0.99987	0.0051	0.9999	0.0051
MGWA	m2	0.70978	0.2573	0.0007	NA
MODO	m1	0.89999	0.0949	0.5500	0.1113
NAWA	m1	0.59332	0.1612	0.0007	NA
NOBO	m2	0.00010	0.0014	0.0007	NA
NOFL	m1	0.48121	0.1713	0.4499	0.1112
NRWS	m1	0.35553	0.2494	0.0401	0.0404
OCWA	m3	0.64985	0.1067	0.5385	0.1179
OSFL	m3	0.80028	0.1788	0.0007	NA
PISI	m1	0.48121	0.1713	0.0007	NA
PIWO	m3	0.59985	0.2191	0.1996	0.1788
PUFI	m2	0.99997	6.00E-04	0.2043	0.1666
RBNU	m1	0.35553	0.1763	0.3555	0.2494
RBSA	m3	0.99998	0.0018	0.5933	0.1612
RECR	m3	0.59986	0.2191	0.1668	0.1494
RNPH	m3	0.26596	0.1141	0.0007	NA
RTHA	m1	0.25873	0.1413	0.9999	0.0051
RUGR	m2	0.00000	1.00E-04	0.0007	NA
RUHU	m2	0.99995	0.0013	0.4400	0.0993
RWBL	m1	0.99987	0.0051	0.9999	0.0051
SORA	m1	0.04011	0.0404	0.0007	NA
SOSP	m1	0.73233	0.1153	0.9999	0.002
SPTO	m1	0.75982	0.0854	1.0000	0
STJA	m3	0.99998	0.0018	0.3555	0.144
SWTH	m1	0.23991	0.0856	0.6464	0.1094
TOWA	m2	0.00000	0	0.0007	NA
TRES	m1	0.04011	0.0404	0.4849	0.2029
TUVU	m1	0.96009	0.0391	0.1604	0.0761
UEFL	m1	0.16038	0.0761	0.0007	NA

VGSW	m1	0.66380	0.1244	0.0801	0.0544
WAVI	m2	0.42975	0.2108	0.0007	NA
WBNU	m1	0.74926	0.0976	0.0017	0.1205
WCSP	m1	0.59332	0.1612	0.0007	NA
WEBL	m3	0.59985	0.2191	0.0401	0.0404
WEME	m2	0.00004	3.00E-04	0.0007	NA
WESJ	m3	0.39978	0.2192	0.9999	0.0051
WETA	m1	0.84992	0.0799	0.0401	0.0404
WEWP	m2	0.78956	0.1794	0.4413	0.1418
WISN	m2	0.96507	0.2039	0.0007	NA
WODU	m1	0.35553	0.2494	0.9999	0.0051
YBCH	m2	1.00000	0	0.0007	NA
YWAR	m3	0.44986	0.1112	0.6160	0.1892

Appendix G - Beta Diversity Values

Table G.1. Modified Raup-Crick pairwise beta diversity values for all detection types. Values represent the probability that the number of shared species between any pair of communities is equal to or lower than expected by chance, re-scaled to range between -1 and 1 (Chase et al. 2011). Higher numbers represent communities that are more dissimilar than expected, while lower numbers represent communities that are less dissimilar than expected.

		1952					2013			
		Coniferous	Marsh	Mixed	Oak	Willamette	Coniferous	Marsh	Mixed	Oak
1952	Marsh	0.98								
	Mixed	0.16	-0.56							
	Oak	-0.96	0.30	-1.00						
	Willamette	-0.11	-0.70	-1.00	-0.76					
2013	Coniferous	-0.93	0.99	0.29	-0.05	0.94				
	Marsh	1.00	-0.71	0.15	0.70	0.43	0.98			
	Mixed	0.98	0.92	-0.96	-0.85	-0.98	0.11	-0.63		
	Oak	0.62	0.95	-0.92	-0.93	-0.60	-1.00	0.18	-1.00	
	Willamette	0.86	0.56	-0.50	-0.45	-0.11	-0.69	-0.99	-1.00	-0.99

Table G.2. Modified Raup-Crick pairwise beta diversity values for visually detected species only.

		1952					2013			
--	--	------	--	--	--	--	------	--	--	--

		Coniferous	Marsh	Mixed	Oak	Willamette	Coniferous	Marsh	Mixed	Oak
1952	Marsh	1.00								
	Mixed	0.53	-0.21							
	Oak	-0.88	0.60	-1.00						
	Willamette	0.28	-0.45	-0.99	-0.57					
2013	Coniferous	0.51	0.85	0.51	0.31	0.88				
	Marsh	1.00	-0.84	0.49	0.91	0.27	0.78			
	Mixed	1.00	0.91	-0.82	-0.35	-0.94	0.22	-0.80		
	Oak	0.92	0.78	-0.41	0.41	0.04	-1.00	0.18	-0.92	
	Willamette	0.95	0.05	-0.52	-0.57	-0.57	-0.79	-0.99	-0.99	-1.00

Appendix H - Shifts in Categorical Abundance

Presented below are histograms with the number of species in each abundance category on the y-axis. Sites outlined in black rectangles showed statistically significant changes in distribution between years based on either Fisher's Exact or Chi-square tests, regardless of detection type.

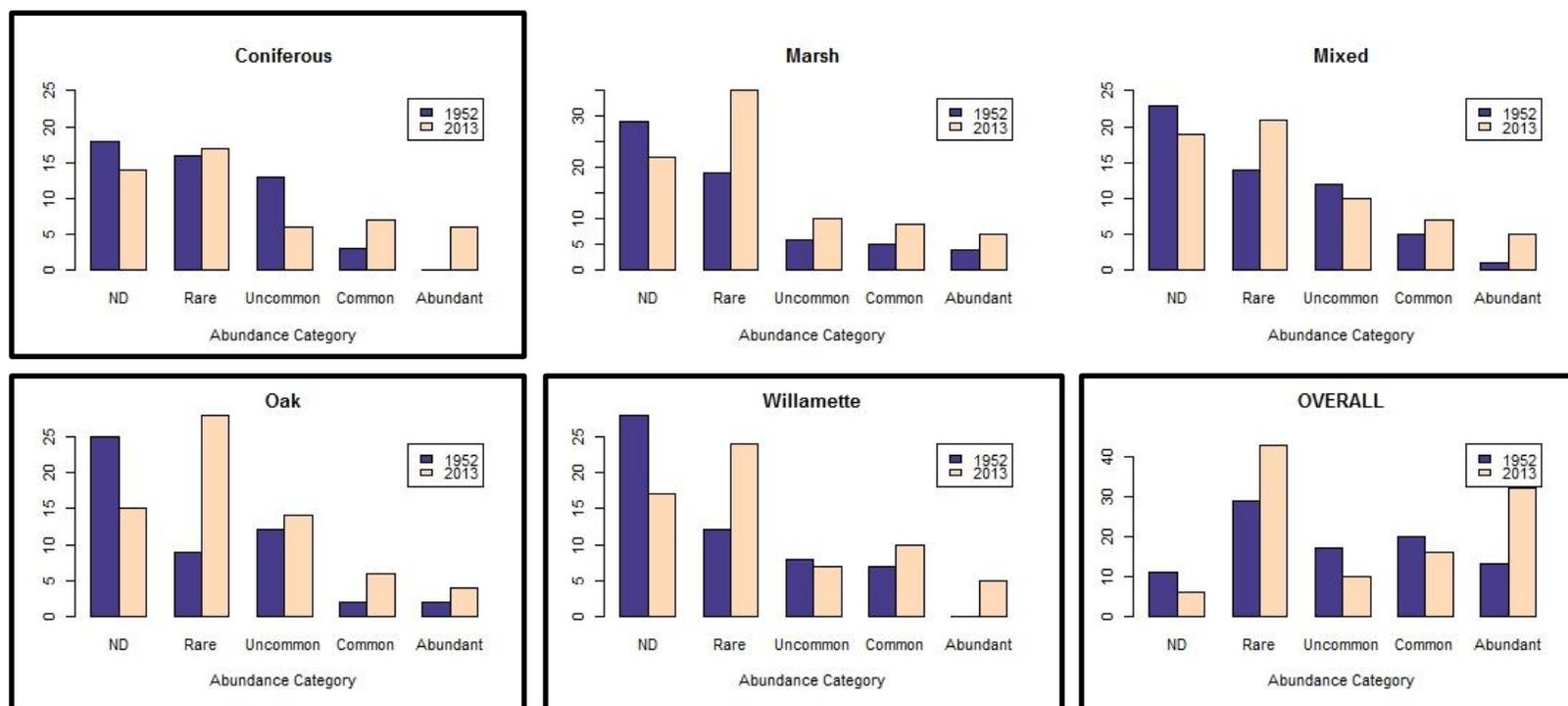


Figure H.1. Histograms of species abundance categories for both survey periods considering all detection types.

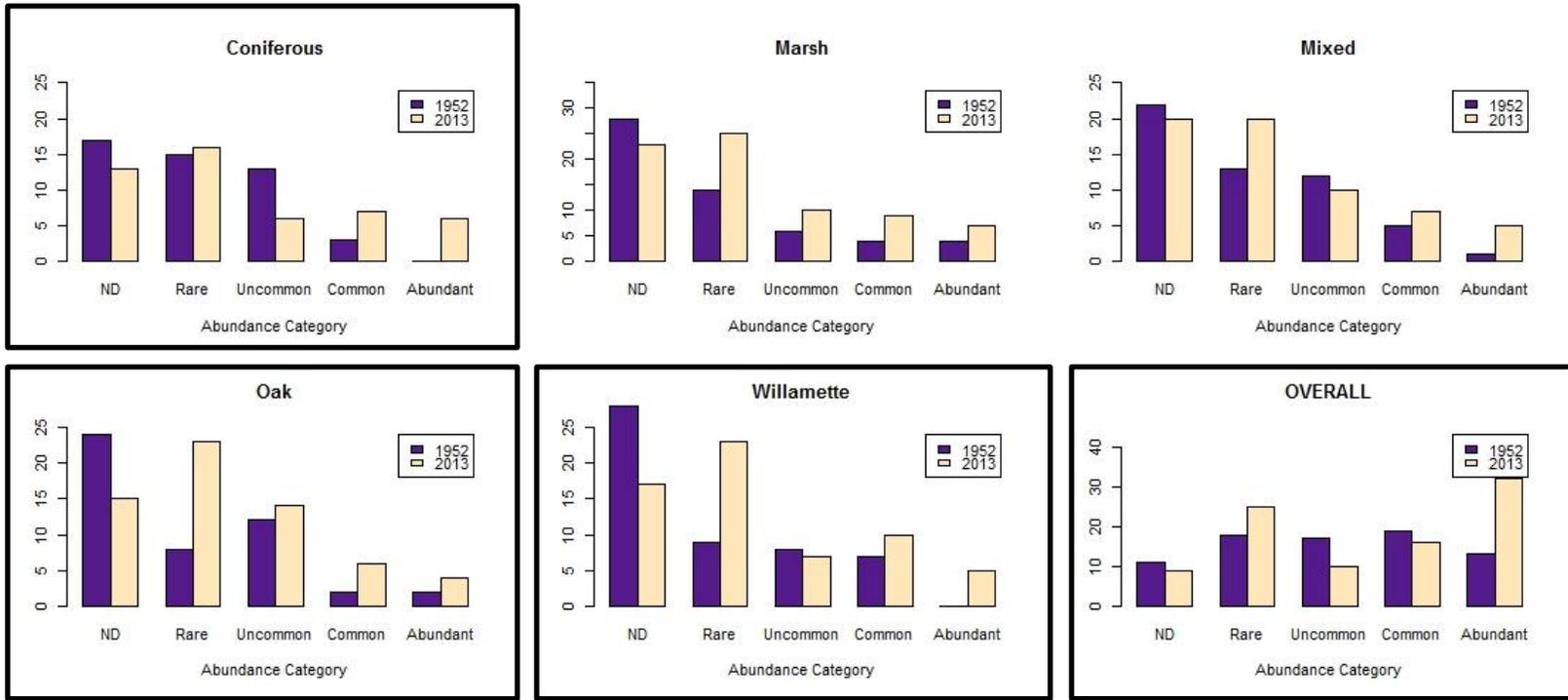


Figure H.2. Histograms of species abundance categories for both survey periods considering all detection types with rare species removed. Rare species are defined as species detected only once during five visits to a given site.

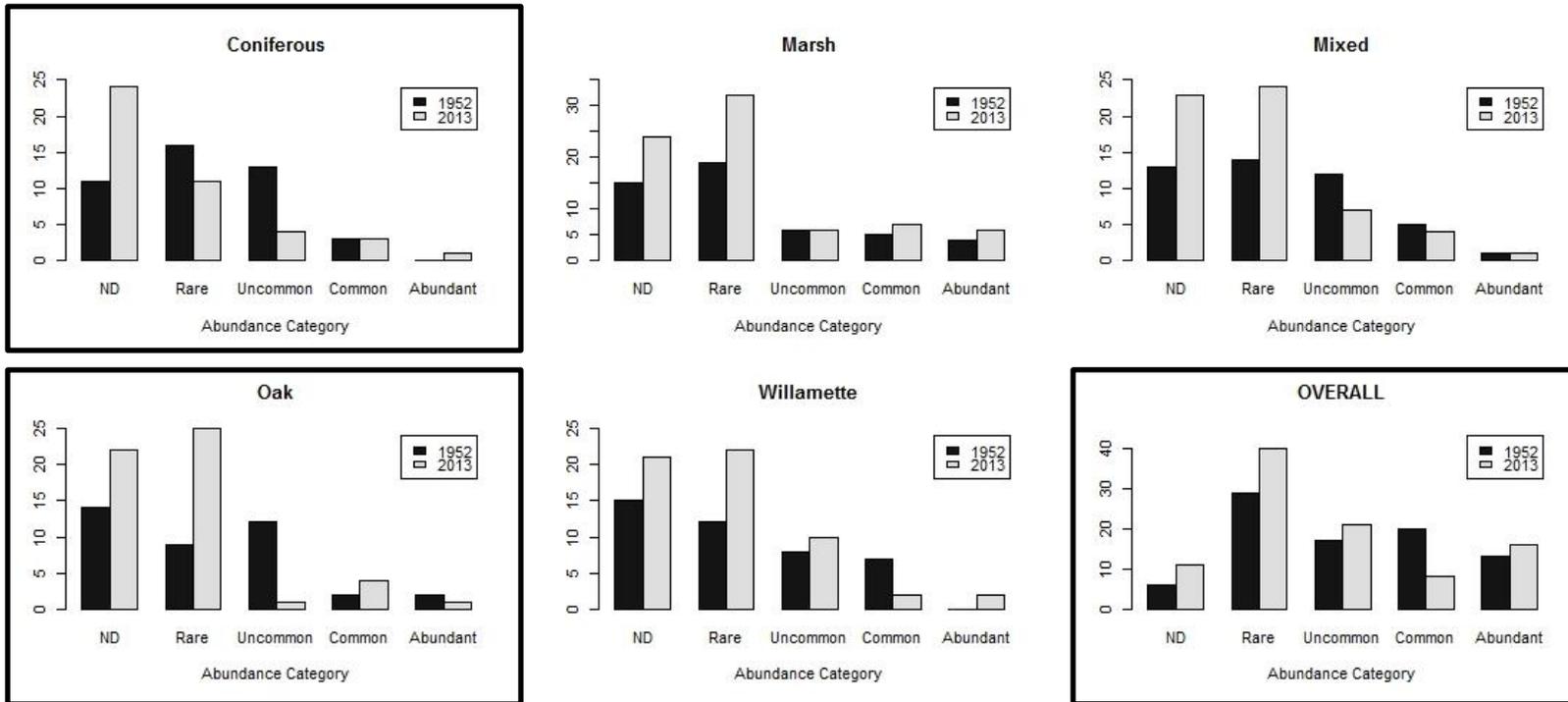


Figure H.3. Histograms of species abundance categories for both survey periods considering only visual detections.

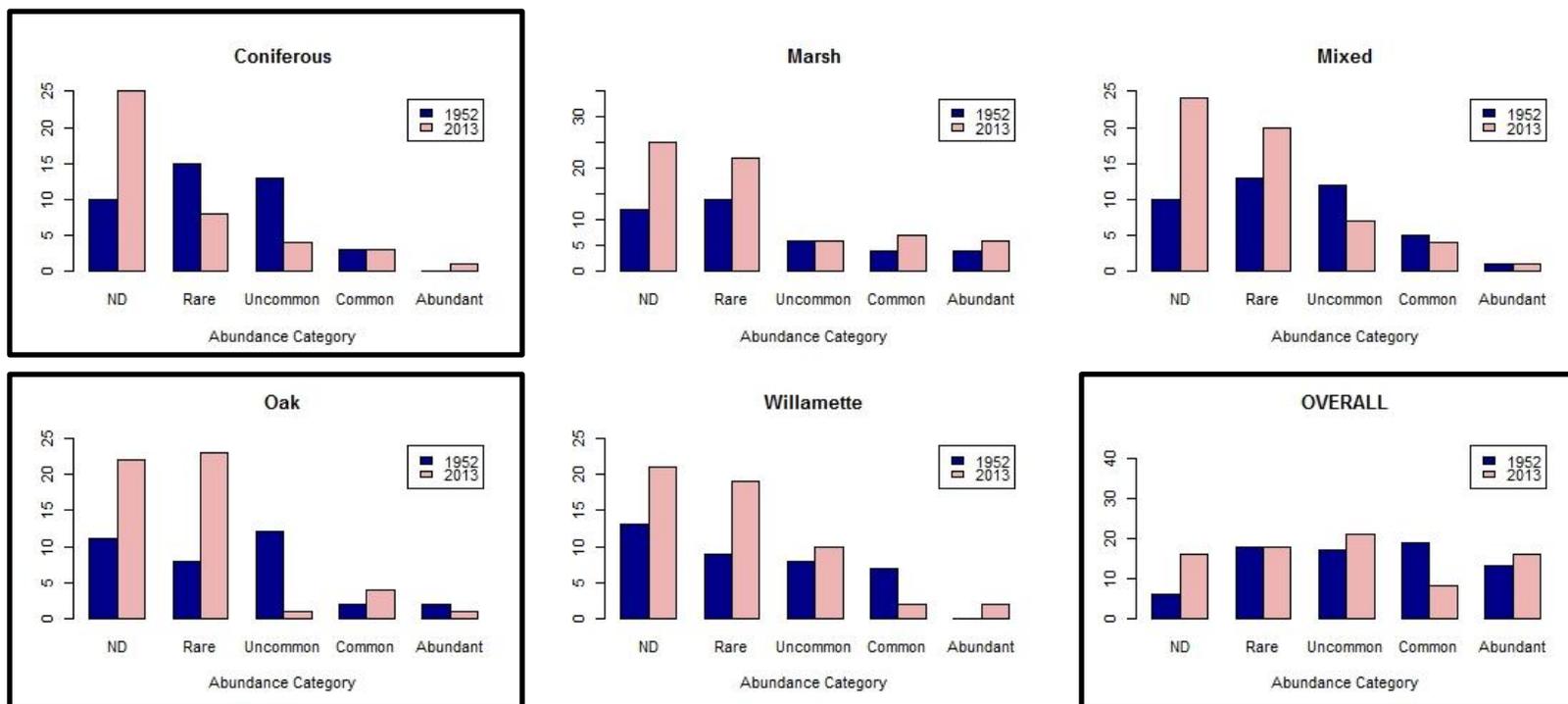


Figure H.4. Histograms of species abundance categories for both survey periods considering only visual detections with rare species removed. Rare species are defined as species detected only once during five visits to a given site.

Appendix I - Qualitative Explanations for Missing Species

Table I.1. Qualitative possible explanations for species detected in 1952 but rarely or not detected in 2013. BBS trends for Oregon and the Northern Pacific Rainforest obtained from Sauer et al. 2014. See Appendix C for list of species common and scientific names.

Species	Possible Explanation for Observed Population Decline	BBS Trend (OR)	BBS Trend (Northern Pacific Rainforest)
Species Common or Abundant in 1952			
California Quail	Changes in surrounding habitat and succession. Seen only at Willamette site.	-0.2	0.4
Chipping Sparrow	Regionally declining, vegetation succession.	-2.8	-3.0
Golden-crowned Kinglet	Regionally declining, changes to understory.	-3.4	-2.4
House Sparrow	Changes in surrounding habitat, vegetation succession. Seen only at Willamette site.	-1.9	0.3
Nashville Warbler	Vegetation succession, changes to understory. Seen only at Oak woodland site.	-0.8	0.1
Northern Rough-winged Swallow	Regionally declining, intra-annual changes in emergent insect levels.	-3.1	-3.1
Western Tanager	Sampling differences. Jenna detected, but not visually.	0.3	1.1
Species Uncommon in 1952			
Brewer's Blackbird	Regionally declining. Jenna detected, but not during 2 hour survey period.	-2.7	-3.6
Band-tailed Pigeon	Sampling differences. Jenna detected, but not visually.	-0.3	-2.5
Black-throated Gray Warbler	Sampling differences. Jenna detected, but not visually.	-2.9	-1.6
Cassin's Vireo	Vegetation succession at Mixed Deciduous site. All other sites: Jenna detected, but not during 2 hour survey period.	-0.9	-1.0
Common Nighthawk	Regionally declining, changes to surrounding habitat.	-1.0	-3.8
Hairy Woodpecker	Sampling differences. Jenna detected, but not visually.	0.3	0.2
House Wren	Vegetation succession, closure of canopy, and changes to understory. Regionally declining. Seen only at Oak woodland site.	-3.4	-3.7
MacGillivray's Warbler	Widespread regional decline. Changes to understory.	-2.0	-2.2
Northern Bobwhite	Introduced species, regionally declining. Changes in surrounding habitat.	-6.6	-4.6

Olive-sided Flycatcher	Regionally declining, changes to canopy layer, vegetation succession	-3.1	-3.8
Ruffed Grouse	Changes to understory layer, closure of canopy at Coniferous site.	1.3	-1.8
Townsend's Warbler	Suspected late migrants.	-0.6	0.1
White-crowned Sparrow	Changes to understory layer, vegetation growth, and closure of canopy at Coniferous site.	-3.7	-0.4
Western Bluebird	Changes to understory layer, vegetation growth, and closure of canopy at Coniferous site.	1.3	-0.8
Species Rare in 1952			
American Bittern	Sampling differences. Jenna detected, but not visually.	-3.0	-1.6
American Kestrel	Regionally declining, changes in surrounding habitat.	-1.4	-2.3
Common Merganser	Sampling differences. Jenna detected, but not visually.	-0.9	-1.7
Fox Sparrow	Species likely misidentified (probably SOSP).	-0.2	-1.6
Gray Jay	Jenna detected, but not during 2 hour survey period.	1.1	-0.9
Pine Siskin	Regionally declining. Intra-annual differences in resource availability and resulting distribution shifts.	-5.2	-4.0
Pileated Woodpecker	Jenna detected, but not during 2 hour survey period.	1.5	0.2
Ring-necked Pheasant	Introduced species, regionally declining. Changes in surrounding habitat.	-3.2	-6.2
Sora	Jenna detected, but not visually and not during 2 hour survey period. Eddy made efforts to flush secretive birds.	-0.8	1.7
Unid. <i>Empidonax</i> Flycatcher	Jenna was able to identify all <i>Empidonax</i> sp. to the species level.	--	--
Warbling Vireo	Sampling differences. Jenna detected, but not visually.	0.0	0.7
Western Meadowlark	Urban development, vegetation succession, and changes to surrounding habitat.	-1.3	-5.4
Wilson's Snipe	Sampling differences. Jenna detected, but not visually.	-1.4	-4.3
Yellow-breasted Chat	Area no longer grazed, succession and changes to surrounding vegetation. Seen only at Marsh site.	-0.9	-0.6

Table I.2. Qualitative possible explanations for species detected in 2013 but rarely or not detected in 1952. BBS trends for Oregon and the Northern Pacific Rainforest obtained from Sauer et al. 2014. See Appendix C for list of species common and scientific names.

Species	Possible Explanation for Observed Population Decline	BBS Trend (OR)	BBS Trend (Northern Pacific Rainforest)
Species Common or Abundant in 2013			
European Starling	Regional range expansion.	-0.9	-2.0
Unknown Duck	Eddy was able to identify all ducks to species level, Jenna was not.	--	--
Wilson's Warbler	Unknown. Likely vegetation succession and changes in understory density/composition.	-1.5	-2.0
Species Uncommon in 2013			
Brown-headed Cowbird	Regional range expansion.	-1.8	-3.7
Cinnamon Teal	Area no longer grazed, increase in standing water at Marsh site. Only seen early in season while open standing water was available.	-4.8	-1.2
Evening Grosbeak	Inter-annual differences in resource availability and resulting distribution shifts. Eddy unlikely to visually detect.	-5.3	-2.8
House Finch	Regional range expansion. Eddy described within city limits but did not detect during surveys.	-1.4	-0.1
Pied-billed Grebe	Area no longer grazed, increase in standing water at Marsh site.	1.2	-0.9
Spotted Sandpiper	Changes to shoreline composition along Willamette River. Increase in gravel shores and beds.	-1.5	-2.0
Species Rare in 2013			
Acorn Woodpecker	Regionally increasing. Maturation of canopy at Oak woodland site.	3.0	0.0
Anna's Hummingbird	Regional range expansion.	12.3	1.8
Bald Eagle	Regionally increasing, range expansion.	5.8	2.5
Black Phoebe	Regional range expansion.	4.3	2.8
Canada Goose	Regionally increasing. Increase in nests along Willamette River.	4.9	7.9
Common Raven	Sampling differences, Eddy unlikely to have visually detected. Regionally increasing.	2.2	1.4
Eurasian Collared-dove	Regional range expansion.	143.6	125.6
Great Egret	Regional range expansion. Area no longer grazed, increase in standing water at Marsh site.	-0.2	9.9
Greater Yellowlegs	Area no longer grazed, increase in standing water at Marsh site. Only seen early in season while open standing water was available.	--	--
Green-winged Teal	Area no longer grazed, increase in standing water at Marsh site. Only seen early in season while open standing water was available.	-0.2	-1.0

Hammond's Flycatcher	Eddy did not identify <i>Empidonax</i> flycatchers to the species level.	1.1	2.7
Osprey	Regionally increasing. Sampling differences, Eddy unlikely to have visually detected.	5.0	3.1
Pacific-slope Flycatcher	Eddy did not identify <i>Empidonax</i> flycatchers to the species level. Eddy unlikely to have visually detected.	-2.7	-1.0
Savannah Sparrow	Flushed from adjacent unmowed grass field. Surrounding habitat no longer grazed. Seen only at Marsh site.	-2.3	-2.7
Sharp-shinned Hawk	Regionally increasing. Sampling differences, Eddy unlikely to have visually detected.	3.8	3.0
Unknown Hummingbird	Multiple hummingbird species not present in 1952. Eddy was able to identify all hummingbirds as Rufous.	--	--
Virginia Rail	Regionally increasing. Sampling differences, Eddy unlikely to have visually detected.	2.0	1.6
Willow Flycatcher	Eddy did not identify <i>Empidonax</i> flycatchers to the species level.	-6.0	-3.1
Yellow-headed Blackbird	Local range expansion.	-2.2	-5.4

Appendix J - Metadata and Archival Process

General Metadata

- Data owner contact information
- Data key words
- Citations for relevant protocols used
- Definitions for database fields/columns
- Data quality and completeness
- Data accessibility and sharing information

Geospatial Information

- Geodetic datum (NAD 1983)
- Geographic coordinate system (Decimal Degrees)
- Coordinates for site centroids
- Coordinates for point count points
- Coordinates for individual detection locations from spot mapping
- Site boundary polygons (archived as JPEG maps and ArcGIS Shapefiles)
- List of site names and abbreviations

Observation Information

- List of bird detection codes
- Definitions for detection types

Bird Related

- List of scientific names

- List of common names
- List of 4-letter abbreviated species codes

Habitat Related

- List of scientific names
- List of common names (where appropriate)
- List of 4-letter abbreviated species codes

Statistical Analyses

- Raw R code used for analyses
- Outputs from R code (where appropriate)
- List of terms used in models
- Definitions of terms used in models

All data and metadata collected in conjunction with this research will be digitally archived in the Oregon State University Scholar's Archive. This includes databases of observations from each point count and spot map survey in FileMaker Pro 12.0 format (Filemaker Inc., version 4). Additionally, avian observations and associated metadata will be submitted to eBird for public access.