Sarah Rabeda EEB 381 8.14.2008

The Effect of Successional Age on Bird Species Composition in Northern Lower Michigan and Testing the Intermediate Disturbance Hypothesis for Bird and Tree Diversity

Abstract

The purpose of this study was to determine the effects of forest succession on bird species composition and to test the intermediate disturbance hypothesis. We surveyed three forest plots – an early successional logging plot, a mid successional aspen plot, and a mature hardwood forest, in lower Northern Michigan where forests follow succession from aspen and beech to hardwood and pine. At each site we determined tree species, diameter at breast height, and distance from the point of our point-quarter center method along two transects. We also conducted bird surveys along the same transects, using the line transect method, and recorded all birds heard or seen. The red-eyed vireo and eastern wood-pewee were the most prevalent bird species at each of our three sites. Our comparisons of variables (tree density, H', richness, and ground cover) between each forest plot were significant, indicating differences due to successional stages. Bird richness followed the predictions of the intermediate disturbance hypothesis, being highest in the mid successional plot. Our results for bird and tree diversity were entirely opposite the intermediate disturbance hypothesis, being lowest in the mid-successional plot. We found one significant positive correlation between bird species diversity and tree density. This result leads us to believe that the density of trees has the greatest effect on bird populations. We can conclude that each forest plot is at a different successional stage, and that bird richness is affected more by density of trees than the type, size, or understory composition.

Introduction

The intermediate disturbance hypothesis predicts that communities with intermediate disturbance rates will have the greatest species diversity compared to communities with high and low frequency disturbances. Therefore, a recently disturbed area should be dominated by early-colonizing species or ruderal species. A late successional area is predicted to be dominated by strong competitors, and a mid successional area by a mixture of the two (Molles 2008).

The change in plant diversity and richness over time may affect associated birds. May (1982) concluded from his study that bird species diversity and richness increase with forest succession. Several factors could explain this trend, including tree species composition, density, and size of the trees. Melhop (1986) found that bird species diversity was highest in a mid-successional forest, but only showed a weak correlation with forest succession. Willson (1974) found that intermediate percentages of foliage were correlated with greatest bird species diversity. It has been shown that bird species diversity reaches a peak once a forest reaches the mature stage in succession (Melhop 1986).

The structure of vegetation is an important factor in bird habitat determination. MacArthur (1958) illustrated the partitioned use of tree height by five warbler species. Each warbler inhabited a different level of the forest with minimal overlap. Resource use and partitioning explain this separation of species; varying levels of the forest provide different nesting sites, and food such as nectar and insects. Each bird species found within a forest has its specific needs, as some species will nest higher above ground, and others will forage and build nests in the ground cover. Forests provide numerous niches and can therefore support a number of bird species.

The purpose of our study was to examine the effects of differently aged forest plots on their corresponding bird populations. We were interested in the composition of each forest, and how tree species, density, and size affect the bird species diversity and abundance of birds. We examined the forest composition of three successional plots to determine if differences of forest composition variables exist between successional stages. We also examined bird species diversity in correlation with the intermediate disturbance hypothesis and forest succession. Between the forests, we hypothesize that there will be distinct variations in tree species, size, and basal area due to succession. We also predict that the types of birds found will differ in each forest plot because of the differences in successional stages. We hypothesize that as a forest matures, bird diversity will increase, peaking at the intermediate stage of succession in accordance with the intermediate disturbance hypothesis.

Methods

Study Sites:

We chose three forest plots on the University of Michigan Biological Station (UMBS) property in Pellston, Michigan. Our early-successional (ES) plot was located at the NW corner of Bryant and Riggsville Roads, where extensive logging took place during 1981-1982. Aspen and beech sapling were very dense and also the dominant tree species. The small size of the trees resulted in a low, sparse canopy. There are a few mature trees within this plot leftover from logging. In comparison to our other sites, ground cover at the ES plot was high. The topography includes a slope near the center of our transect, and a small clearing near the edge. We created a 75-meter buffer between the first transect and Bryant to minimize edge effect. The surrounding area was a continuation of similar habitat.

Our mid-successional (MS) plot is found on Grape Vine Point. This site has been undisturbed since the 19-teens. Because aspen dominates this plot, this forest is reaching the end of the aspen life-span and is likely to succeed toward hardwood and pine (Etterson 2007). The topography is relatively flat, and the forest is fairly open and ground cover is minimal. Edge effect is minimal, as Grape Vine Point has a large undisturbed expanse of similar habitat.

We used Colonial Point, an old growth forest, as our late-successional (LS) plot. Colonial Point has enough area to reduce edge effect. There too the ground is flat and ground cover very minimal. All trees were mature, and very minimal numbers of saplings were found. The area of Colonial Point where we conducted our survey was a mixture of hardwoods and hemlocks.

Experimental Design:

Because of the small size of our sample areas, we used the line transect method. At each site, we ran two 300-meter transects which we divided in half to create four transects per site. To estimate our distance along the transect while birding, we marked off each 30-meter segment. To ensure no double counting of birds, we separated the transects by 150-meters. We used a 25-meter listening zone on each side of the transect for birding. This left us with a 100-meter buffer zone between transects.

We collected bird data the last week of July 2008. The line transect method entails walking each transect at a steady pace and recording all birds seen or heard within our 50-meter bound (Bibby et al. 2000). Our group included a team of three birds students, and to eliminate observer bias, we rotated bird surveying for each site. We collected bird data for four mornings, beginning at around 6:15 am each time. Conditions were favorable, with mostly partly cloudy skies during all censuses.

To collect forest data, we used the point-quarter center method at each 30-meter interval along our six transects. At each point, we collected data for the nearest tree greater than five centimeters in diameter. Our measurements included distance from the center point (meters), diameter at breast height (centimeters) and the tree species. We randomly placed a square-meter plot at each point to determine ground cover. Within each plot, we recorded percent cover and number of forbs and woody plant species.

We used the Shannon-Weiner index to calculate bird and tree species diversity. The proportion of each species at each site was calculated for each birding session so that there were four estimations of bird diversity for each forest site. To test our data, we used univariate ANOVA and curved and linear regression, with an alpha value of 0.05. Our ANOVA tests included comparing bird richness, abundance and H' among the three forests. We also used ANOVA tests to compare basal area, tree density, richness, abundance, cover richness and percentage of cover among the three sites. We also compared each forest variable (density, richness, cover, H') to each bird variable (richness, H', and abundance) using linear and curved regressions.

Results

All variables for the forests – basal area, tree richness, H', and density – were significantly different between the successional plots ($p < 0.05$: table 1). We found that basal area was much higher at the late successional plot, at 17696.96 cm^2, and was lowest at the mid successional plot at 6368.057 cm^2 (Fig. 1). Average tree richness decreased from the early plot (6) to the mid plot (4.5) and again to the late plot (4: Fig. 1). Tree H' was lowest at the MS plot, but we found that density was the greatest there. Our only significant regression was between bird richness and tree density (df= 1,11, F=11.11, p =0.008, R^2=0.526: Fig. 2). At a density of five trees per 100m^2, there was an average of four bird species. As tree density increased to 26 trees per 100m^2, bird richness increased to an average of eight species. We found that bird richness was correlated with tree density positively but nonlinearly. All other regression analyses were not significant ($p>0.05$).

We found that bird communities differ at each forest site; namely bird species richness (df=3, 12, F= 30.38 p=.000) and the abundance (df=3, 12, F= 22.61, p=0.000) differed significantly by site. Bird species richness was highest in the MS plot with a mean of seven species (Fig. 3). We found that H' for birds was also significantly different between the sites (df=3, 12, F= 84.77, p=0.000). Our H' calculations show that the MS plot has the lowest value of total bird species diversity (Fig. 4). Bird abundance was also lowest at the mid successional plot with an average of 12.5 birds (Fig. 3). The ES plot had an average of 13.25 birds, and the late plot had an average of 13. Our early plot had a mean richness of 6, compared to the high of 7, but had the highest bird abundance (Fig. 3).

The two most dominating birds at all three sites were the red-eyed vireo and eastern wood-pewee (table 2). We found that the red-eyed vireo was most prevalent in the early successional plot at 23 occurrences. The mid successional plot had 16, and 8 were recorded at the late successional plot. We recorded the wood-pewee 4, 10, and 14 times at the early, mid, and late plots, respectively. Hairy woodpeckers were seen at an intermediate value (3,6,6, for early, mid, and late, respectively). We found that two species of birds, the American Redstart and Black-capped Chickadee, were relatively evenly distributed among the forest plots. All other birds were a unique occurrence within their respective plot, or were spotted only once.

Discussion

We conclude that the three forests we sampled are in differing stages of succession. Each forest varies significantly in tree density, richness, basal area, and understory cover. We can explain the increasing basal area with increasing forest age. As trees age, they increase in diameter. Percent cover can also be attributed to forest age. As a forest matures, the canopy thickens and limits the amount of light penetration, which inhibits the ability of understory plants to grow. Our results are consistent with these patterns. Sakai et al. (1985) noted that the aspen forests surrounding UMBS are nearing their life-span. Because aspen are an early successional species, they grow rapidly and in large numbers, and begin to decline in biomass at about 70 years (Cooper 1981). Our MS plot, where aspen are dominant had the highest density. This could be due to the turnover of species, as red maple and American beech were also present.

Our ES plot shows higher than expected tree density and a relatively large basal area. In this study, we chose to exclude all trees less than five centimeters in diameter. Our measurements therefore do not reflect the exact make up of the early successional plot, which was heavily populated with small saplings. Sakai et al. (1985) documented that early successional species included big tooth aspen, trembling aspen, and paper birch, which were found in our early successional plot. Sakai et al. (1985) also concluded from her seven-year study of forest successional change at UMBS that our early successional plot was undergoing a transition to a hardwood forest in 1985. A few scattered mature trees were left over from the logging activity two decades ago, and these trees factor into our richness and abundance results for the ES plot.

Our results did not follow the predictions of the intermediate disturbance hypothesis. The MS plot is predicted by the intermediate disturbance hypothesis to have the greatest diversity of tree and bird species due to its intermediate successional stage between early species (aspen, beech) and late successional species (Sakai et al 1985). The only variable which was highest in the MS plot was tree density. This indicates that forest succession may not follow the intermediate disturbance hypothesis because species diversity was lowest at the MS plot. The site with the greatest bird richness, tree richness and tree diversity was the ES plot (Fig. 1), and the LS site showed the highest bird species diversity (Fig. 4). Many studies have supported the increase in bird diversity with forest succession (Johnston and Odum 1956). Johnston and Odum (1956) found that as succession progressed to a mature hardwood forest, bird diversity increased, as our results also indicate.

Although the MS plot was predicted by the intermediate disturbance hypothesis to have the highest species diversity, its low abundance levels decreased the overall diversity. Ring (1998) found that bird species diversity was not significant between ecosystem types in the Pellston area. Our species diversity results appear to follow a trend opposite of intermediate disturbance hypothesis, but they may not be strongly significant between sites. The LS site, due to its age and the large size of trees, is able to provide more diverse niches, and therefore has the greatest total bird diversity. Many singletons were recorded at the LS plot, indicating the need for further sampling, but also greater capacity of the forest to support a variety of species. The ES plot has new and remaining trees from logging activity to increase its tree richness, and it can therefore support a larger number of bird species than a similar homogenous early successional forest.

We found that bird richness was highest in the MS plot, which is predicted to occur by the intermediate disturbance hypothesis. Our results are in agreement with those of James and Wamer (1982) who found that second growth forests in successional transition had greater numbers of species than the mature woods they studied. They also found that the lowest density of birds in their study occurred in aspen and birch forests with low canopy and a high density of small trees, similar to our early successional plot.

We found that the red-eyed vireo dominates the ES plot at 23 occurrences. The next highest values were for the black-capped chickadee and wood-pewee, each at 4. Yahner (2003) from his study of an ES habitat and found that the red-eyed vireo was present in both his control and cut plot. He found that the red-eyed vireo increased significantly once the plot had been cut. Our results show a high number of red-eyed vireos in the most recently disturbed site, with a decreasing trend as forest successional age increases. The eastern wood-pewee showed a reverse trend, being lowest at the early plot, and most prevalent at the LS plot. Eastern wood-pewees prefer mature hardwood forests, as in our LS plot. The red-eyed vireo prefers second growth forests that are relatively open. Our ES plot was fairly young, and had patches of open space ideal for the red-eyed vireo (Bewer et al 1991). The varying factors between forest plots such as density, basal area, and cover could influence the habitat selection of these birds.

Possible complications exist that may have had an effect on our data collection and results. Because our research group was newly exposed to birding techniques, observer level must be taken into consideration. More experienced birders would be better able to locate and identify birds by sound and sight. Because of the lower level of observer experience, some birds were left unidentified and therefore our results for bird abundance and diversity may be lower than expected. Greater observer experience may have yielded differing trends in richness and diversity. We recorded the unidentified birds with a corresponding number. If we heard the same unidentified call further down a transect, we would not mark it as a new species. This way, we were still able to observe bird richness and calculate bird species diversity. We also began surveying late in the breeding season, and many of the songbirds had already stopped singing, thus decreasing our overall richness and diversity estimates, and possibly influencing the trends we found.

Forest composition highly influences bird species diversity, and has important conservation implications. The late successional plot resulted in the highest H' and bird abundance of the three stages of succession. It is therefore important to preserve old growth areas, which are able to support more species and more individuals. Birds require various habitat qualities, such as food sources, nesting sites, and levels for foraging. Activity such as agriculture, development, and logging put bird populations at risk. Tree density had the highest effect on bird richness, and must be taken into consideration when logging, thinning, or conserving a forest.

Our study of forest succession and bird community structure according to the intermediate disturbance hypothesis yielded surprising results. Unlike our predictions, bird and tree diversity followed a reverse trend, being lowest in the MS plot. We found that density was the determinate factor for bird species richness, which indicates that habitat selection may not be due to tree composition or age of a forest. Based on our study, the forests near UMBS are in varying successional stages and support various bird species. Continued surveys of successional variation and its effect on bird richness, abundance, and diversity will be valuable to conservation efforts and a greater understanding of the interactions between vegetation and the birds it can support.

Table 1. Summary of statistical analyses. All variables were tested using ANOVA to observe the presence of differences between the forest plots. The only significant regression is listed. Variable 1 (forest) includes ES, MS, and LS (early, mid, and late successional, respectively).

Variable 1	Variable 2	df	P	F	R^2
Forest	Bird Richness	(3,12)	0.000	30.38	
Forest	Bird Abundance	(3,12)	0.000	22.61	
Forest	H' Birds	(3,12)	0.000	84.77	
Forest	Basal Area	(3,12)	0.006	8.133	
Forest	Density	(3,12)	0.001	14.84	
Forest	Tree Richness	(3,12)	0.000	91.46	
Forest	H' Trees	(3,12)	0.000	154.3	
Forest	Avg. Cover spp	(3,12)	0.000	21.54	
Forest	Avg. % cover	(3,12)	0.003	10.19	
Bird Richness	Density	(1,11)	0.008	11.11	0.526

Table 2. Counts of each bird species found over a total of four sampling days at the early-successional plot (ES), mid-successional plot (MS), and late-successional plot (LS).

Bird	ES	MS	LS
American Crow	1	0	2
American Redstart	3	2	4
Black-capped Chickadee	4	5	2
Blue Jay	1	0	0
Red-eyed Vireo	23	16	8
Eastern Wood-pewee	4	10	14
Hairy woodpecker	3	6	6
Pine Warbler	1	0	0
Ovenbird	1	0	0
Winter Wren	1	0	1
American Robin	2	1	6
Black-throated green warbler	0	1	1
Hermit Thrush	0	0	1
Red-breasted Nuthatch	0	0	1
Red-headed Woodpecker	0	0	1
Swainson's Thrush	0	0	1
White-breasted Nuthatch	0	1	1
Brown Creeper	0	0	1

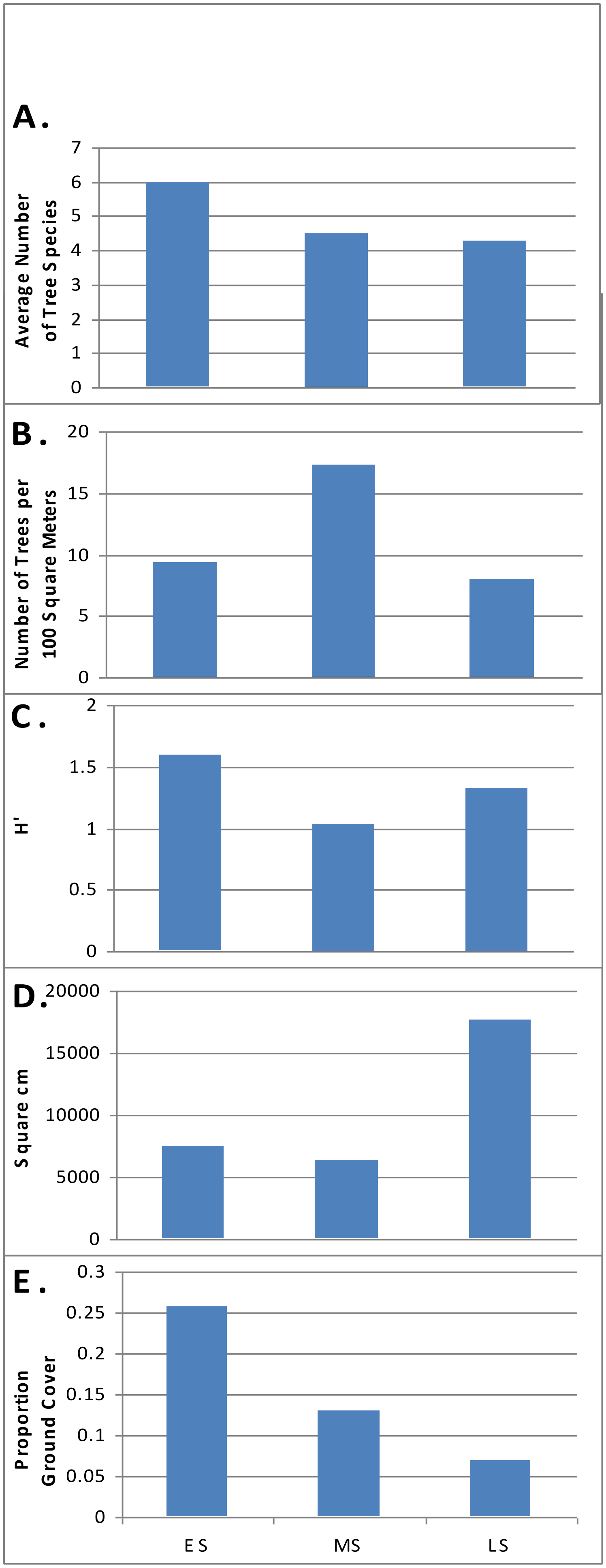

Figure 1. ES = early-successional, MS = mid-successional, LS= late-successional. The average number of tree species as calculated from four transects per site (A). Density of trees (cm^2) per 100 square meters, taken as an average of four transects per site (B). Average total tree species diversity calculated using the Shannon-Weiner index (C). Average basal area per site in square cm (D). Average proportion of ground cover at each site (E).

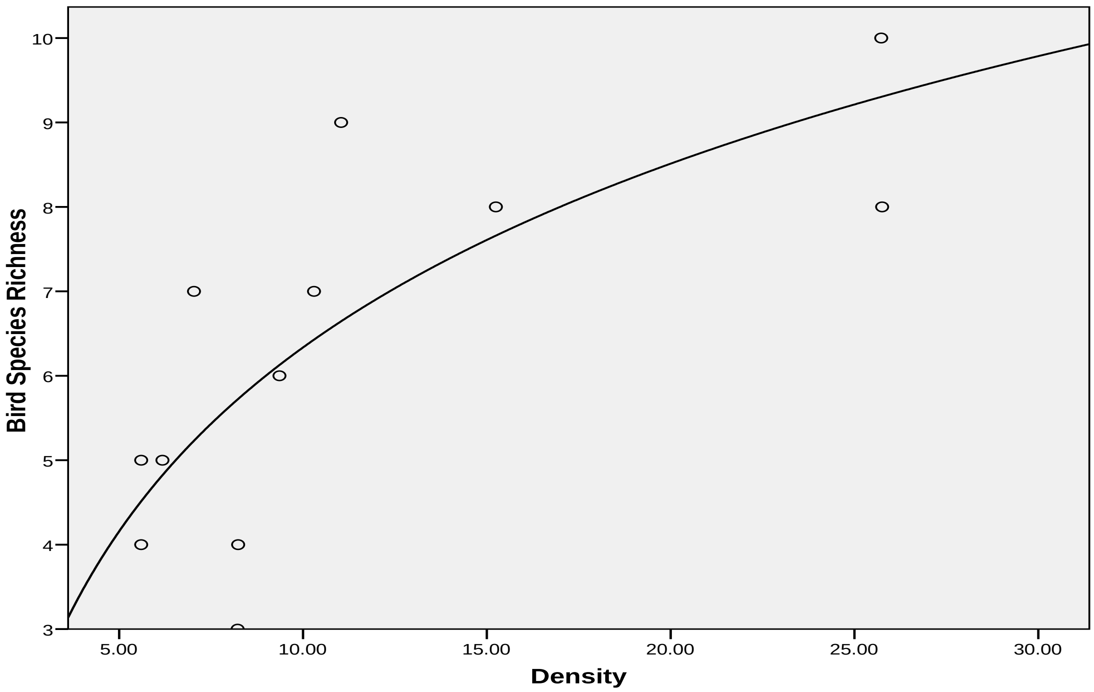

Figure 2. The relationship between tree density (number of trees per 100 square meters) and bird species richness was our only significant regression. As density of trees increases, bird richness increases non-linearly. Correlation coefficient = 0.526, P=0.008.

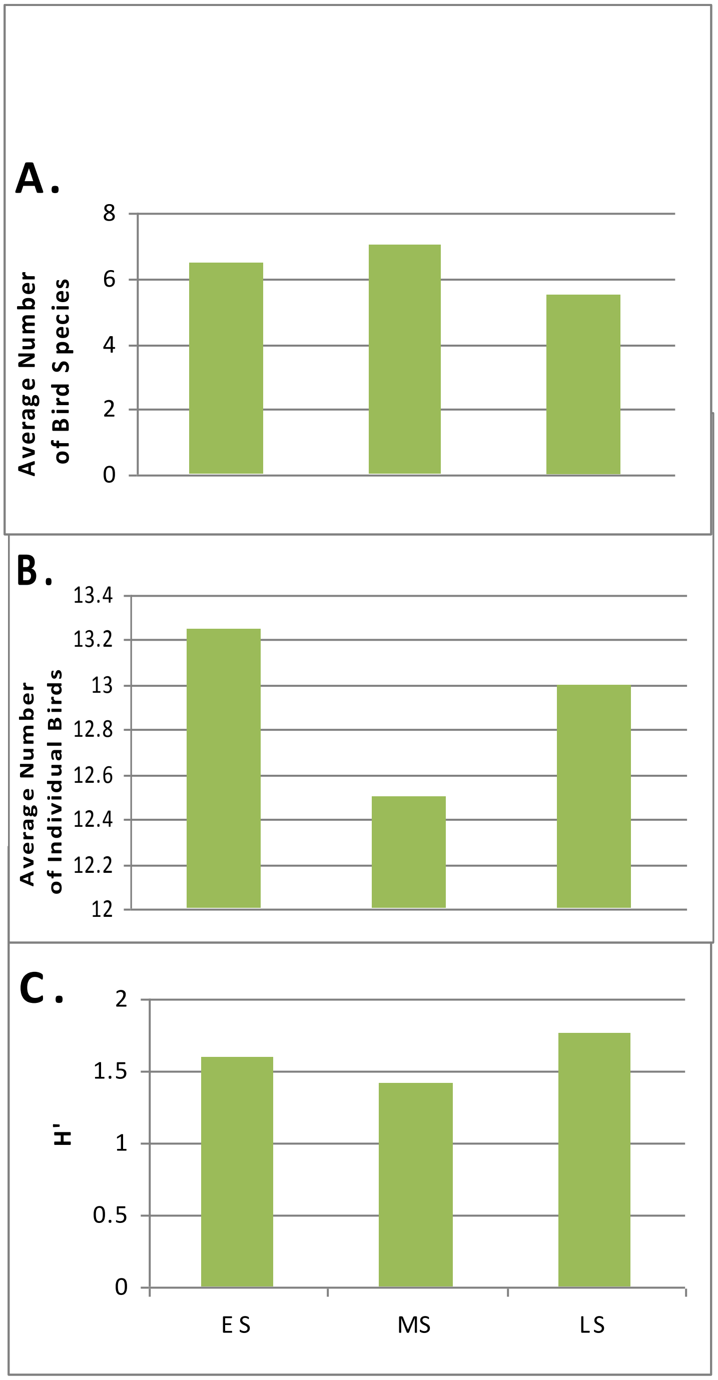

Figure 3. ES= early-successional, MS = mid-successional, LS= late-successional. A comparison of average number of bird species from four sample days at each site, also known as bird richness (A). A comparison of average bird abundance measured from four sample days (B). Average total bird diversity at each site calculated using the Shannon-Weiner index (C)

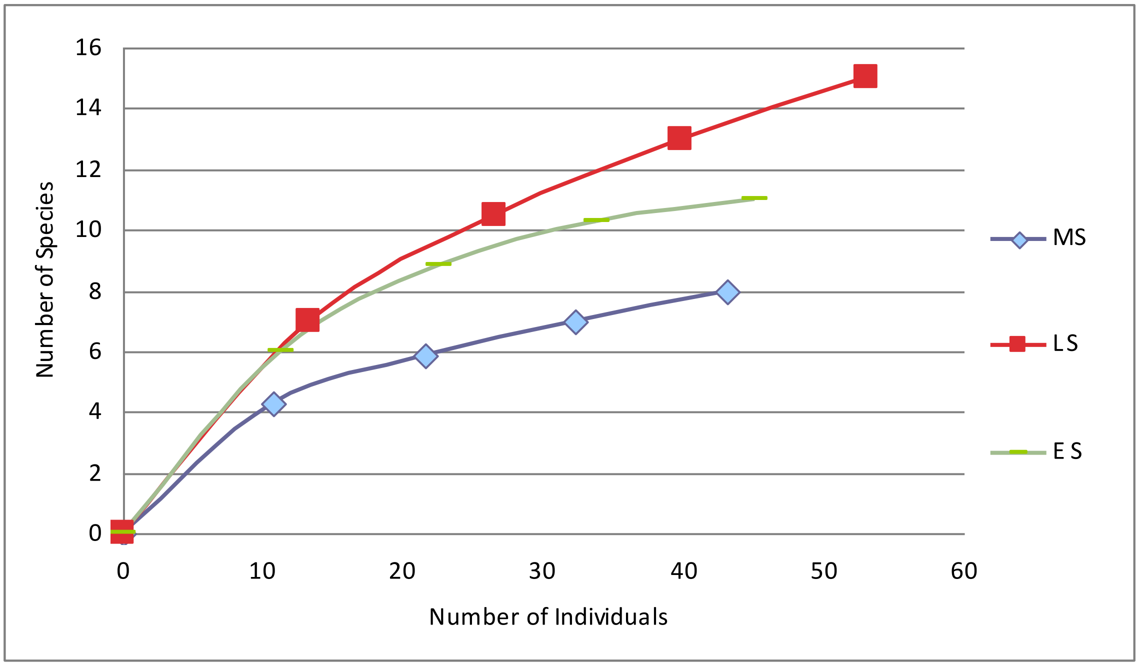

Figure 4. Species abundance at each site, calculated using EstimateS program, using 100 randomizations. ES= early-successional, MS = mid-successional, LS= Late-successional.

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