Examining the species-area relationship among birds in patches of montane conifer forest on the National Bison Range

UNDERC West 2015

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Abstract

Landscape changes and habitat alteration can affect the spatial distribution of individuals across a landscape. Birds are particularly sensitive to disturbances that cause habitat fragmentation. Within habitat changes also affect their distribution, as more heterogeneous areas tend to host a wider array of species than more homogenous areas. This study aimed to test whether bird diversity and abundance in patches of montane conifer forests on the National Bison Range, MT were more strongly affected by patch size or by patch heterogeneity. An active (point count) and passive (Soundscape) avian sampling technique was employed to reduce sampling bias. Vegetation characteristics were sampled to measure habitat heterogeneity. I found a correlation between patch size and bird diversity for both active and passive sampling techniques. Multiple linear regression showed that area was more influential to determining species richness than habitat heterogeneity. However, separate linear regressions of habitat heterogeneity (determined by coefficient of variation CV) vs. species richness showed that there was a positive correlation between CV of tree DBH and species richness, and CV of percent cover was marginally significant. More homogenous stands of Douglas fire that have been allowed to dominate Ponderosa Pine due to fire suppression tended to have lower species richness, abundance and diversity than more heterogeneous stands. Understory clearing for easy passage by ungulate species has taken away shrubs, an important structural vertical layer of vegetation for birds. Overall, forest area seemed to be the most important factor in determining the spatial dynamics of bird populations in this study, however habitat heterogeneity still plays an important role in providing different areas for species associated with them. Managing for habitat heterogeneity will promote the preservation of bird diversity on the National Bison Range.

Introduction

Earth's landscape today has become increasingly fragmented due to anthropogenic disturbances. Humanity's needs continue to put a strain on the environment resulting in a "patchwork quilt" of drastic ecological consequences. Patterns of worldwide extinctions, population declines, and declines in biodiversity have been described in detail, with habitat destruction being the leading cause (Dirzo *et al*. 2014; Haddad *et al*. 2015). Birds have become increasingly sensitive to habitat fragmentation, which is the creation of a greater number of habitat patches smaller in size than the original contiguous tract (Bender *et al.* 1998). To most bird species, the direct loss of habitat is detrimental to their populations, while some avifauna thrive in areas of natural or anthropogenic disturbances (Berg 1997; Scheick 1995).

In contrast to habitat fragmentation, natural landscape heterogeneity results from changes in physical and biological structure, producing a gradient of distinct vegetation patches with specific ecological functions (Rotenberry and Wiens 1980; Pickett and Cadennasso 1995). The spatial arrangement of these natural patches within a landscape can often determine population and community structure (Dunning *et al*. 1992; Pickett and White 1985). While the effects of habitat fragmentation within managed forests on avian diversity and abundance is well documented, (Fahrig 2003; Brawn *et al*. 2001; Rosenburg and Raphael 1986; McGarigal and McComb 1995), little research has been focused on their diversity and abundance within natural forest mosaics (Opdam 1991).

In a variety of environments, avian diversity can be influenced by habitat structure, patchiness, and complexity (Wiens 1974). For example, in eastern deciduous forests the diversity of breeding bird species in a community increases with overall heterogeneity and vertical layering of vegetation (MacArthur and MacArthur 1961). Therefore, a more heterogeneous forest could support more bird species because of varying preferences among the species for particular vegetation structure and/or composition (Freemark and Merriam 1986).

The species-area relationship (SAR) is one of the oldest and most well known patterns within biogeography that explains the uneven spatial distribution of individuals within species (Gleason 1922). Larger areas tend to contain a higher number of species within a taxonomic group, and empirically, the relative numbers seem to follow systematic mathematical relationships (Preston 1962). The pattern is so common among a wide variety of taxa and ecosystem types, some ecologists consider it the closest thing to a rule within the field of study (Rosenzweig 1995). There are two main models that exist that focus on mechanistic explanations of parameters within their mathematical descriptions. Both result from the way in which

individuals are distributed among species. The first, the "exponential model" developed by

Williams (1964) is the species/log area transformation. The "power function model" is the log

species/log area transformation (Preston 1962). For the purposes of this paper, the power

function model is used since it is the most widely accepted (Connor and McCoy 1979)

There are two principal theories that have been proposed to account for the significant

positive correlation often observed between numbers of species and area. The famous theory of

island biogeography suggests that the number of species increases with greater area *per se*, often

becoming asymptotic for the largest areas because of lower extinction probabilities for larger

populations permitted by larger islands (MacArthur and Wilson 1967). Alternatively, Williams'

(1964) habitat-diversity hypothesis argues that as the amount of area sampled is increased, new

habitats with their associated species are encountered, and thus species number increases with

area. Although there is well documented evidence that larger areas contain more species, there is

still considerable debate about the exact form of the relationship, along with the meaning of the

shape and slope of the curve (Connor and McCoy 1979). Among avian studies, Anjos and Boçon

(1999), and Rahbek (1996) have demonstrated a positive correlation between species number

and area.

There are three primary factors related to the spatial distribution of individuals that can

affect the slope, shape, and scale of SARs. The first is related to sampling; since the majority of

species are rare, most will not occur in all sampled areas and will only be sampled in larger

areas, even when their distribution is random (Preston 1962). In effect, sampling may increase

the relationship between species and area. The second factor is habitat heterogeneity, showing

that larger areas tend to have more complex structural habitat types, enabling the coexistence of

more species associated with specific habitats (Rosenzweig 1995). This relationship is well

documented in birds (e.g., MacArthur and MacArthur 1961, MacArthur 1964, Recher 1969). The third factor is related to habitat heterogeneity in that the spatial population dynamics of species such as local immigration and extinction along with aggregation can lead to the spatial clustering of individuals (Storch *et al.* 2003).

Given that all of these factors can and possibly do affect the spatial distribution of species, it becomes difficult to determine each factors' relative importance separately. However, through measuring habitat heterogeneity and the sampling effect through vegetation sampling and two different methods of sampling bird diversity and abundance, one can test to some extent what factors do not attribute to SARs.

Measuring avian diversity and abundance using traditional techniques such as point-counts is still widely used in the scientific community (Royle and Nichols 2003). However, with any technique that aims to measure animal abundance and diversity, there is always the problem of detectability. Rarely does any technique ever detect all animals present in the surveyed area or sample unit. Especially with an active sampling technique such as point-counts that require the observer to be present, human presence can influence the detection probability of individuals (Mackenzie *et al*. 2005). A passive sampling technique such as Soundscape recording offers some advantages over traditional active sampling techniques. Soundscape recording units are less invasive, can be left out for extended periods of time and collect data at regular intervals (Gage *et al.* 2008).

This study aims to determine which factors determine avian abundance and diversity within naturally occurring montane forest patches on the National Bison Range. I hypothesized that larger patches of forest will have an overall higher avian species richness, diversity, and

abundance than smaller patches. I predicted that patches with more habitat heterogeneity will have an overall higher species richness, diversity, and abundance than more homogenous ones. Comparisons of observer-generated point-count data to remotely recorded Soundscape data should reveal a difference in observer detection and influence on the sampling method. Overall, I hoped to tie together how the forest management practices of the USFWS on the NBR effect the distribution of birds across the landscape.

Methods

Study Area

The National Bison Range (NBR) in Dixon, Montana (47.326299 N, -114.226053 W) is comprised mostly of intermountain bunchgrass palouse prairie with naturally isolated forest patches occuring between 2800 and 4800 feet. Forest composition varies from Ponderosa Pine (*Pinus ponderosa*) and Douglas Fir (*Pseudotsuga menziesii*), with *P. ponderosa* found mostly at lower elevations and in dryer soils. *P.menziesii* comprises a majority of higher elevation forests. I selected six forest patches of differing sizes that were the most accessible to utilize for study areas, and measured their area in hectares using the polygon tool in ARCMAP (ESRI 2015; Figure 1). Forest edge was determined based on observed forest densities in the field, and comparison to USGS Topographic maps that had the forests outlined. Some forests became too sparse in some areas sampled that I decided to treat them as single patches. Patches varied in size from 7.18- 35.70 ha (Table 1).

The NBR has been a part of the National Wildlife Refuge system under the U.S. Fish and Wildlife (FWS) service since 1908. As part of managing habitat on the range for Bison (*Bison bison*), and many other large ungulates, the FWS has implemented management practices favoring fire suppression and understory clearing. Historically, most of the forests on the range

were old-growth stands of *P.ponderosa* that are more fire tolerant than *P.menziesii*. Once the

FWS started the fire suppression and salvage logging, *P.menziesii* started to dominate as second

growth to become in most areas, a climax species. These stands have been referred to as "dog

hair" because of how thick they become. The primary means of woody vegetation control done

by the FWS on the NBR is chainsaw clearing of second growth douglas fir, followed by piling

and burning the slash (USFWS 2003).

Point Counts

A fixed-radius point count method was used to measure avian diversity and abundance

(Silvy 2012). Point counts were conducted within forest patches at five random points. Point

counts were conducted daily for five days at each of the six forest patches (n=30). Point counts

took place during the morning (5-9 am) to maximize bird observations and allow a more accurate

representation of bird abundance and diversity within forest patches. Specific point count

methodology was conducted according to Ralph et al. (1995). Counts began 1 minute after

arriving at the station, and lasted for 10 minutes. The number of individual birds of each species

was recorded within a 50m radius. Shannon-Wiener's diversity index and species richness were

calculated for each plot.

Remote Acoustic Soundmeter Recordings

Remote recordings were made using the Wildlife Acoustics Soundmeter 2 (Wildlife

Acoustics 2015). The soundmeters were programmed to record one minute of sound every 30

minutes at 22,050 Hz (Gage 2008). The resulting recording is called a "soundfile", and is stored

in an on-board memory chip in .wav format. The soundmeters were placed near the center of

three forest patches and continuously recorded data daily, often coinciding with the point counts.

The sound meters were left in a patch for 13 days, and then moved to three different patches for

13 days for samples at six sites total, all within the month of July 2015. Soundfiles from only

5am-9am were listened to personally by the author, to sample during the same time frame as the

point counts. Maximum species richness was calculated for every soundfile, and then averaged

for each day for a total of (n=78) sample files.

Vegetation Sampling

To better understand habitat characteristics within patches, several habitat variables were

measured at five random plots within the forest patch for a total of five plots per patch (n=30).

Plot site selection was determined by taking a random distance and direction from the

soundmeter station using a random numbers table. Distance was measured by pace. An 11.2m

radius ($400m^2$) was used for each plot by stretching out a pre-measured rope tied to a stake. All

trees larger than 15cm in diameter within each plot were identified to species, and DBH was

measured. The total number of trees in each plot was counted. Percent canopy cover was

estimated using a spherical densiometer (Model A-R.E. Lemmon forest densiometers) in each

cardinal direction and then averaged. Percent ground cover was visually estimated into four

classes (soil/rock, grass/forb, shrub, and litter) within the plot (Linder and Anderson 199

Statistical Analysis

For generating species area-curves utilizing a linear regression, forest area (in hectares),

and species richness was log transformed to reduce skewness in the distribution of forest sizes

and to linearize the bird-species relationship (Connor and McCoy 1979). The Shannon-Wiener

diversity index was used to calculate species diversity (Magurran 2004). To compare avian

abundance and diversity with area of the forest patches, a linear regression was used without the

log transformation. Due to the inability to obtain an accurate estimate of abundance from the Soundscape technique, only the abundance and subsequently diversity estimate from the point count sampling technique was used.

Coefficient of variation (CV) was used as an index of habitat heterogeneity. CV was calculated for tree DBH and percent canopy cover and was run through a linear regression against species richness. CV was expressed as a percent. Visual estimates of percent ground cover were run through separate linear regressions against species richness to determine what habitat structural component influenced species richness the most.

Multiple linear regression was used to analyze relationships between avian species richness, forest area, and habitat heterogeneity(CV for tree DBH and percent canopy cover) and to examine whether area or habitat heterogeneity had the strongest influence on avian species richness. Multiple linear regression was also used to examine relationships between avian diversity, forest area, and habitat heterogeneity. All statistical analyses were conducted using SYSTAT 13.0 (Systat Software, Inc., Chicago, IL, USA).

Results

Species richness was strongly correlated with area in both the active ($p<0.0001$) and passive ($p=0.029$) bird sampling techniques. The increase in log forest area explained 84.0% and 73.4% of the variation in the increase of the number of species for the active vs. passive bird sampling technique, respectively (Fig. 2). Abundance ($p=0.005$) and diversity ($p<0.0001$) were also both positively correlated with area, explaining 54.2% and 74.1% of the variance, respectively (Fig. 3).

Coefficient of variation for tree DBH was positively correlated with species richness (p=0.05), explaining 55.0% of the variation in tree DBH. Percent canopy cover showed a slight negative correlation with species richness, but was not significant (p=0.086, R^2=0.383; Fig.4). Coefficient of variation for tree DBH was also positively correlated with diversity (p=0.05), explaining 56.1% of the variation in tree DBH. Percent canopy cover showed the same negative correlation with diversity, but was still insignificant (p=0.124, R^2=0.310; Fig. 5).

Separate linear regressions of visually estimated percent ground cover showed that percent shrub (p=0.010, R^2=0.212), grass and forb (p=0.644, R^2=0.008), and litter (p=0.080, R^2=0.105) had no influence on species richness. Percent soil and rock (p=0.001) did however have an influence on species richness, explaining 31.6% of the variance (Fig.6).

Multiple linear regression for forest area vs. species richness vs. CV for tree DBH showed that area (p<0.0001) explains 86.7% of the variance, whereas CV for tree DBH has no significance in determining species richness (p=0.623). A similar trend was found in the multiple linear regression for forest area vs. species richness vs. CV for percent canopy cover. Area (p<0.0001) explains 87.6% of the variance, whereas CV for percent canopy (p=0.130) has no significance in determining the species richness.

A similar trend was found when replacing species richness with diversity in the multiple linear regression. Multiple linear regression for forest area vs. diversity vs. CV for tree DBH showed that area (p<0.0001) explains 74.5% of the variance, whereas CV for tree DBH has no significance in determining diversity (p=0.530). A similar trend was found in the multiple linear regression for forest area vs. diversity vs. CV for percent canopy cover. Area (p<0.0001)

explains 75.2% of the variance, whereas CV for percent canopy (p=0.277) has no significance in determining avian diversity.

Discussion

The point count data show a significantly positive trend that as forest area increases, so does species richness, abundance, and diversity, as predicted. There was no observed difference between the active or passive sampling technique, indicating that observer-based sampling was unbiased in determining species richness. Both avian sampling techniques showed high R^2 values that explain most of the variation, and both have slopes approaching one (Fig.2). These slope values indicate a near isometric relationship, with a strong positive correlation (Connor and McCoy 1979).

One limitation of the passive technique lies within using technology itself. Without eyes and ears there to determine "how many of who" is singing, I was unable to collect abundance (and subsequently diversity) data. Only the maximum species richness heard during the sampling period (5-9am) was able to be collected, and averaged across the 13 day sample period. The range of the Soundmeter could have been different than human hearing capabilities as well. It was often hard to hear bird songs especially on windy days. Even though there was a similar trend between the two techniques, I strongly believe traditional point count sampling techniques are better and more comprehensive than a passive technique such as Soundscape.

Interestingly, for forest patches sampled later in July one family of birds was missing from sampling that was present in the earlier sampling period. The wood warblers (Passeriformers:Parulidae), are migratory song birds that utilize North American forests for breeding. The two species that were observed during the early sampling period (July 1-14) were:

MacGillivray's warbler (*Geothlypis tolmiei*), and the Yellow-rumped warbler (*Setophaga coronata*). These species were not observed during the later sampling period (July 15-29th). This could be due to the sensitive nature of the breeding season; migrants could have left before the second sampling period (Bibby 2000). Ideally, all six forest patches would have been sampled at the same time to reduce sampling bias.

In determining whether habitat heterogeneity or area was more influential on species richness, multiple linear regression showed that area is the primary factor determining species richness. However, a separate linear regression of CV for tree DBH against species richness showed a significant relationship, indicating that habitat heterogeneity still slightly influences the spatial distribution of individuals, but forest area is the overall factor that determines species distribution. However, habitat homogeneity could influence this relationship.

Reading through archival annual reports from the National Bison Range, I found some interesting information regarding their forest management practices. Their main goal is fire suppression and to reduce woody encroachment (USFWS 2003). Through fire suppression, they are allowing thick stands of *P.menziesii* to overtake *P.ponderosa* as climax vegetation. *P.ponderosa*, a more fire tolerant species is reliant on fires to regulate second-growth of *P.menziesii* (Arno *et al.* 1995). Without regular fires, thick stands of *P. menziesii* have overtaken forests on the NBR. These thick stands have a relatively homogenous low DBH and high percent cover, and the understory is almost always 100% grass (Personal observation, Fig 4.). I found a correlation between low DBH and low species richness, and even though it approaches significance, high percent cover seems to have a negative effect on birds indirectly through the lack of understory vegetation. Forests of this type may be having a negative effect on the spatial distribution of birds on the NBR. The homogenous habitat is only being used by a few species

that can tolerate it. The thick overstory is cutting off light to the understory, restricting shrub growth that seems to be marginally significant to birds (Fig.6). The removal of this vertical layer of vegetation could be distributing the birds to better quality patches with more heterogeneity.

Overall, I think the interplay of a variety of factors influence the spatial distribution of birds on National Bison Range. Forest area certainly seems to be the key determinant in regulating species richness, abundance, and diversity; however habitat characteristics still seem to influence the relationship. Homogenous habitats likely only lead to few species being present, due the specialized nature of a niche. More heterogeneous habitats offer different specialized areas where species associated with those areas can be detected. In this study, the "area per se" hypothesis seems to be supported, however I think that with a larger sample pool, habitat diversity may have shown a more significant role. Ideally, sample sizes would have been larger, and sampling would have taken place during a shorter period of time. Future studies should use larger study areas and more forest patches to gain a better perspective on changes throughout the landscape. More focus on habitat should also be critical if future studies aim to tease out different theoretical hypotheses.

Tables and Figures

Table 1.) Areas (in hectares) and average species richness estimates from point counts (PC) and

the average maximum species richness estimated from the soundscape (SC) sampling technique.

| Site	Area (ha)	AVG Spp. Rich (PC)	AVG Max Rich. (SC)
Hill	9.94	4	4.15
Bear	16.77	10.8	12.08
Gate	35.7	16.8	16.85
EC1	7.27	3.6	5.64
EC2	13.96	10.2	11.14
EC3	7.18	5.25	6.57
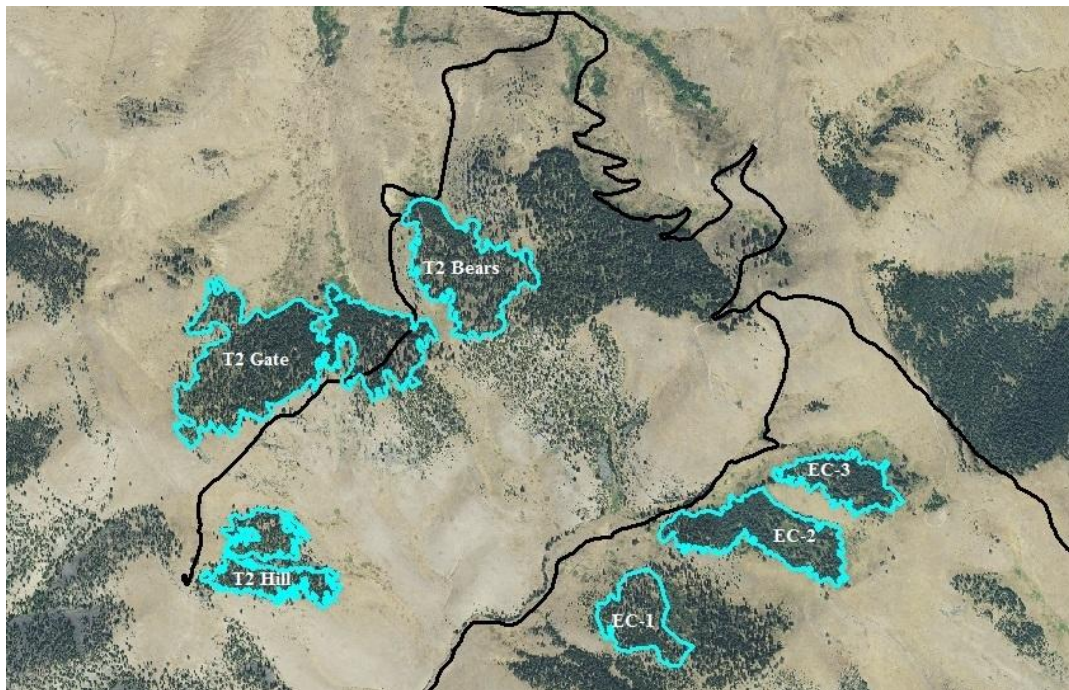
Figure 1. A map of the six study forest patches on the National Bison Range. Blue outlines the

forest edge. Black outlines the roads.
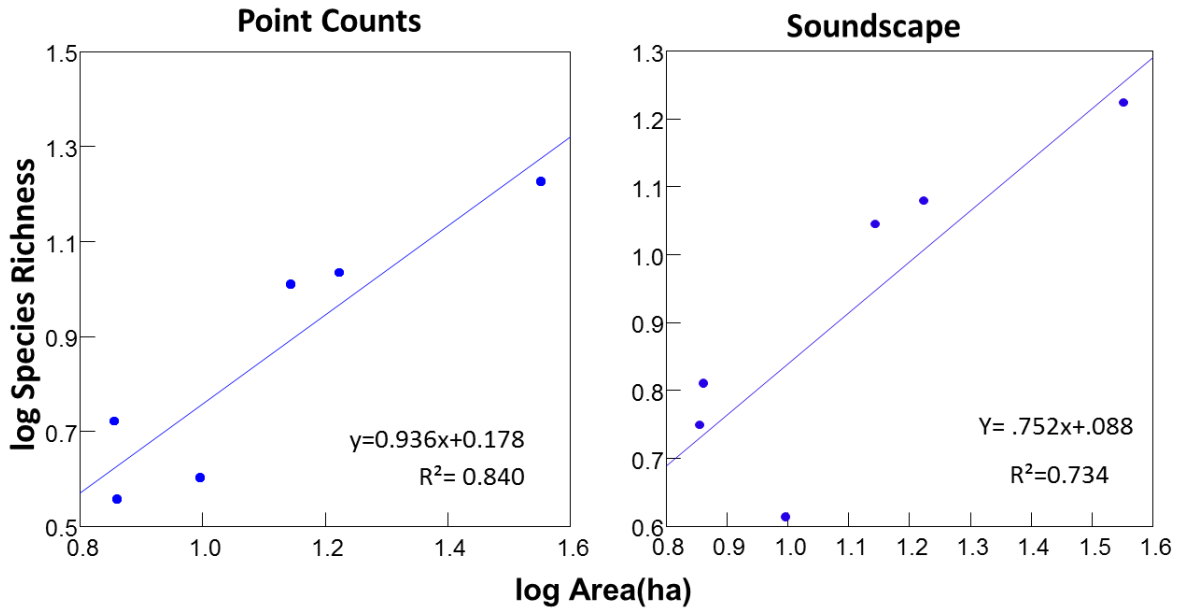
Figure 2. Species-area curves (mean) for both point count(left) and Soundscape (right) avian sampling methods. Axes are on a log scale.
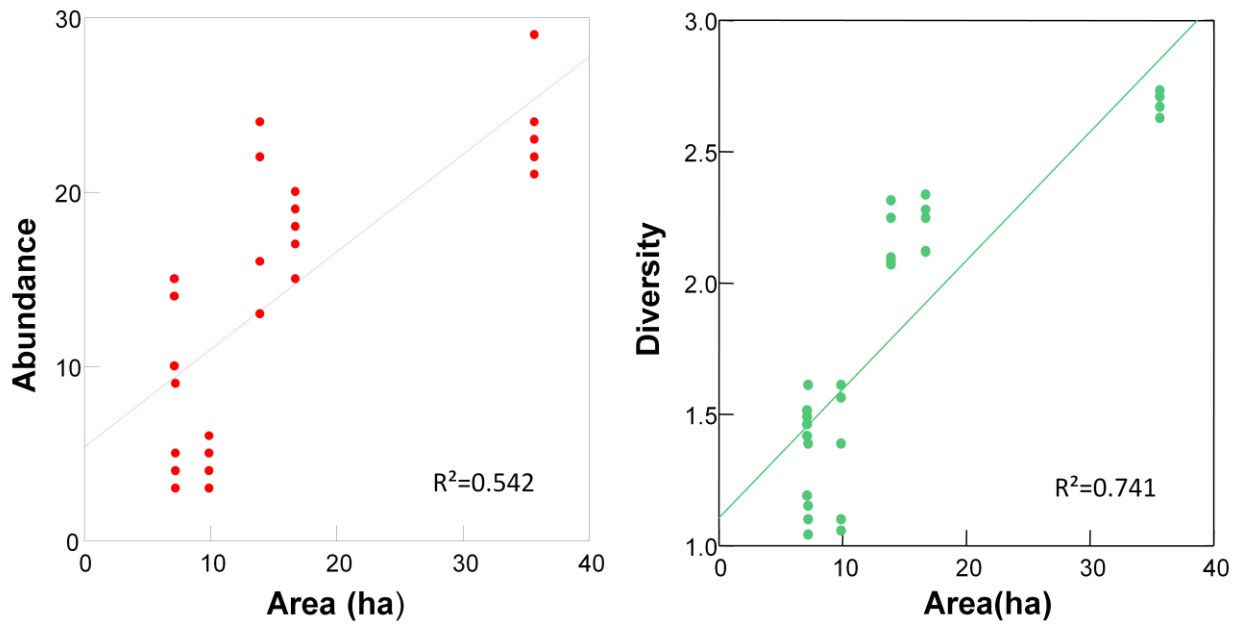
Figure 3. Scatter plots for avian abundance (red) and diversity (green) estimated from point-count data plotted against forest area.
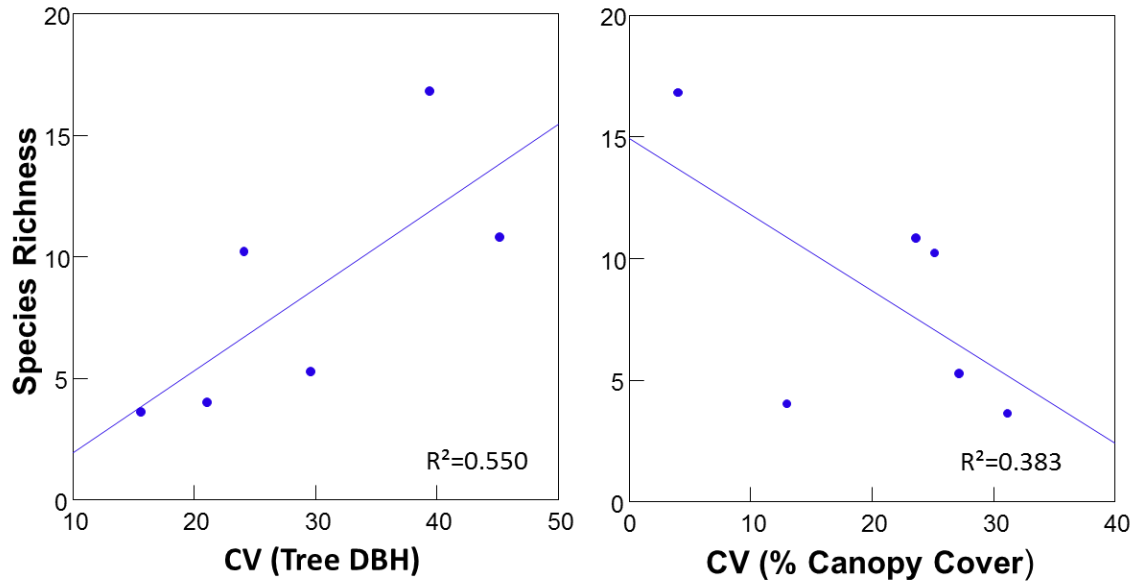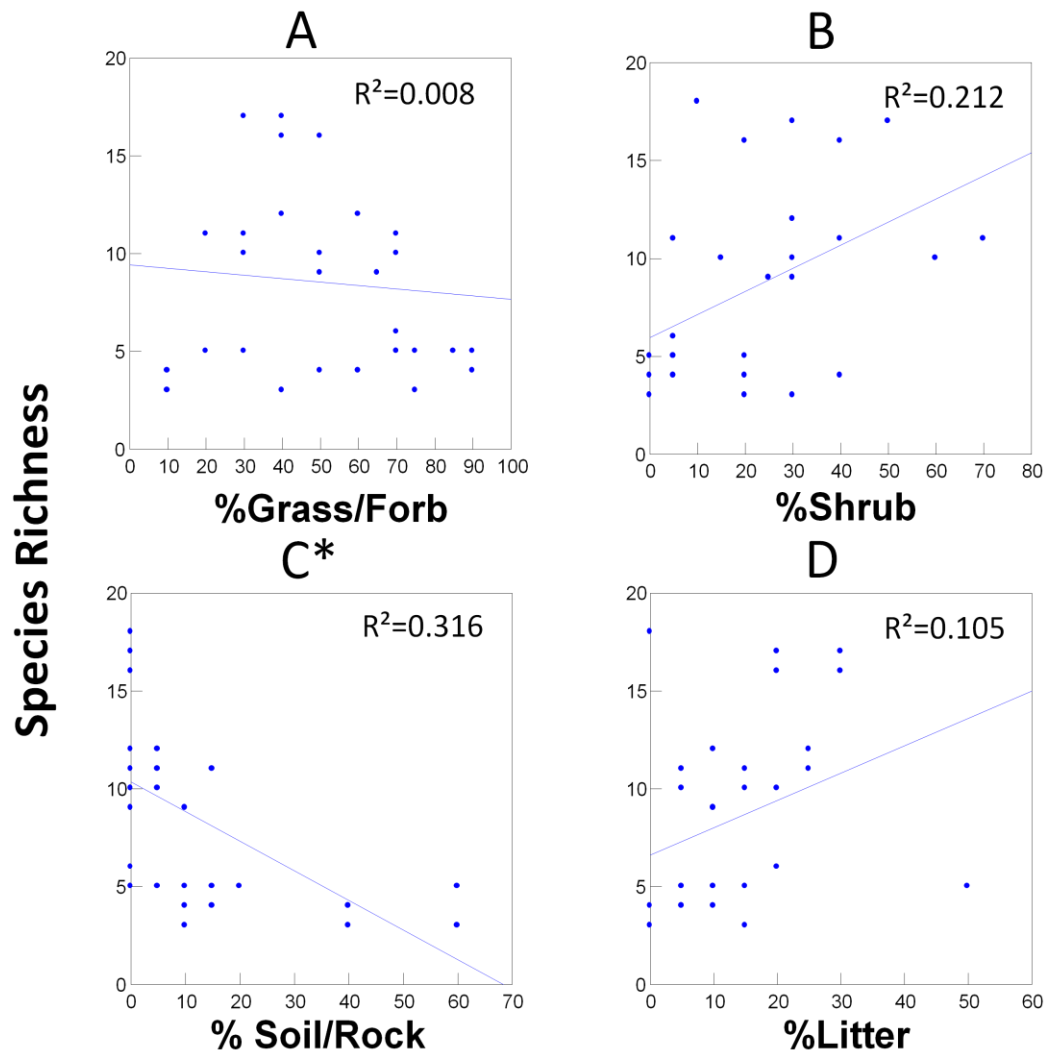
Figure 4. Scatter plots for mean coefficient of variation (CV) for tree DBH (left) and percent canopy cover (right) plotted against avian species richness. CV is expressed as a percent.
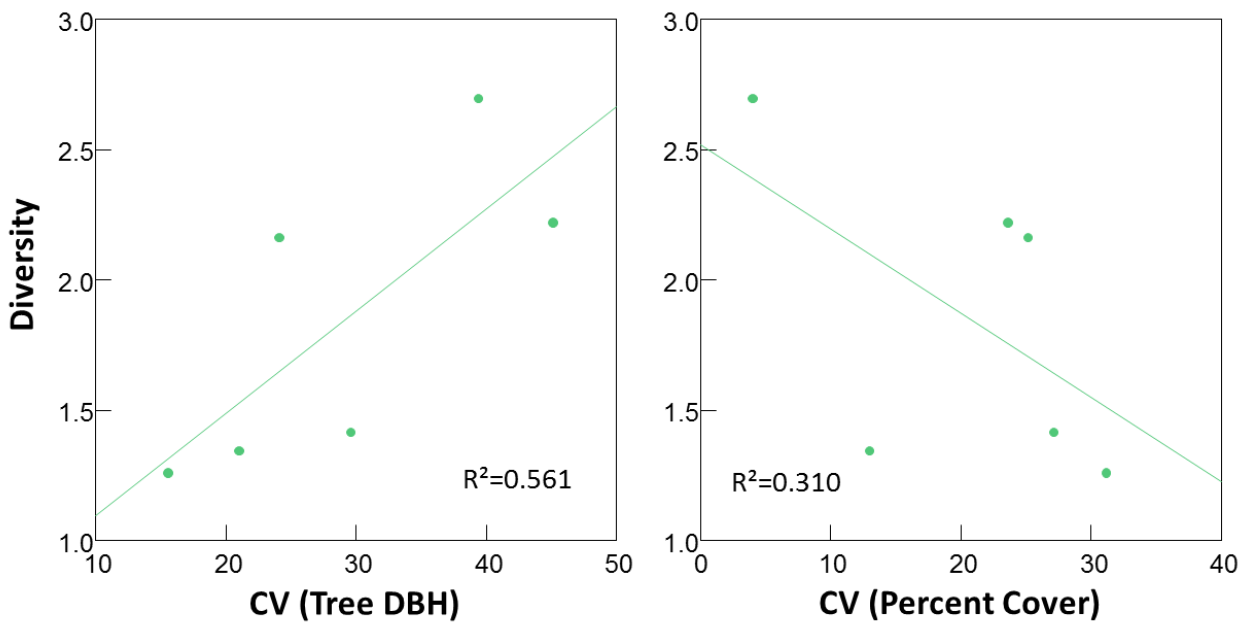
Figure 5. Scatter plots for mean coefficient of variation (CV) for tree DBH (left) and percent canopy cover (right) plotted against avian diversity. CV is expressed as a percent.

Figure 6. Scatter plots for visually estimated percent ground cover plotted against species richness. (*) indicates significance through linear regression.

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